Population Dynamics

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7.1 Introduction

Predators and parasitoids are important components of all insect communities and are therefore of central interest to ecologists studying the complex factors driving the dynamics of species interactions and community structure. Knowledge gained from studies of predator and parasitoid populations is also of immense practical value in insect pest management (Hassell & Waage, 1984; Murdoch et al., 1985; DeBach and Rosen, 1991; Van Driesche et al., 2010; Heimpel & Mills, 2017; Hajek & Eilenberg, 2018; McEvoy, 2018; Segoli et al., 2023).

In this chapter, we aim to demonstrate how ecologists and biological pest control researchers can assess the role of natural enemies in insect population dynamics, and how the information obtained can be put to use in biological control. We begin by reviewing methods for demonstrating and quantifying predation and parasitism (Sect. 7.2). We then examine the different techniques for determining the effects of natural enemies on insect population dynamics empirically and through mathematical modeling (Sect. 7.3). Finally, we examine ways in which this and other information can be used in choosing appropriate biological control agents for introduction (Sect. 7.4).

7.2 Demonstrating and Quantifying Predation and Parasitism

7.2.1 Introduction

Most studies of pest control by predators and parasitoids examine pest and natural enemy presence and/or abundance and then qualitatively infer their impact. While this provides useful data to address a range of ecological questions, a quantitative measure of impact is critical for guiding pest management decision-making. For

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example, Mace and Mills (2017) argued that to encourage adoption of conservation biological control, metrics need to be developed that can predict current activity and future potential of biological control. They evaluated natural enemy metrics to explore how well they performed in predicting current and future biological control of the walnut aphid, *Chromaphis juglandicola*, in California walnut orchards. Some metrics based on direct measures of natural enemy activity, such as percent parasitism and predator–prey ratio, were effective indicators of current biological control activity. However, Mace and Mills (2017) highlighted that predicting future control through the season using natural enemy metrics can be misleading due to the confounding effect of within-year density dependence in the pest population.

Furlong and Zalucki (2010) reported that less than half the studies of lepidopteran pests and their natural enemies used methodologies that would allow measurement and objective assessment of the impact of natural enemies. Similarly, a meta-analysis of the response of pests and natural enemies to landscape complexity found only 13 of 46 studies included a measure of natural enemy impact (Chaplin-Kramer et al., 2011). Merely examining species presence and/or abundance and inferring impact means it is difficult to make informed pest control decisions incorporating natural enemy activity, as there is no quantitative evidence of impact. Direct estimation of natural enemy impact can provide a tangible metric for determining the point at which the impact no longer maintains populations of pests below economic damage thresholds (Macfadyen et al., 2015).

In this section we present techniques that can be applied to both field and laboratory populations of natural enemies and their prey (1) to demonstrate that natural enemies can have a significant impact upon host and prey populations, and (2) to quantify rates of predation and parasitism to provide indices of the impact of biological control of value to pest management.

7.2.2 Exclusion of Natural Enemies

Natural Enemy Exclusion

Exclusion methods, in which pest abundances are monitored in the absence and presence of natural enemies, are widely used to estimate the impact of predation and parasitism in the field. Suitably designed exclusion barriers coupled with careful non-destructive population sampling has been used, in combination with life-table construction, to effectively demonstrate the impact of predator and parasitoid complexes on pest populations under a range of conditions (Furlong et al., 2004b, 2008). The principle behind their use is to quantify natural enemy impact by comparing the growth in prey population in plots (any habitat unit, from part of a plant to a whole plant or a group of plants) from which natural enemies have been excluded with that in control plots to which natural enemies have free access. In the context of predation, although it is commonly assumed that prey missing in the field have been eaten by predators, this may not always be the case and Castellanos et al. (2015) have documented the bias that can result from non-consumptive effects of predation in exclusion experiments (Sect. 7.2.5).

Various exclusion techniques have been employed, including mesh cages placed over individual plants or groups of plants, mesh sleeve cages placed over branches or leaves, clip cages attached to leaves, greased plastic bands tied around tree branches and trunks, and vertical barriers, constructed of plastic or wood, around plants. The most appropriate technique will depend upon the natural enemies being investigated, and whether the aim is to exclude all natural enemies or to exclude particular species or groups of species. For example, a terylene mesh/gauze cage placed over a plant ought, if the mesh size is sufficiently small, to exclude all aerial and surface-dwelling insect natural enemies. By increasing the mesh size slightly, small parasitoid wasps may be allowed in, while increasing the mesh size further will allow larger types of natural enemy to enter as well. Using a cage with its sides raised slightly above the ground allows ground-dwelling predators such as carabid beetles and ants to have access to aphids on cereals, while excluding adult hoverflies and flying parasitoids. Conversely, a trench or a barrier can prevent access to ground-dwelling predators but allow access to aerial predators and parasitoids. Barriers that exclude only a sub-set of the natural enemies that attack a pest can be used to illustrate the importance of specific enemy groups to biological control (Bográn et al., 1998; Medina and Barbosa, 2002; Gardiner and Landis, 2007; Xiao and Fadamiro, 2010; Martin et al., 2013; Rusch et al., 2013). When paired with population models, exclusion methods can provide valuable insight into the direct economic impact of certain biological control agents (Östman et al., 2003; Landis et al., 2008).

Exclusion barriers can be used to enclose already existing populations of prey, in which case the density of the prey at the start of the experiment will need to be estimated and recorded. Alternatively, exclusion barriers can be used to enclose plants or plant parts that were free of, or have been cleared of, prey and that can then be loaded with a fixed number of prey. The latter approach has the advantage that equivalent starting densities of prey/hosts can be used in both exclusion and control plots, and that the potential for immature stages of parasitoids being present within pre-existing hosts can be eliminated from the experimental plots. It may be necessary to use a systemic insecticide when eradicating prey such as leafhoppers or planthoppers from a plot, in order that any prey eggs present within plant tissues are killed. Of course, loading with prey cannot take place until one can be sure that the plant is free of the insecticide.

Exclusion studies need to account for both the effectiveness of the barrier and its effect on the survivorship or population growth of the focal herbivore. For example, mesh cages can alter microclimatic factors such as light intensity, humidity, and temperature. To account for this, exclusion cages that prevent all predators are sometimes paired with sham cages with a larger mesh size or cutouts allowing predator access (e.g., Costamagna et al., 2007). This approach has been used in several studies (Costamagna et al., 2008; Costamagna & Landis, 2011; Samaranayake & Costamagna, 2018). Medina and Barbosa (2002) used cages with varied mesh size along with sticky barriers to examine predation of large and small tussock moth (*Orgyia leucostigma*) larvae by flying invertebrates, crawling invertebrates, and birds. Large larvae were more frequently removed from cages allowing access by birds. However, the results for small larvae illustrated the importance of using adequate controls, as just as many small larvae disappeared from the treatment that excluded all predators as from the control treatment allowing access to all predators.

In order to separate the effects of microclimate and natural enemy exclusion upon prey populations, it is necessary to use exclusion techniques that are either: (1) as similar as possible in construction, or (2) very different in construction, but which nevertheless provide similar microclimatic conditions in their interiors. Kaser and Heimpel (2018) conducted an exclusion-cage experiment designed to isolate the impact of an accidentally introduced parasitoid of the soybean aphid (*Aphis glycines*) in North America from the other resident natural enemies of the soybean aphid. They designed five exclusion cages, including a sham cage. The sham cages were intended to simulate the microclimatic conditions of predator and total exclusion cages, but to allow natural enemies to enter in a manner similar to open cages. They found no significant differences between sham cages and open cages in aphid densities or aphid population growth rates; therefore, cage microclimate did not differentially affect birth and death rates of the aphids between treatments.

If the prey or hosts are mobile, both immigration and emigration may differ between exclusion and inclusion treatments, which can be a problem (Kindlmann et al., 2015). In order to rule out the possibility that aphid densities in fully caged cereal plots were augmented as a result of prevention of emigration of alatae, Chambers et al. (1983) removed all alate aphids that settled on the insides of some of the experimental cages whilst allowing them to remain in other experimental cages. Removal of alatae was found to not alter the pattern of population change in the cages. Therefore, recolonisation of shoots inside experimental cages was unlikely to have been a cause of the difference observed in aphid densities between caged and open plots.

If prey densities increase in the exclusion plots, they may do so to such an extent that predator species (e.g., coccinellids, hoverflies) other than the ones that are excluded (e.g., carabid beetles) are preferentially attracted to the exclusion plots through their aggregative responses (Sect. 1.15.2). The impact of the excluded natural enemy species may thus be underestimated. This limitation applies particularly to the use of barriers and trenches, where the enclosed plants remain exposed to invasion by a variety of aerial predators. In addition, total exclusion of natural enemies is difficult to achieve and, consequently, it is important to check for the presence of natural enemies and to count them in the exclusion plots either during or at the end of an exclusion experiment. Exclusion methods employing barriers that are far from completely effective in excluding natural enemies are, strictly speaking, interference methods (see below).

Whilst exclusion methods can reveal that natural enemies have a significant impact upon prey populations, other methods generally need to be applied before the predator–prey interaction can be quantified. The results need to be related to the density of predators present in the habitat if realistic estimates of predation rates are to be obtained. Additionally, exclusion experiments provide minimal information, if any, on the dynamics of the predator–prey or parasitoid–host interaction, a limitation that applies also to several of the other methodologies described below. This problem can be at least partly overcome by the construction of paired life tables for the insects in exclusion and control plots (Van Driesche & Bellows, 1996; Itioka et al., 1997) (Sect 7.3.4).

Gardiner et al. (2009) used data from exclusion cages to develop a biological control services index (BSI) to quantify the extent of natural enemy control in crop fields, where:

$$BSI = \frac{\sum_{p=1}^{x} \frac{Ac,p-Ao,p}{Ac,p}}{x} \tag{7.1}$$

Ac is the number or density of prey in each exclusion plot p a given number of days following the initiation of the experiment, Ao is the corresponding number or density of prey in each open plot p with access to natural enemies, and x is the number of replicate plots. Gardiner et al. (2009) found that BSI values for an invasive aphid, *Aphis glycines*, in soybean fields in north-central USA increased with landscape diversity. Similarly, Woltz et al. (2012) found BSI values to be high in soybean fields in Michigan, USA regardless of local habitat management or the diversity of the surrounding landscape.

Natural Enemy Interference

Although physical removal is considered a method of predator exclusion it is, as mentioned above, rarely completely effective and is thus better described as ‘interference’. For large, relatively slow-moving predators it involves removal by hand while small, active predators and parasitoids can be removed using an aspirator. This method has advantages in that confounding microclimatic effects can be ruled out (since cages are not used), and the contribution of particular natural enemy species to parasitism and predation can be relatively easily assessed. However, the method also has the disadvantage that removal of natural enemies is very labour intensive. For the method to provide more than just a crude measure of natural enemy effectiveness, a 24-h per day watch needs to be kept on plants, and several observers need to be involved in removing insects. Additionally, removal of natural enemies may disturb prey and thereby increase prey emigration, and predators and parasitoids may have the opportunity to kill or parasitise hosts before they are detected and removed.

A related ‘biological check’ method of interference exploits the fact that honeydew-feeding ant species, when foraging for honeydew sources

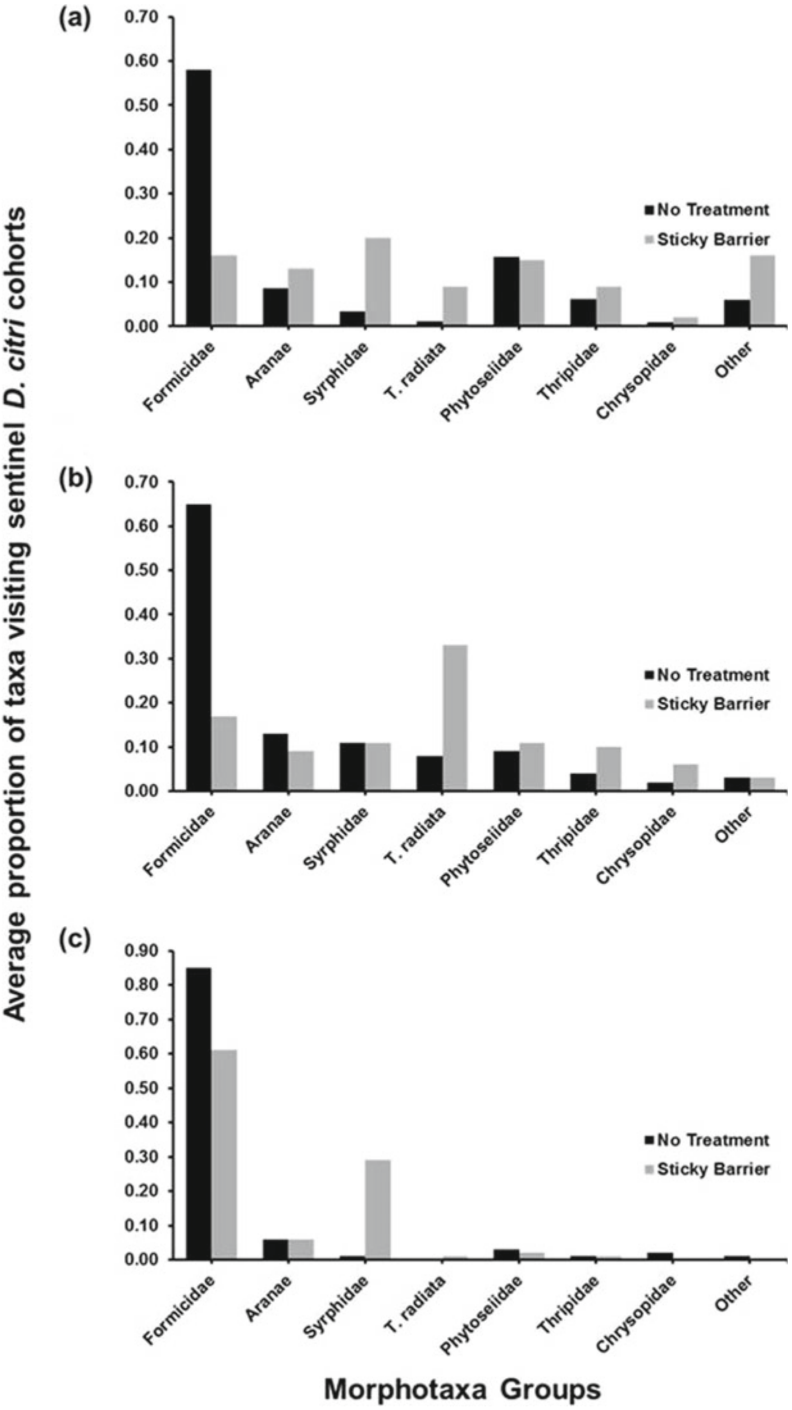


Fig. 7.1 The average proportion of taxa observed visiting sentinel *Diaphorina citri* cohorts under no and sticky barrier treatments at three localities. **a** Biocontrol Grove, **b** Lochmoor, and **c** Jurupa sites in Riverside County, California, USA. The "Other" category is comprised of uncommon predatory taxa including Coccinellidae, Anthocoridae, Mantidae, Forficulidae, and the brown garden snail, *Cornu aspersum* (from Kistner et al., 2017, with permission)

and tending homopteran prey, interfere with non-ant predators and parasitoids (Fig. 7.1), either causing them to disperse or killing them. In one set of plots, ants are allowed to forage over plants, whereas they are excluded from the other set. Natural enemies have access to both types of plot, but they are subject to interference by ants in the former. The method can be used with prey that do not produce honeydew, provided either natural or artificial honeydew is made available to the ants. This method has several of the disadvantages of other interference and exclusion methods.

For the insecticidal interference method, test plots are treated with an insecticide, so as to eliminate the natural enemies, and the control plots are untreated. The insecticide used is either a selective one, or a broad-spectrum one that is applied in such a way as to be selective (e.g., reduced concentrations), affecting only the natural enemies. The main advantages of the method are that potential confounding effects of microclimate can be ruled out, and very large experimental plots can be used. As an alternative to blanket spraying of test plots, an insecticide trap method can be used. Ropes of plaited straw treated with insecticide, trenches dug in the soil and containing formalin solution or insecticide-soaked straw, or some other insecticide-impregnated barrier, can severely reduce the numbers of natural enemies entering test plots. Asiimwe et al. (2016) used this method to reduce natural enemies in treatment plots compared with unsprayed controls through applications of broad-spectrum insecticides, and to show that natural enemies exert a greater influence than plant quality on the seasonal dynamics of the whitefly pest *Bemisia tabaci* in cotton fields in Arizona, USA.

A limitation of insecticidal interference is that the numbers of prey may be inadvertently reduced due to the toxic effects of the insecticide (i.e., either the insecticide turns out not to be selective in action, or drift of a broad-spectrum insecticide has occurred) or they may be inadvertently increased due to some stimulatory, sublethal effect of the insecticide upon prey reproduction (e.g., prey fecundity may be increased). Insecticides can be tested in the laboratory for their possible sublethal effects upon prey reproduction. As for other interference methods (see above), total elimination of natural enemies from the test plots may not be achieved and so the full potential of natural enemies to reduce prey numbers is often underestimated. Additionally, limited information is provided on the dynamics of the predator–prey interaction, even where densities of natural enemies are known.

Combining Exclusion with Inclusion

One solution to the problem of achieving similar conditions in the different exclusion treatments is to carry out an exclusion/inclusion experiment. This involves the use of identical cages for the two inclusion treatments, an experimental treatment in which a known number of prey/hosts are added to the cage, and a control treatment in which a known number of predators and/or parasitoids as well as a known number of prey/hosts are added to the cage (e.g., Lingren et al., 1968; Rusch et al., 2016). This type of experiment has the added advantage that the densities of natural enemies are more precisely known and that *per capita* predation and parasitism rates can be calculated provided the densities used reflect those normally recorded in the field (taking aggregative responses of the enemies into account; Dennis and Wratten, 1991). A major disadvantage of inclusion experiments is that the cages can severely restrict or prevent the dispersal of natural enemies. The long-distance searching behaviour of foraging predators and parasitoids, in response to kairomones, may also be interfered with.

7.2.3 Sentinel Prey and Hosts

One method of examining predation and parasitism by invertebrates is to actively manipulate prey/host availability by establishing patches of sentinel prey/hosts and recording the rate of prey disappearance or accumulation of detectable traces of predation, or the rate of parasitism after a set period of exposure in the field. While the use of sentinel prey/hosts often includes ‘non-natural’ elements, such as inflated densities, non-natural distributions, and immobilisation of prey/hosts, which may distort the natural enemy–host interaction, it is suitable for comparative purposes.

Real, live or dead, sentinel prey/hosts in field experiments were initially used to measure parasitism (Ôtake, 1967) or predation (Speight & Lawton, 1976) more than 50 years ago, and have been used productively since (e.g., Wratten & Pearson, 1982; Perez-Alvarez et al., 2019). However, several studies have documented important differences in predation between live and dead, and mobile and immobile prey. For example, the probability of removal of immobilised prey may be higher than for unmanipulated prey that are able to escape or defend themselves (Zou et al., 2017). Natural enemies may also have a preference for either mobile or immobile prey (Nagy et al., 2020). For example, Brooks et al. (2009) found higher predation of live, mobile prey than of dead, immobilised prey in a freshwater macroinvertebrate system, while Steward et al. (1988) reported that predatory wasps (Vespidae) preferred pinned to unpinned caterpillar prey. Hence, the method of prey manipulation can affect the estimation of predation rates.

A further important aspect of determining the validity of the sentinel method is to assess whether the predator of immobilised prey also consumes the prey in unmanipulated settings. Direct observation (Sect. 7.2.4) can provide first-hand information about the predators involved in pest suppression (Pfannenstiel & Yeargan, 2002; Westerman et al., 2003), but this method is laborious and less practical at night or under adverse weather conditions. Video recording of exposed prey can resolve these limitations as it allows continuous monitoring for extended periods under a wide range of environmental conditions (Frank et al., 2007; Grieshop et al., 2012; Nurdiansyah et al., 2016; Zou et al., 2017; Perez-Alvarez et al., 2019).

Predation can also be assessed using artificial prey. A rather superficial similarity to real prey is often sufficient to attract predators, though such artificial prey cannot move, defend themselves, or behave as true prey would, and the absence of chemical cues may conceal prey identity (Howe et al., 2009; Lövei & Ferrante, 2017). Artificial sentinel prey was first used by Edmunds and Dewhirst (1994) and have since been used successfully to quantify predator impacts against caterpillars in the field (e.g., Seifert et al., 2015, 2016; Clayborn & Koptur, 2017). Although artificial sentinel prey is less natural, traces of predation left by different predators are sometimes identifiable, making them suitable for comparative studies and the partitioning of total predation pressure by predator types (Lövei & Ferrante, 2017). Artificial sentinel prey is also cheaper to use than live prey, do not require rearing, can be simple to produce (as in the case of caterpillar models; Howe et al., 2009), can be standardised across sites (Roslin et al., 2017), and their density and distribution can be easy manipulated. For these reasons, the artificial sentinel method has been recommended for obtaining quantitative estimates of predation as an ecosystem service under field conditions (Meyer et al., 2015). However, it can only be used for generalist predators and not for specialist predators or for parasitoids.

While sentinel prey is often used to quantify predation, hosts can also be placed in the field for a set exposure period to estimate the impact of parasitoids (e.g., Letourneau et al., 2012; Thomson & Hoffmann, 2013). This is most commonly used for studies of egg (e.g., Keller & Lewis, 1985; Glenn & Hoffmann, 1997) and pupal parasitoids (Geden et al., 2020; Nieto et al., 2021), but can also be used for larval parasitoids (Todd et al., 2018; Rutledge et al., 2021). This allows comparisons of standardised parasitism rates across different crop types, at different times throughout the season, and across multiple habitats in agricultural landscapes (e.g., Thomson & Hoffmann, 2013; Macfadyen et al., 2015).

7.2.4 Direct Field Observation

Predation and parasitism can be observed directly in the field, which is valuable to identify relevant species interactions (Rosenheim et al., 1999), and to understand and quantify searching behaviour (Waage, 1983; Schenk and Bacher, 2002; Brechbuhl et al., 2010) and prey defence (Nelson, 2007). When sufficient observations are made it can also be used to quantify rates of predation or parasitism (van Nouhuys & Ehrnsten, 2004; Costamagna and Landis, 2007;

Latham and Mills, 2010; Naranjo & Ellsworth, 2017). Increasingly, video is being used for observation of relatively sedentary prey. This is efficient because multiple videos can be viewed by researchers at high speed, allowing systematic data collection and observation of even infrequent events. Additionally, infrared cameras can be used to record activities at night. Video cameras are generally less disruptive than human observation of natural interactions, though the installation of cameras can still be disruptive (Grieshop et al., 2012; Hemerik et al., 2018).

The Asian citrus psyllid, *Diaphorina citri*, is an economic pest of citrus because it vectors a bacterium that causes the lethal citrus disease huanglongbing. Kistner et al. (2017) studied predation and parasitism of *D. citri* colonies with and without access for ant mutualists in urban citrus. Based on a total of 19,200 h of video they were able to identify the natural enemy community and to show that when ants were excluded by a sticky barrier, visitation by syrphids, which are key predators, and the imported psyllid parasitoid, *Tamarixia radiata*, increased (Fig. 7.1).

Relatively few observational field studies include data that is sufficiently extensive and systematic to be used quantitatively. Those that do quantify the rates of predation or parasitism use many different approaches. As a classic example, Kiritani et al. (1972) estimated that, depending on season and leafhopper instar, between 10 and 63% of rice leafhoppers in a field are eaten by spiders, by estimating the number (n) of rice leafhoppers killed by spiders per rice hill per day as follows:

$$n = FC/P \tag{7.2}$$

where F is the number of predators seen feeding per rice hill during the observation period, C is the number of hours in a day that predators are actively feeding, and P is the average time, in hours, taken to eat a prey individual. Also studying spiders, Sunderland et al. (1986) quantified predation of aphids by web-spinning spiders based on:

$$n = prk \tag{7.3}$$

where n is the number of aphids killed/m^2/day, p is the proportion of ground covered by webs, r is the number of aphids falling from plants per m^2/day, and k is the proportion of aphids entering webs that are killed (determined from field observations and laboratory experiments). Using this approach, Sunderland et al. (1986) estimated that aphid populations could be reduced by up to 40% by spider predation.

7.2.5 Non-consumptive Effects of Predators and Parasitoids

Although the direct effects of predation and parasitism on prey abundance are critical to understanding population and community dynamics, indirect effects through prey responses that reduce the risk of predation and parasitism can also play an important role (Sih, 1986). Responses of insect prey to the threat of predation and parasitism include changes in behaviour (Ballantyne and Willmer, 2012; Siepielski et al., 2014) , life-history (Elliott et al., 2015; Sitvarin et al., 2015; Xiong et al., 2015), and physiology (Thaler et al., 2012; Rendon et al., 2016). Natural enemy-mediated changes in prey traits that do not involve direct consumption are termed non-consumptive effects (NCEs), risk effects or trait-mediated interactions (Hermann & Landis, 2017).

The majority of studies to date link NCEs to changes in behaviour, including changes in feeding (Rypstra & Buddle, 2013; Thaler et al., 2014), oviposition (Wasserberg et al., 2013; Sendoya et al., 2015), colonisation or dispersal (Ninkovic et al., 2013; Bucher et al., 2015; Kersch-Becker and Thaler, 2015), host-plant preference or habitat use (Wilson & Leather, 2012; Sidhu & Wilson Rankin, 2016) and increased predator avoidance (Hoefler et al., 2012; Lee et al., 2014). In general, prey tend to respond to natural enemies behaviourally to become less apparent and reduce encounters, which can often lead to a reduction in fitness due to reduced food intake and reproductive success.

The non-consumptive effects on prey from natural enemies can be quantified by manipulation of predator mouthparts (physical removal or gluing them shut), physical isolation of natural enemies from hosts using a barrier, or by isolation of individual natural enemy cues (such as visual or chemical cues). Such approaches allow different mechanisms of natural enemy detection to be studied and their impacts on prey fitness quantified (Hermann & Landis, 2017).

NCEs of natural enemies can be stronger than their consumptive effects and can have indirect effects that act at the ecosystem level (Preisser et al., 2005; Creel & Christianson, 2008; Buck et al., 2018). For example, Fill et al. (2012) studied the NCEs of an aphid parasitoid *Aphidius colemani* on both *Myzus persicae*, a host aphid, and *Acyrthosiphon pisum*, a non-host aphid. They found that the parasitoid reduced the population growth rate of the non-host aphid, probably through direct encounters while foraging for the host aphid, which caused the non-host aphid to drop from its host plant in response to the risk of attack. Thus, even specialist natural enemies have the potential to cause non-target impacts on insect herbivores in the broader community via NCEs. Similarly, Ingerslew and Finke (2017) extended this same study system to include a second aphid parasitoid *Aphidius ervi* that only parasitises *A. pisum*. The outcome for aphid suppression was influenced by interference in the consumptive effects of the two parasitoids, but also by additive contributions from both parasitoids to their NCEs. This illustrates that NCEs can arise from responses to both enemy and non-enemy species, adding further to the complexity of quantifying the impacts of predation and parasitism.

7.2.6 Molecular Approches for Determining Species Identities and Trophic Relationships in the Field

Electrophoresis was among the first molecular approaches used to quantify predation by fluid-feeding arthropod predators (reviewed by Solomon et al., 1996). However, this technique has been superseded by more sensitive methods of molecular gut content analysis (MGCA) that include both serological and DNA-based techniques (Symondson, 2002). Immunoassays using polyclonal antisera plus enzyme-linked immunosorbent assay (ELISA) have been used extensively for predator gut content analysis. For example, Sunderland et al. (1987) used this approach to compare different polyphagous predator species and the detectability of cereal aphid proteins in their gut contents. They found that antibodies to aphid proteins could be detected in the gut of a predator for relatively long time periods, and that 'maximum detectability times' were longer for spiders and staphylinid beetles than for some other predators. Two key problems with use of polyclonal antisera were a lack of reproducibility and a tendency to cross-react with proteins from other prey species (Symondson, 2002). An alternative monoclonal antibody-ELISA approach has been developed to overcome these limitations but has not been extensively used due to the extensive time and high cost associated with production of a suitable clone. The specificity of monoclonal antibodies can extend to detection of different life stages of conspecific prey in predator gut contents. It was used by Sigsgaard et al. (2002) to investigate cannibalism in the corn earworm, *Helicoverpa zea*. The related technique of immunomarking, in which prey items are marked with a generic immunoglobulin G (IgG) that can be detected in the gut contents of predators using an IgG-specific ELISA, has the distinct advantage that it avoids the need for development of prey-specific monoclonal antibodies (Hagler, 2006; Hagler et al., 2018). Prey items marked in this manner can also be used to identify cannibalism and to determine whether the gut contents of predators represent true predation events or result of scavenging and the consumption of carrion.

Following the demonstration that shorter DNA sequences increased the amount of time that prey are detectable in predator guts, and that detectability was improved by using primers that amplified sequences from multiple copy DNA (Zaidi et al., 1999), drastic advances were made in the development of DNA-based detection techniques (Furlong, 2015). DNA markers have become the most widely used approach for the analysis of trophic interactions, with conventional and multiplex polymerase chain reaction (PCR) approaches based on specific primers being sufficient for detection of parasitism and predation by known natural enemy species, and next-generation sequencing based on universal primers providing an opportunity to investigate more complex species interactions that might include unknown species (Gonzalez-Chang et al., 2016; Schmidt et al., 2021).

Polymerase chain reaction primers have not only been used for quantifying predation, but also to provide accurate estimates of parasitism rates and identification of immature parasitoids dissected from hosts (Jones et al., 2005). In addition, as secondary parasitoids can be difficult to identify using morphological characters, Chen et al. (2006) developed specific primers for identification of two secondary parasitoids of *Lysiphlebus testaceipes*, a common generalist parasitoid of aphids. More recently, DNA metabarcoding (Sect. 3.2.2) has also been used to identify the primary parasitoids of the millet head miner *Heliocheilus albipunctella* in Senegal, where it was used as a viable alternative to host rearing for estimating rate of parasitism (Sow et al., 2019). Parasitoid richness and parasitism rates at four field sites were consistently higher for DNA metabarcoding than for host rearing, indicating that this technique shows promise for quantifying the importance and complexity of host–parasitoid interactions in the field. Liang et al. (2018) also developed a reliable and robust molecular technique to characterise the competitive interaction between two parasitoids *Diachasmimorpha longicaudata* and *Fopius arisanus* of the oriental fruit fly *Bactrocera dorsalis*.

Recent developments in the MGCA of predators include the field application of real-time PCR to estimate the number of copies of prey DNA in predator guts (Zhang et al., 2007), quantitative PCR to determine prey consumption indices for different predator species (Lundgren et al., 2009), ligase detection reaction (LDR) PCR (Li et al., 2011), terminal restriction fragment length polymorphism (tRFLP) (Juen et al., 2012) and next-generation sequencing (NGS) techniques (Pinol et al., 2014) for the investigation of predator diet breadth and detection of multiple predation events. One challenge in the application of NGS for MGCA is the excessive amount of predator DNA relative to prey DNA produced using universal primers. A cost-effective method to enrich prey DNA without the need to block predator sequences in PCR amplification can be achieved through DNA extraction from the gut only, coupled with a long lysis time and size selection for low molecular weight DNA (Krehenwinkel et al., 2017, 2019). In parallel with these technological advances, protocols designed to maintain the integrity of field-collected predators for MGCA have been developed following the field testing of different predator collection methods (Greenstone et al., 2011, 2012).

While molecular approaches provide several advantages over classic methodologies (e.g., natural enemy exclusion and direct observation) for the identification of trophic linkages involving predators, these tools still lack the quantitative rigour that clearly links prey detection to the number of pests killed (Furlong, 2015). For example, Firlej et al. (2013) used large field cages to measure the impact of predation by Carabidae on soybean aphid populations and found that predators identified to be of importance from MGCA did not provide suppression of aphid populations in field cages. A key advantage of molecular approaches, however, is that they provide a more accurate assessment of the diet breadth of generalist predators.

Macfadyen et al. (2015) stated that predators are often described as "generalist" feeders that consume a wide range of prey despite a lack of evidence. Using a PCR approach to determine what generalist predators have recently eaten, it is now clear that some species are not as "generalist" as previously thought (Chapman et al., 2013). Similarly, DNA-based approaches have the advantage that they can effectively reveal interactions within natural enemy communities as well as interactions with a target pest. For example, Traugott et al. (2012) found that more than half of the parasitoid DNA detected in the gut contents of generalist predators stems from direct predation of adult parasitoids.

Molecular methods are used to study biological control interactions involving small and sometimes cryptic predators and parasitoids (reviewed by Symondson, 2002; Harwood and Obrycki, 2005; Gariepy et al., 2007; Harwood et al., 2009; Weber and Lundgren, 2009; Furlong, 2015; Schmidt et al., 2021). They have also proved to be a valuable approach for assessing the occurrence of intraguild predation in the field (Aebi et al., 2011; Schoeller et al., 2012; Traugott et al., 2012; Davey et al., 2013; Rondoni et al., 2015). Such techniques not only enable researchers to accurately identify interactions between natural enemies and host or prey insect pests in the field, but also to quantify, at least in the case of parasitoids, their contributions to pest control services. Both are critical elements for building successful and sustainable IPM strategies for crop pests and will undoubtedly benefit from further technological advances (Schmidt et al., 2021).

7.3 The Role of Natural Enemies in Insect Population Dynamics

7.3.1 Introduction

Having reviewed some of the methods by which insect mortality due to natural enemies can be quantified, we now turn to the task of assessing the significance of mortality, due to natural enemies, for the dynamics of hosts or prey populations. Mortality factors acting on an insect population can decrease insect population size or induce fluctuations in population sizes, and potentially contribute to the regulation of population size toward a stable equilibrium. Population regulation is directly relevant to the process of the pest control using natural enemies. For a factor, such as parasitism or predation, to regulate, the strength of its action must be dependent on the density of the population affected. That is, it needs to be prey density dependent, so that the effect of the predator or parasitoid is proportionally larger at high prey population densities and smaller at low prey densities (Fig. 7.2). Negative density dependence operates through negative feedback on population size. This is most often considered as due to host or prey mortality, but may also involve decreased reproductive rate, dispersal, and immigration. If the proportion of hosts parasitised varies with changing host density, either temporally or spatially, this can profoundly affect the dynamics of the species. Density-dependent factors can also affect average population sizes (Sects. 7.3.4 and 7.3.7) and can, under certain conditions, induce perturbations (Sect. 7.3.4).

We begin by addressing the pros and cons of using percentage parasitism estimates as a metric to assess the impact of parasitoids on host population dynamics (Sect. 7.3.2). We then discuss the simple technique of assessing the impact of natural enemies by assessing the correlation of

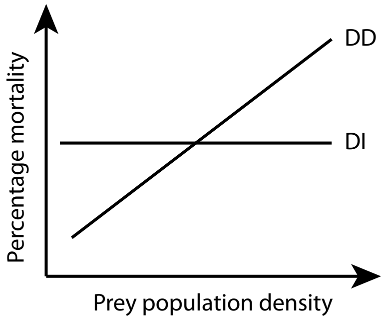


Fig. 7.2 A density-dependent mortality factor (DD) in which proportional prey mortality increases with population prey density and a density-independent factor (DI) in which proportional prey mortality is unrelated to prey population density

their numbers with those of the host populations (Sect. 7.3.3). We then review classical life-table analysis (Sect. 7.3.4) used to parse the contribution of each host stage and mortality factor to the dynamics of the host population. Next, we move to experimental rather than observational approaches to quantifying pest population control by natural enemies using manipulation and factorial experiments (Sect. 7.3.5). Following this, we discuss the influence of landscape fragmentation and metapopulations on natural enemy–host dynamics (Sect. 7.3.6) before reviewing the structure and stability properties of discrete-time and hybrid parasitoid–host models (Sect. 7.3.7) and closing the section with how to confront population models with field data (Sect. 7.3.8).

7.3.2 Percent Parasitism

The percent parasitism is the fraction of the host population that is observed to be parasitised. A high 'percent parasitism' of an insect pest population suggests that a parasitoid has a large impact on the host population size. While a high rate of parasitism will reduce the host population size, it does not necessarily reflect host population regulation, or long-term pest control.

First, the percent parasitism reported in a publication is the percent of a sample of the host population. It can either under- or over-estimate the impact of parasitoids on host population dynamics, depending on the size of a sample, the timing of the sample relative to the phenology of the species, and where the sample is taken from, relative to the distributions of both species. A life-table study of the host population (Sect. 7.3.4) can be used to assess a parasitoid's contribution to host population mortality locally. However, because it is not generally possible to obtain all of the information needed to make a life table, it is worthwhile to consider percent parasitism of a sample taking into account its limitations.

When samples are taken over time, say over a generation of a host, the percent parasitism will vary temporally depending on the phenologies of both species. Specific aspects of phenology that are relevant to how percent parasitism should be considered, such as whether generations are discrete or continuous, the length of time the host is susceptible, when the parasitoid is active during that time, and the development time of the parasitoid relative to the host (Godfray et al., 1994; van Nouhuys & Lei, 2004).

Phenological asynchrony of the host and parasitoid can be accounted for by measuring recruitment to both the host and the parasitoid (parasitised hosts) populations continuously. The ratio of total parasitoid recruitment to total host recruitment provides an unbiased estimate of total losses to parasitism. Another method uses the attack rate from field samples (Bellows et al., 1992). If individuals are collected at frequent intervals, reared under field temperatures, and the proportion dying from each cause recorded from one sample to the next, then the original percentage of the sample that was parasitised can be estimated. Gould et al. (1990) and Buonaccorsi and Elkinton (1990) provide equations for the calculations. The method requires that all hosts have entered the susceptible stage before the first sample and that no host recruitment occurs during the sampling period. Details and examples of these and other techniques for determining rate of parasitism can be found in Van Driesche and Bellows (1988), Furlong et al. (2004a), Toepfer and Kuhlmann (2006), Jenner et al. (2010) and Asiimwe et al. (2016).

The sampling method used will introduce a further error into the estimate of parasitism rate as methods are biased towards either parasitised or unparasitised hosts. In the above scenarios, samples are collected over time, generally covering the whole susceptible life stage of a host that has relatively discrete generations. In many instances, samples are taken less frequently or only once. If the sample is taken early, the percent parasitism for the host generation will likely be underestimated. If it is taken late, it may be overestimated. Similarly, rate of parasitism is generally spatially heterogeneous, at many scales (Hassell, 2000a; Segoli, 2016). Parasitism also varies among hosts in a population depending on what plant part they are on, the age of the plant and the plant species or variety (Kaiser et al., 2017). For instance, Kishinevsky et al. (2016) found that parasitism of the whitefly *Bemisia tabaci* by *Encarsia* parasitoids varied among host plant species within a field, and was low on flowering host plant individuals. Parasitism rate also differs in different parts of a field (Ferguson et al., 2006) due to both local host density (Gunton & Pöyry, 2016) as well as location relative to field edges (Cronin, 2009), different parts of an agricultural landscape (Segoli et al., 2020), and in different types of landscapes (Marino & Landis, 1996; Tscharntke et al., 2007; Grab et al., 2018). Thus, sampling location, distribution of sampling points, and field site can either under- or over-estimate the rate of parasitism. Finally, the percent parasitism can underestimate the role of parasitoids for the dynamics of host populations if there are other forms of parasitoid-induced mortality. Host feeding (Jervis & Kidd, 1996; Zang & Liu, 2008; Emerick and Singh, 2016), unsuccessful parasitism and non-consumptive effects (Abram et al., 2019) contribute to host mortality and sometimes outweigh the effects of parasitism.

7.3.3 Correlation Methods

A useful indication of the impact of natural enemies can often be obtained by statistically correlating their numbers against those of their hosts. A high positive correlation may indicate a degree of prey specificity on the part of the natural enemy, that might reflect a rapid numerical response to variations in host density. Blubaugh et al. (2018), for example, found that the density of aphid parasitoids, primarily *Diaeretiella rapae*, was positively associated with aphid density on broccoli on farms with few lepidopteran pests (Fig. 7.3a). But on farms with many lepidopteran pests there was no association between parasitoid and aphid densities (Fig. 7.3b). They conducted an experiment and concluded that aphid parasitism was reduced by the presence of lepidopteran herbivores, presumably due to indirect effects of lepidopteran feeding influencing host plant cues used by foraging aphid parasitoids.

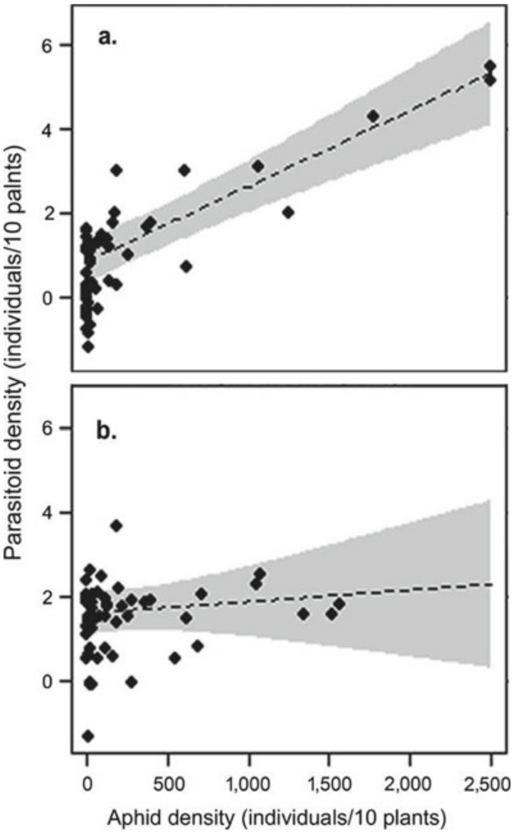


Fig. 7.3 Regression plots of a mixed-effects model of aphid densities and aphid parasitoid densities from a 2014–2015 survey of 52 organic farms where **a** lepidopteran herbivores rarely occurred ($n = 54$) and **b** where lepidopteran herbivores co-occurred with aphids at densities > 0.5 larvae/plant ($n = 50$). The dashed lines show the expected value of the linear regression, conditional on the random factors in the model, which were sample date and farm. The grey bands are 95% confidence intervals around expected values. The points are partial residuals, showing the association between aphid and parasitoid densities given the other factors in the model, sample date and farm (from Blubaugh et al., 2018, with permission)

Negative correlations, on the other hand, may indicate a slow or lagged numerical response by a predator to changing prey density. These responses are commonly shown by highly polyphagous predators that may 'switch' to feeding on a prey type only after it has increased in relative abundance in the environment. Negative correlations are also more likely to be associated with prey species that tend to show rapid changes

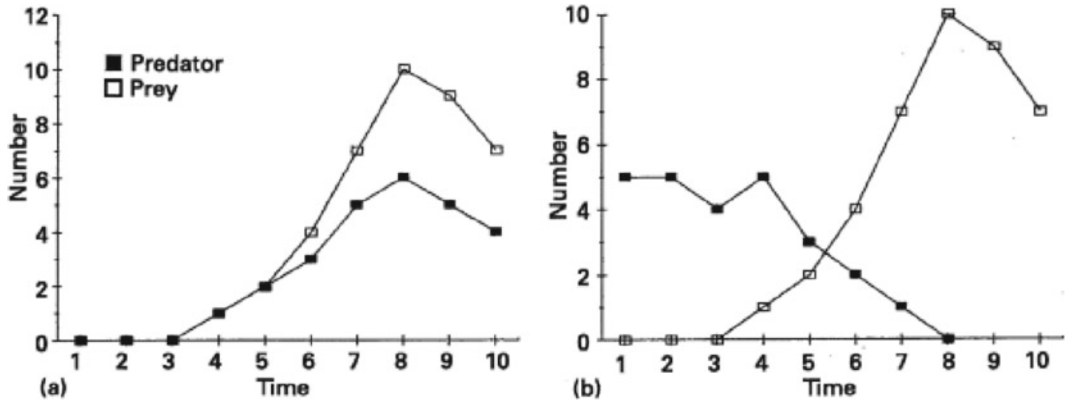


Fig. 7.4 Relationships between predator and prey population numbers which produce either positive or negative correlations: **a** a positive correlation between predator and prey numbers produced by a slow rate of prey increase coupled with a relatively low predator attack rate, such that prey numbers are not reduced, while predator numbers are still rising; **b** a negative correlation between predator and prey numbers caused by predators depressing prey numbers, which only increase after predator numbers have declined

in abundance, or with predators having a high attack rate (Fig. 7.4) (Murdoch, 1969).

Negative correlations are often found between aphids and their natural enemies because the aphids colonise a crop early in the season and increase rapidly. Enemies follow at different rates. For example, Bannerman et al. (2018) found a strong negative association between the soybean aphid (*Aphis glycines*) and its coccinellid predator *Harmonia axyridis* in soybean in Minnesota, USA. The coccinellid was absent early in the season as the aphid population increased. The population density of the aphid peaked at about seven weeks, and the coccinellid population peaked three weeks later, probably forcing the already declining aphid population to crash.

While in many cases natural enemies do cause host densities to decline, correlations can be created just as easily by predator populations tracking changes in prey numbers, rather than by bringing about those changes. Also, absence of a correlation should not be taken to imply that predators do not have any impact (Hassell & Waage, 1984). Therefore, conclusions based on correlation should be drawn with caution, and then only with an appreciation of the biology of the species involved and follow-up experiments.

7.3.4 Life-Table Analysis

Introduction

A life table shows, for each age, stage or time period, what the probability is that an individual will die before reaching the next age, stage or time period. It is especially useful in the study of insects, where developmental stages are discrete and mortality rates, and the causes of mortality, may vary widely from one lifecycle stage to another. Life tables are used to analyse the mortality of insect populations and determine key factors responsible for the pattern of change in total generation mortality within a population. They can further be used to determine how specific mortality factors, such as natural enemy species, affect prey or host population dynamics (Bellows et al., 1992). Below we show how types of processes relevant for pest control or population regulation can be identified and quantified using life tables. For instance, key lifestages for explaining population growth or decline under different conditions can be identified (e.g., Malabusini et al., 2022), density-dependent mortality can be distinguished from density-independent mortality, and delayed or over-compensating density dependence can be detected. Because some insect populations (e.g., aphids) tend to have generations which overlap in time, while others do not, two quite different approaches have been developed for each category: the age-specific life table and the time-specific life table, respectively.

Age-specific Life Tables

The life-table approach was pioneered for insect populations in a study of *Drosophila melanogaster* by Pearl and Parker (1921). Varley and Gradwell (1960) extended the approach to discrete generations of the winter moth (*Operophtera brumata*) in the UK using key factor analysis, based on Haldane's (1992, reprinted from his 1949 publication) logarithmic method for comparing the contribution of successive mortality factors to total mortality (*K*). Varley and Gradwell's (1960) approach has some shortfalls (Royama, 1996) and in practice has been replaced by more powerful and sophisticated techniques focused on population growth rate rather than total mortality, and accommodating overlapping generations as well as sex (Brown et al., 1993; Sibly & Smith, 1998; Coulson et al., 2005; Chi et al., 2020). However, because the concept of key factor analysis, as presented by Varley and Gradwell (1960) , provides an intuitive way of quantifying and analysing the immediate cause of changes in population size, we illustrate it below.

The usefulness of Varley and Gradwell's (1960) approach depends on the availability of sequential life tables for several generations of a univoltine insect population. In temperate regions, for example, it is common for insect populations to overwinter as eggs and develop through a series of discrete stages in the spring and summer (Fig. 7.5). The adults then mature in the autumn to lay a new generation of overwintering eggs before dying. In this situation, generations remain separate. By obtaining population density estimates for the numbers entering each stage in the life-cycle, it is then possible to construct a composite life table from a sequence of life tables for each generation (Table 7.1). The numbers entering each stage can be estimated by direct assessment of recruitment (for example, by measuring fecundity or fertility), or by indirect calculation from counts of each stage. Several techniques are available which provide an estimate by the second route, and these are reviewed by Southwood and Henderson (2000).

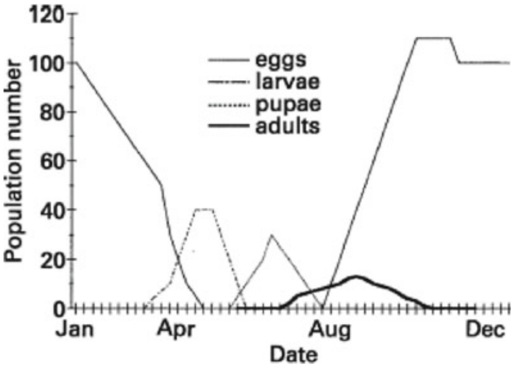


Fig. 7.5 Schematic life-cycle of a typical temperate zone univoltine insect population

Where stage mortalities can be partitioned into a number of definable causes, such as parasitism, predation and desiccation, they can be quantified separately in the table. In this way it may be possible to build similar life tables for particular natural enemies. By converting the numbers entering each stage in Table 7.1 to logarithms ($\log_{10}$), we can calculate for each successive mortality in any generation:

$$k = \log_{10}\text{number before mortality} - \log_{10}\text{number after mortality} \qquad (7.4)$$

where *k* is a logarithmic measure of the proportion dying from the action of the mortality factor. Within each generation, we can thus determine a sequence of *k*-values, k_1, k_2, k_3, … k_n, corresponding to each successive mortality factor up to the adult stage. Mortality during the adult stage can be counted as one or more *k*-factors acting on the adults, or alternatively as a *k*-mortality acting on the next generation of eggs (Varley et al., 1973). The final post-reproductive mortality to act on a generation, i.e., that which brings generation numbers to zero, contributes nothing to between-generation variation in numbers and is not included in the analysis. The advantages of using *k*-values instead of

Table 7.1 Composite life tables for six generations of a hypothetical insect population with discrete generations. Each k-value is calculated as $k = (\log_{10}$ before mortality $- \log_{10}$ after mortality). $K = k_1 + k_2 + k_3$

Year	Eggs	k_1	Larvae	k_2	Pupae	k_3	Adults	K
1	1000	0.824	150	0.398	60	1.080	5	2.302
2	800	0.426	300	0.685	62	1.190	4	2.301
3	1200	0.681	250	0.455	50	0.824	12	1.960
4	700	0.942	50	0.204	50	0.699	10	1.845
5	500	0.553	140	0.301	70	0.766	12	1.620
6	1200	1.000	120	0.150	85	1.230	5	2.380

Note while such life tables have traditionally been presented in columns, putting them in rows, as is done here, makes spreadsheet regression calculations easier) (see also Fig. 7.6)

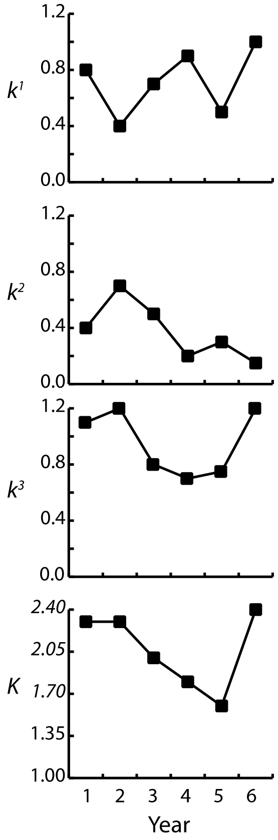


Fig. 7.6 Key factor analysis of the mortalities acting on a hypothetical insect population (see Table 7.1 for data)

percentage mortalities lie in the ease of calculation and the fact that k-values can be added together to give a measure for total generation mortality (K) (adding percentages would have no meaning because they would sum to well over 100%).

Plotting the k-values against generation may be enough to reveal the key factor(s) causing population change (Fig. 7.6). Here, variations in k_3 between generations most closely follow variations in overall mortality (K), indicating that k_3, is the key factor. Note that the key factor is not necessarily the factor causing greatest total mortality (k_1 in this case).

Detecting Density Dependence

Assessing which factors contribute to regulation of the population again involves plotting each k-value, this time against the $\log_{10}$ density on which it acts (i.e., before the mortality). In our example (Fig. 7.7) the plot of k_1 against log density of eggs contains six data points, corresponding to each generation. Similarly, k_2 is plotted against $\log_{10}$ density of new larvae, again with six data points, and so on. Positive relationships for any of these plots indicate that mortality is acting in a density-dependent fashion. A horizontal slope indicates density independence, while a negative slope indicates inverse density dependence. Regression analysis is generally used to calculate the significance of the slopes. Here, the only significant density dependence is found in k_2. However, the problem of statistical validity arises because as k-values are calculated in the first place from $\log_{10}$ densities, the two axes are not independent. Moreover, the independent variable ($\log_{10}$ density), estimated from population samples, is not error-free.

If density dependence is accepted, then the slope of the regression, b, can be taken as a measure of the strength of the density dependence. The closer b is to 1, the greater the stabilising effect of the mortality. A slope of $b = 1$

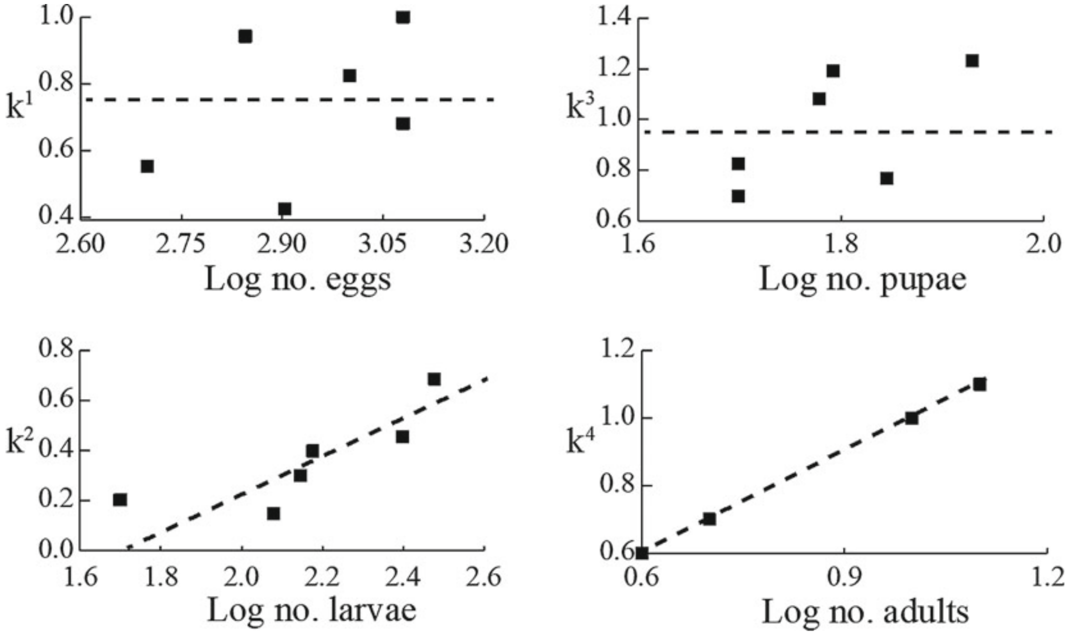


Fig. 7.7 The identification of density-dependent factors from life-table data. *k*-values for the different mortalities are plotted against the population densities on which they acted. In this case, only k_2 is significantly density-dependent (k_2 = 0.86L–1.52; R^2 = 0.84; k_1 = 0.74; k_3, = 0.96). k_4 is the last mortality to act, bringing numbers down to 0 (or in this case 1, which was used to make the log calculations workable). This remaining mortality is, by its nature, always density dependent but is not included in the analysis, as it contributes nothing to population variation or regulation

will compensate perfectly for any changes in density at this stage, while a slope of $b < 1$ will be unable to compensate completely for any changes (undercompensation). Slopes of $b > 1$ suggest overcompensation.

A Case Study: The Winter Moth

Varley and Gradwell's (1968, 1970) own study of the winter moth (*Operophtera brumata*), together with the various follow-up studies in England and Canada, are the best understood and most widely quoted examples of the use of age-specific life tables. We will briefly review some of the features of this study and use it to illustrate some of the potential problems in using key factor analysis.

The winter moth feeds on a wide range of mainly deciduous trees, and occasionally defoliates oaks. The life-cycle at Wytham Wood, near Oxford, UK, where the study was carried out, is as follows: eggs are laid in early winter in the tree canopy and hatch in spring to coincide with bud burst. The caterpillars feed on the foliage until fully grown, whereupon they descend to the forest floor on lines of silk and pupate in the soil. Adults emerge in November and December and females ascend the trees to mate and oviposit in crevices on the bark. There is, therefore, one generation each year (univoltinism).

Data collected between 1950 and 1962 reveal that 'winter disappearance' (k_1), during the period between the egg stage and that of the fully grown larvae, is the key factor explaining population variation between years. Parasitism, disease, and predation (k_2–k_6) are relatively insignificant in this respect (Fig. 7.8). The only significant regulating factor to be detected, however, was predation on pupae (k_5, Fig. 7.9), subsequently shown to be caused mainly by shrews and ground beetles (Frank, 1967; East, 1974; Kowalski, 1977). Parasitism showed no sign of being density dependent, either at the larval stage (k_2) or at the pupal stage (k_6), leading the authors to suggest that the wide variations in

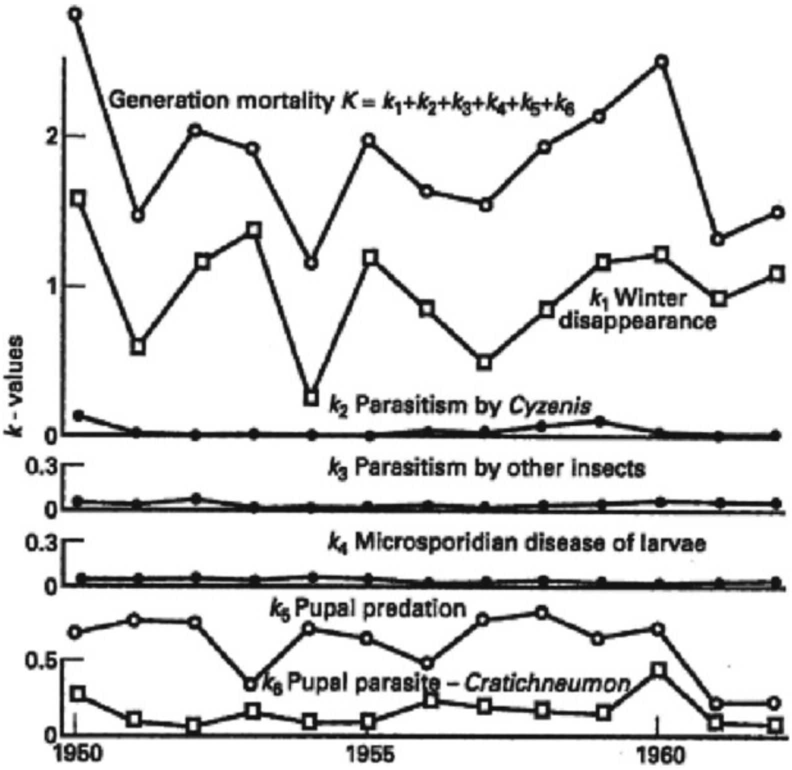


Fig. 7.8 Key factor analysis of the mortalities acting on the winter moth (from Varley et al., 1973, reproduced by permission of Blackwell Publishing)

densities from year to year, caused by the key factor 'winter disappearance', may be obscuring a possible delayed density-dependent relationship. The lack of any detectable regulating potential by the larval parasitoid *Cyzenis albicans* (k_2) was particularly surprising as this tachinid fly had been introduced in 1955 as a very effective biological control agent against winter moth in Nova Scotia, Canada (Roland & Embree, 1995). This difference could perhaps be explained by higher levels of *C. albicans* mortality in the UK. The parasitoid, although attacking the moth in the larval stage, continues to develop within the moth pupae throughout the summer and early winter and is therefore exposed to the same mortality factors as the moth pupae. Varley and Gradwell (1968, 1970) recorded as much as 98% mortality of *C. albicans* puparia. This is higher than that for winter moth pupae, but understandable as *C. albicans* spends 4 to 5 months longer in the soil, emerging in the spring.

Disadvantages of the Approach

The difficulty of obtaining sufficient field data highlights the single biggest problem of the approach, namely that of securing a long enough sequence of data to perform the analysis with a reasonable likelihood of detecting statistically significant relationships (Hassell et al., 1987). For insect populations having one generation a year, there is no guarantee of success with even a decade of data. This is especially a problem in the face of environmental change that alter processes affecting a species over the duration of the study. Moreover, the approach depends heavily on knowing all of the important factors to include in a study at the outset. There is not much scope for incorporation of new components at a later stage. There are several additional problems: (1) Several agents may act at the same time on a life-cycle stage, which can be accounted for using the marginal death rates which represent the proportion dying due to a factor in the absence of other independent factors that may act

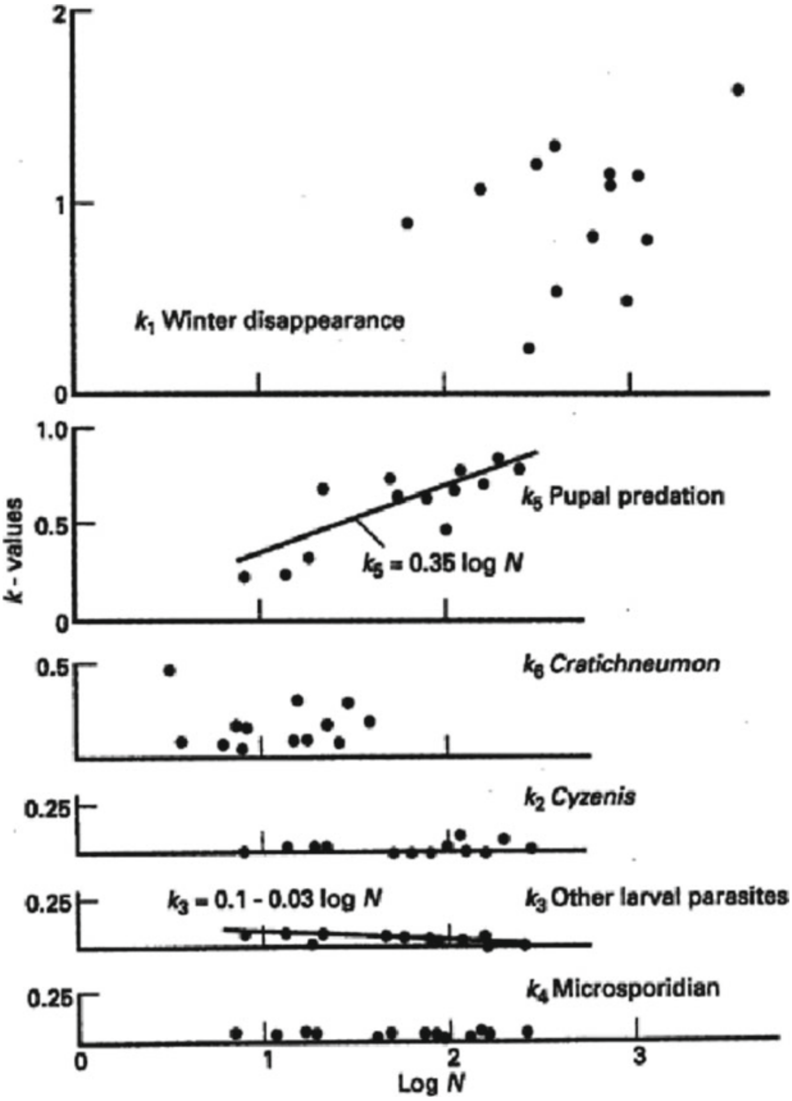


Fig. 7.9 *K*-values of the winter moth mortalities plotted against the population densities on which they acted. k_1, k_2, k_4 and k_6 are density independent; k_3 is weakly inversely density dependent; k_5 is strongly density dependent (from Varley et al., 1973, reproduced by permission of Blackwell Publishing)

at the same time (Elkinton et al., 1992). (2) Some of the mortality categories in the life table may contain, or mask, a number of others which could be important key or regulating factors. This is particularly likely to be the case with poorly understood, broad categories, such as ‘winter disappearance’ in the winter moth example. (3) Life-table analysis methods are based on correlation, so do not provide an unambiguous estimation of cause-and-effect relationships. (4) It is possible for strongly regulated populations to show little variation from equilibrium, and this may make statistical detection of the processes of regulation difficult using traditional life-table methods.

Time-Specific Life Tables

Time-specific (or vertical) life tables are suitable for use with populations in which the generations overlap, due to a short development time of the immature stages relative to the reproductive period of the adults (Kidd, 2010). At equilibrium, such species (such as humans and aphids) achieve a stable age distribution (Lotka, 1922) in which the proportion of the population in each age group or stage remains constant. In this situation, all the ecological processes affecting the population are, at least in theory, operating concurrently. This means that the relative numbers in each age group at any instant in time provide an indication of the proportional mortality from one age group to the next. We cannot deduce from this what mortality factors are operating, or whether any regulation is occurring, so the value of a time-specific life table is limited in this respect.

Estimating mortality from parasitism is difficult when generations overlap. Van Driesche and Bellows (1988) provide an analytical method for doing this. Hughes (1962) developed a technique based on the time-specific life-table approach, which could be used for analysing aphid populations with a stable age (i.e., instar) distribution. Using a graphical method to compare population profiles at successive physiological time intervals, Hughes (1963) was able to partition the mortalities acting on the different instars, for example, parasitism, fungal disease and ‘emigration’. As Hughes (1972) pointed out, there is, however, no easy way of estimating errors in the construction of these life-table diagrams. In fact, the technique is dependent on the assumption of a stable age distribution. Whilst Hughes’ (1972) method is now considered to be of limited applicability, his work did lead to the development of the earliest simulation models for analysing insect populations with relatively complex population processes, such as density dependence (Knape and de Valpine, 2012; Andow & Kiritani, 2016). For field populations with overlapping or partially overlapping generations, the use of such models is now the only sensible way forward. These techniques are discussed in detail below (Sect. 7.3.8).

7.3.5 Manipulation and Factorial Experiments

The problems of detecting density dependence from life-table data have already been discussed (Sect. 7.3.4). One way of testing directly whether density-dependent mechanisms are operating is to carry out a ‘convergence experiment’ (Nicholson, 1957), in which subpopulations are manipulated to achieve artificially high or low densities and are then monitored through time (Harrison & Cappuccino, 1995). Convergence to a common density is then taken as evidence for density-dependent regulation. Practical difficulty in manipulating the density of some species, and knowledge of what densities are high or low, may limit the usefulness of this technique. Among successful studies, Brunsting and Heessen (1984) manipulated densities of the carabid predator *Pterostichus oblongopunctatus* in field enclosures and found evidence for convergence within two years. Criticisms can be levelled at this technique in that enclosures may prevent emigration. Gould et al. (1990) manipulated densities of gypsy moth by artificially loading eight forest areas with different densities of egg masses to achieve a wide range of infestation levels. This method revealed previously undetected density-dependent mortality in the larval stage, primarily due to two parasitoid species.

Factorial experiments can be used to determine whether factors potentially capable of limiting population numbers combine in a simple additive way or show more complex patterns (synergistic or antagonistic interactions; Chap. 9). A fully factorial experiment is designed to include all possible combinations of two or more factors, and each of the levels within the factors. To be useful, the factorial experiment must be replicated and last long enough to produce time-series data sufficient to assess equilibrium population levels around which numbers fluctuate (Rosenheim, 1998; Sih et al., 1998). Such experiments are used to examine the emergent effects of multiple enemies on prey populations primarily due to intraguild predation (e.g., Mitchell et al., 1992; Costamagna and Landis, 2007; Straub and Snyder, 2008; Frago and Godfray, 2014; Wu et al., 2016; Chailleux et al., 2017; Alhadidi et al., 2019), and how multiple prey species may indirectly impact the role of natural enemies for one another. For example, using field enclosures (Sect. 7.2.3) in an alfalfa field, Cardinale et al. (2003) manipulated the presence of two important predators, the coccinellid beetle *Harmonia axyridis* and the damsel bug *Nabis* sp., and one parasitoid, *Aphidius ervi*, each individually and in all combinations. They followed the population dynamics of the natural enemies and the prey species, pea aphids *Acyrthosiphon pisum,* and found that the pea aphid was suppressed most in the treatment with all three natural enemies, suggesting a synergistic (greater than additive) effect (Fig. 7.10). However, closer inspection of the data from all treatments and the field revealed that this suppression was mediated by a second prey species, the cowpea aphid *Aphis craccivora*. The cowpea aphid inhibited parasitism of the pea aphid by *A. ervi.* So, when the cowpea aphid was suppressed by the two predators, the parasitoid population increased and suppressed the pea aphid population (Fig. 7.10). These same factorial experimental methods are also used to explore the effects of abiotic factors (Miller et al., 2017) or agricultural manipulations such as mulching (Schmidt et al., 2004), in conjunction with natural enemies.

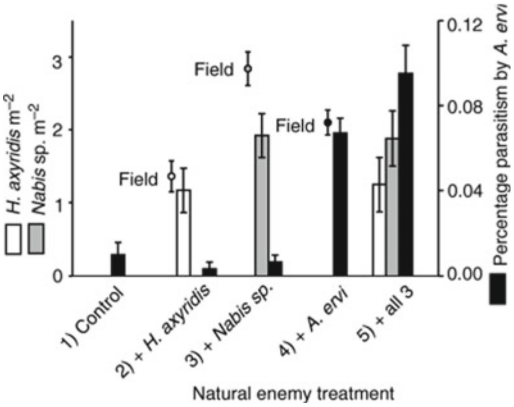


Fig. 7.10 Natural enemies of the pea aphid (*Acyrthosiphon pisum*) treatments on the final date of the study. The densities of predators *Harmonia axyridis* and *Nabis sp.* are based on the final numbers of individuals captured per cage. Parasitism by *Aphidius ervi* is compared among treatments with the ratio [(mummies stem^{-1})/(mummies + *Acyrthosiphon pisum* stem^{-1})]. Bars are the mean ± SE of n = 3 cages for treatments 1–4, and n = 4 cages for treatment 5. For comparison, data points give the naturally occurring densities of enemies in the alfalfa field (from Cardinale et al., 2003, with permission)

7.3.6 Landscape Scale Patterns, and Metapopulation and Metacommunity Dynamics

An insect herbivore usually occurs on a crop or natural plant species that is present at multiple sites in a region, with variable conditions spatially and temporally. In order for a natural enemy to have an impact on the pest, and persist in the long term, it must do so on a landscape scale. The structure of a landscape, such as its configuration, complexity or the fraction of the area cultivated, can determine the regional long-term persistence of an individual natural enemy species, or the composition of the community of natural enemies, and their effectiveness against insect pests. The dynamics of populations in agricultural or other heterogeneous or fragmented landscapes can be modelled as metapopulations. By extension, a community of natural enemies and their prey can be seen as a metacommunity.

In this section we first present aspects of landscape ecology that have been used to make predictions about the impact of landscape structure on biological control. Then we present the existing and potential application of metapopulation and metacommunity ecology for predicting the dynamics of pests and their natural enemies.

Landscape Ecology

Agricultural intensification leads to a simplified landscape. This simplification is associated with decreased biodiversity and increases in economically important pests on cultivated crops. In some cases, the increase in pests is due to decreased effectiveness of natural enemies (Tscharntke et al., 2007; Cohen & Crowder, 2017; Perez-Alvarez et al., 2019). Both conservation and importation biological control may be influenced by the landscape context of the crops. Grab et al. (2018) investigated the relationship between landscape simplification and the importation and conservation biological control of Lygus bugs, *Lygus lineolaris*, in cultivated strawberry. They found increased pest density and reduced parasitism rates of crop pests in landscapes with more intensive agriculture

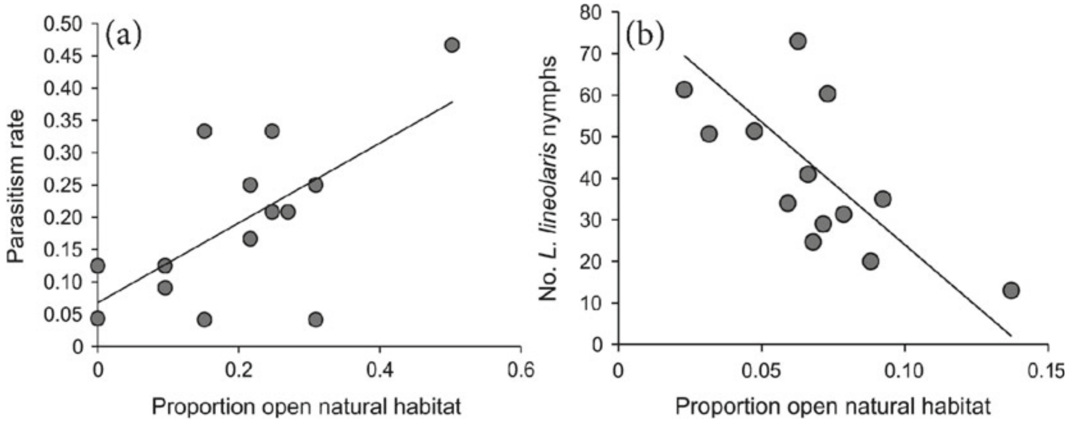


Fig. 7.11 **a** Parasitism rates of *Lygus lineolaris* nymphs by *Peristenus digoneutis* and **b** the average number of *L. lineolaris* nymphs collected from strawberry fields, as a function of the proportion of open semi-natural habitat at 750 m surrounding the sampling location within each strawberry field (from Grab et al., 2018, with permission)

(Fig. 7.11), probably because there were few host and food resources for the parasitoids in simplified landscape (Jonsson et al., 2015). Grab et al. (2018) also found, irrespective of landscape simplification, only introduced parasitoids and no native parasitoids of Lygus bugs in strawberry fields. In this case there was no conservation biological control being provided by parasitoids, even where non-crop habitat was abundant. In contrast, Winqvist et al. (2011) found decreased conservation biological control of aphids on cereal crops by generalist predators in simplified landscapes. However, it is notable that this held for organic farms but not conventional farms (Fig. 7.12), suggesting that landscape at multiple spatial scales is relevant for the maintenance of

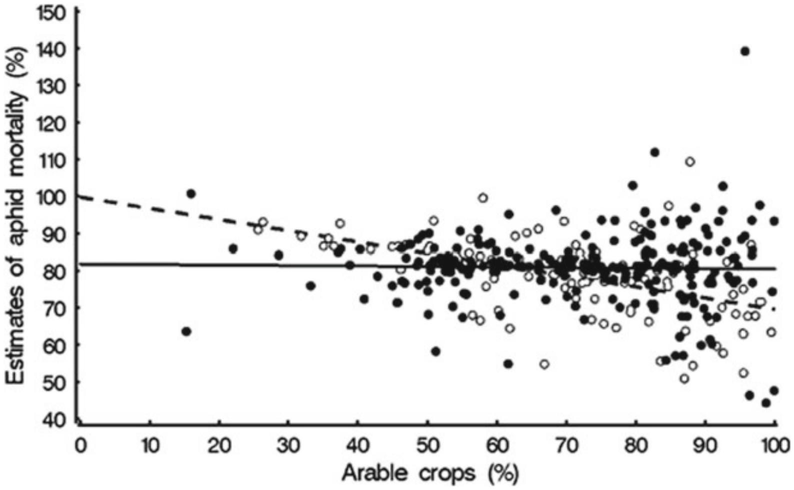


Fig. 7.12 Percentage of aphids eaten (mortality) as a function of percent arable crops in the landscape. The figure was created by plotting residual values for each sampling point (agricultural field) along the landscape gradient. The residual values come from the statistical analysis of variance model, accounting for the variation associated with the random effects of farm nested in region, which leads to apparent aphid mortality of greater than 100% in some fields. Organic fields: open circles and dotted regression line. Conventional fields: filled circles and solid regression line. The interaction is significant, i.e., the significant effect of landscape in the organic fields differs from the insignificant effect in conventional fields (from Winqvist et al. 2011, with permission)

natural enemy populations. These examples illustrate that while biodiversity increases with landscape complexity, increased non-crop habitat in the surrounding landscape does not consistently improve pest management as natural enemy responses can vary from positive to negative (Karp et al., 2018).

Metapopulation and Metacommunity Ecology

The above associations of pests, damage and natural enemies with landscape complexity indicate that the landscape is important for natural enemy populations, and illustrate important ecological patterns, but they do not quantify the dynamics of populations. To do that, we must measure or model change in population sizes over time and/or space. Since most insect pests are distributed in a dynamic patchwork landscape, it is intuitive to place them in a metapopulation context.

A metapopulation is a spatially structured population that persists over time as a set of local populations with limited dispersal between them. Local population processes (reproduction, predation, etc.) occur mostly within the local populations. Between-patch variation in parasitism and predation influence dynamics at the local population level, and dispersal between local populations may account for the persistence of regional populations, despite unstable fluctuations or extinctions at the local level (for reviews see Taylor, 1990, and Hanski, 1998). While the concept existed earlier, the term "metapopulation" was first used by Levins (1969) to describe his model of the potential for insect pest control, including biological control and insecticides, at a regional level. Levins (1969) formulated the rate of change of the fraction of habitat patches occupied by a species in a landscape (p). He used the same logistic differential equation that is used in classical population models (Sect. 7.3.8), but with the number of individuals replaced by the fraction of occupied patches p,

$$\mathrm{d}p/\mathrm{d}t = cp(1-p)ep \tag{7.5}$$

Here, c is the rate constant for colonisation of empty patches and e is the rate constant for extinction of local populations. Levins' (1969) model includes an intrinsic exponential growth rate cp for colonisation as well as a term that inhibits growth once the metapopulation is large ($-cp^2$), at which point there are few available sites left to colonise. Colonisation is the result of immigration from neighbouring populations. The rate of extinction is proportional to the fraction of occupied patches with the probability of extinction of each patch (e) being independent.

Since Levins' (1969) model, more realistic deterministic models have been developed (Adler & Nuernberger, 1994) as well as probabilistic patch occupancy models, such as the incidence function model that accounts for spatial variation of colonisation and extinction probability (Hanski, 1994), and Bayesian models to address spatial and temporal variability of conditions (Smith et al., 2014), as well as individual agent-based models in which the behaviour of each individual animal is accounted for (Uchmański, 2016).

These models consistently show that persistence at the regional level can be enhanced by dispersal between local populations, provided that: (1) local populations fluctuate asynchronously between habitat patches, (2) predator rates of colonisation are not too rapid relative to those of the prey, and (3) some local density dependence is present. While the degree of density dependence may be quite low, resulting in frequent local extinctions, the metapopulation may persist for a long time (Kean & Barlow, 2000; Hanski et al., 2017). For the most part, these models describe the dynamics of a single predator or parasitoid species reliant on a prey or host resource with independent dynamics. However, they are also applied to systems in which predator–prey dynamics are interdependent (Taylor, 1990; Holt, 1997; Fernandes et al 2022). This includes a number of laboratory studies exploring the effects of spatial structure and dispersal on persistence of predator–prey systems (Huffaker, 1958; Pimentel et al., 1963; Holyoak & Lawler, 1996; Bonsall et al., 2002). Pimentel et al. (1963), for example, examined the interaction between a parasitoid wasp and its fly host in artificial environments consisting of small boxes connected by tubes. The interaction persisted longer with more boxes and with reduced parasitoid dispersal. Bonsall et al. (2002) developed a similar system of interconnecting boxes to study a bruchid beetle–parasitoid metapopulation interaction, with comparable results. While agreement with theory may be encouraging, the small scale on which these experiments, by necessity, have been carried out, may not reflect processes at the regional metapopulation level.

Metapopulation processes have been detected in some large-scale field predator–prey systems, but joint metapopulation dynamics of the prey with the predator or parasitoid have rarely, if ever, been identified (Walde, 1995; Harrison and Taylor, 1997; Weisser, 2000; Cronin, 2004; Cosentino et al., 2011). One of the best-studied examples involving an arthropod predator–prey system is provided by the Glanville Fritillary butterfly, *Melitaea cinxia*, and its specialist braconid parasitoid, *Cotesia melitaearum*, in the Åland Islands, Finland. In Åland there are around 3,200 suitable dry meadows, of which several hundred are occupied by the butterfly in any one year, and the parasitoid is present in about 10% of the local butterfly populations (Lei & Hanski, 1997; van Nouhuys and Hanski, 2002; Hanski et al., 2017). The dynamics of the butterfly are predicted by metapopulation theory for the observed areas and isolation of habitat patches. The parasitoid also exists as a metapopulation, greatly influenced by the spatial dynamics of the host. However, due to density-dependent hyperparasitism, parasitoid dispersal limitation, and an overarching dependency of the butterfly on host plant quality, the dynamics of the host do not depend on the parasitoid (van Nouhuys & Hanski, 2002; Øpedal et al., 2020). Clearly, more detailed empirical studies of this nature, especially in biological control systems, are required to provide a ‘reality check’ to the theoretical literature (Cronin & Reeve, 2005).

Insect pests and their natural enemies are part of a community of species in a landscape that is often a patchwork of cultivated and uncultivated land. Thus, the system can be thought of as a metacommunity, which is a community of interacting species made up of local communities linked by dispersal (Leibold et al., 2004). There is a robust literature of metacommunity theory (Logue et al., 2011), but it has not yet been applied quantitatively to questions of efficiency of importation or conservation biological control. Nonetheless, some metacommunity processes are broadly relevant for predicting persistence or dynamics in biological control. One example of this is the consequence of hyperparasitoids for the effectiveness of parasitoids as biological control agents. The patch occupancy model of metacommunity theory (Leibold et al., 2004) predicts that with increasing habitat fragmentation, higher trophic level species such as hyperparasitoids fail to persist because the resources become sparser and more unpredictable at increasing trophic levels (Holt, 2002; Wang et al., 2021). Thus, we predict hyperparasitoids to be present where a plant and insect pest are common in a landscape. This could either stabilise or destabilise effectiveness of biological control (Rosenheim, 1998). A second example of the potential application of metacommunity theory to biological control is the concept of spillover between cultivated and uncultivated parts of the landscape in conservation biological control (Tscharntke et al., 2007; Blitzer et al., 2012). The mass effects model of metacommunity dynamics predicts the movement of individuals within a landscape based on changing resource availability (Leibold et al., 2004). Based on this, a community of natural enemies may persist in a dynamic landscape, such as an agricultural system, in which local populations fluctuate due to changes in resource availability caused by harvest, crop rotation, insecticide application and seasonality.

7.3.7 Analytical Models of Population Dynamics

A continuous-time framework is generally used to model populations with overlapping generations and all-year-round reproduction (Hassell, 2000a, 2000b; Murdoch et al., 2003). In contrast, discrete-time models are more suited for populations with non-overlapping generations that reproduce in a discrete pulse determined by season. We review simple models of host–parasitoid interactions in discrete-time formalism and describe tools for elucidating their dynamical behaviours. One advantage of simple models is that they are often analytically tractable, i.e., their analysis using mathematical tools can provide generic insights into regulatory mechanisms across parameter regions that lead to stable, unstable, or oscillatory population dynamics. While reviewing classical models introduced decades ago, we also highlight new modelling frameworks and results from recent literature. We emphasise that while we primarily focus on discrete-time models in this chapter, many host–parasitoid systems are more appropriately modelled using the continuous-time framework of Lotka–Volterra predator–prey models (Murdoch et al., 1987, 2003; Ives, 1992; Gurney & Nisbet, 1998; Sanchez et al., 2018; Singh, 2021a).

Simple Discrete-Time Models

Discrete-time models have been a tradition in arthropod host–parasitoid systems; their usage is primarily motivated by the univoltine life-histories of insects residing in the temperate regions of the world. A typical life-cycle consists of adult hosts emerging during spring, laying eggs that hatch into larvae. Hosts then overwinter in the pupal stage and emerge as adults the following year. The host becomes vulnerable to parasitoid attacks at one stage of its life-cycle (typically the larval stage). Adult female parasitoids search and attack hosts during this time window of vulnerability. While adult parasitoids die after this time window, the parasitised hosts support juvenile parasitoids, which pupate, overwinter, and emerge as adult parasitoids the following year. Synchronised life-cycles, with no overlap of generations in both the host and the parasitoid makes discrete-time models highly appropriate for these systems.

A model describing host–parasitoid dynamics in discrete time is given by

$$\begin{aligned} H_{t+1} &= RH_t f(RH_t, P_t) \\ P_{t+1} &= kRH_t[1 - f(RH_t, P_t)] \end{aligned} \tag{7.6}$$

where H_t and P_t are the adult host and the adult parasitoid densities, respectively, at the start of year t, and $R > 1$ denotes the host's reproductive rate. Note that $R > 1$ is needed to avoid population extinction of the host. If the host is vulnerable to the parasitoid at its larval stage, then RH_t is the host larval density exposed to parasitoid attacks. Parasitoids attack host larvae during the vulnerable period leading to two categories of hosts within the population: parasitised and unparasitised larvae. The function $f(RH_t, P_t)$ is the fraction of host larvae escaping parasitism (sometimes referred to as the escape response). In the absence of the parasitoid $f(RH_t, 0) = 1$ and the host population grows unboundedly as

$$H_{t+1} = RH_t.$$

Finally, $RH_t[1 - f(RH_t, P_t)]$ is the net density of parasitised larvae, with each larva giving rise to k adult female parasitoids in the next generation. Renaming variables, where now H_t denotes the host larval density, results in

$$\begin{aligned} H_{t+1} &= RH_t f(H_t, P_t) \\ P_{t+1} &= kH_t[1 - f(H_t, P_t)] \end{aligned}$$

and both forms of the model have been used in the literature.

The simplest formulation of Eq. 7.6 is the classical Nicholson–Bailey model

$$\begin{aligned} H_{t+1} &= RH_t exp(-cTP_t) \\ P_{t+1} &= kRH_t[1 - exp(-cTP_t)] \end{aligned} \tag{7.7}$$

where c represents the rate at which parasitoids locate/parasitise hosts, and T is the duration of the host vulnerable stage (Nicholson & Bailey, 1935). The model assumes that parasitoids search for hosts randomly, are never egg limited, and have rapid handling times. Given the random

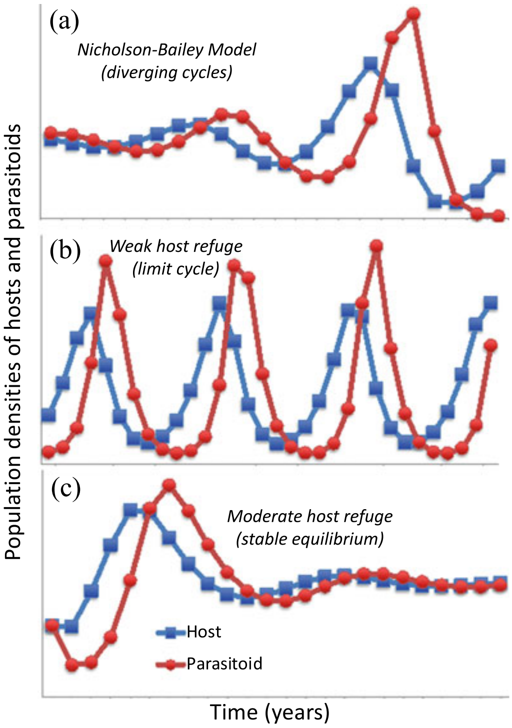


Fig. 7.13 **a** A typical host–parasitoid population time series for the Nicholson–Bailey model (Eq. 7.7), **b** for a model with either a weak host refuge ($\mu = 0.05$ in Eq. 7.12) or c) a moderate host refuge (μ = 0.20 in Eq. 7.12) (Singh & Emerick, 2021, with permission). Host reproductive rate is assumed to be R = 2

host–parasitoid interaction, the number of parasitoid attacks per host follows a Poisson distribution, with mean cTP_t, then the escape response $exp(-cTP_t)$ is the probability of zero attacks in the Poisson distribution. A typical time series of the Nicholson–Bailey model is shown in Fig. 7.13a. Both populations grow at low densities, but at large host densities, the parasitoid begins to overexploit the host. This leads to a crash in the host population, followed by a crash of the parasitoids. These cycles of overexploitation and crashes result in an unstable interaction, with both populations exhibiting diverging oscillations. Before discussing generalisations to the Nicholson–Bailey model, we briefly review mathematical approaches used for dissecting dynamical behaviours.

General Stability Analysis

Given a model of the form represented by Eq. 7.6, one is typically interested in knowing if the model can support a stable host–parasitoid interaction, and if so, then for what parameter values. Simulating the model for a few test parameters (this can be done, for example, in a spreadsheet package, such as Microsoft Excel, by starting with an initial condition and iterating forward in time) can provide the first answers but a systematic quantification of stability regions proceeds along the following steps:

Step 1: Determining the Equilibrium Point

The model's equilibrium or fixed points are the population densities that remain constant across years. Let H^* and P^* denote the host and parasitoid densities at equilibrium, respectively. These equilibrium densities are obtained by first substituting $P_{t+1} = P_t = P^*$ and $H_{t+1} = H_t = H^*$ in Eq. 7.6 and then solving the resulting equations. Note that the model has a trivial equilibrium $P^* = H^* = 0$ where both populations are extinct, but we are primarily interested in the non-trivial equilibrium that represents the coexistence of species. For model 7.6 this non-trivial equilibrium is the solution to the following two equations

$$1 = Rf(RH^*, P^*)$$
$$P^* = k(R-1)H^*$$

Solving these equations for the Nicholson–Bailey (1935) model yields a single non-trivial equilibrium point

$$H^* = \frac{lnR}{(R-1)kcT}$$
$$P^* = \frac{lnR}{cT},$$

where the host equilibrium levels decrease, and the parasitoid equilibrium levels increase, with increasing host growth rate R.

Step 2: Linearising Around the Equilibrium

Real populations are never in equilibrium as environmental fluctuations in model parameters and unmodeled interactions constantly perturb the system out of any equilibrium it may have momentarily reached. If these perturbations transiently decay and the populations return to equilibrium, then the equilibrium point is said to be stable. Alternatively, if perturbations amplify, and the populations increasingly deviate from the equilibrium, then the equilibrium point is said to be unstable. Considering small perturbations $p_t = P_t - P^*$, $h_t = H_t - H^*$ and linearising model nonlinearities in Eq. 7.6 around the equilibrium, results in the following linear discrete-time system

$$\begin{bmatrix} h_{t+1} \\ p_{t+1} \end{bmatrix} = A \begin{bmatrix} h_t \\ p_t \end{bmatrix} \tag{7.8}$$

where A represents a 2×2 matrix whose entries are related to the slope, or sensitivity, of the escape response to population densities (detailed formulas describing each entry of A are provided in the Appendix to Singh & Emerick, 2021). The matrix A is mathematically referred to as the Jacobian matrix and its eigenvalues are intricately linked to the stability of the equilibrium.

Step 3: Checking for Stability

The necessary and sufficient condition for stability of a linear discrete-time dynamical system, such as Eq. 7.8, is that all the eigenvalues of A have an absolute value of less than one (Elaydi, 1996). For a 2×2 matrix, this corresponds to the equilibrium H^*, P^* being stable if the following three conditions all hold

$$1 - Tr(A) + Det(A) > 0$$

$$1 + Tr(A) + Det(A) > 0$$

$$1 - Det(A) > 0 \tag{7.9}$$

where Tr and Det refer to the trace and the determinant of the matrix, respectively. The equilibrium point is unstable if any one of the inequalities does not hold (we refer the reader to Elaydi, 1996, for details on the mathematical terminology used here).

In many cases these stability conditions can be further simplified. For example, if the escape response $f(P_t)$ only depends on parasitoid density, then the first two conditions always hold, and stability is completely determined by the third inequality $1 - Det(A) > 0$. If $1 - Det(A) = 0$ then the equilibrium point is said to be neutrally stable (on the edge of stability and instability), and both host and parasitoid populations cycle with a period of 6 or higher (Singh & Nisbet, 2007). If $1 - Det(A) < 0$ then the equilibrium is unstable, and populations either show diverging oscillations that grow unboundedly (as in the Nicholson–Bailey, 1935, model; Fig. 7.13a), or they settle into bounded population cycles (i.e., a stable limit cycle; Fig. 7.13b).

Interestingly, for a parasitoid-dependent escape response $f(P_t)$ the inequality $1 - Det(A) > 0$ can be rewritten in a different form

$$\frac{dH^*}{dR} > 0 \tag{7.10}$$

which leads to a simple, yet powerful stability condition: the model's equilibrium is stable, if and only if, the adult host equilibrium density increases with increasing host growth rate R (Singh et al., 2009). Recall that H^* in the Nicholson–Bailey model is decreasing with R, and its instability is reflective of this simplified stability criterion. Using the fact that $P^* = k(R-1)H^*$, the above condition on H^* can also be written in terms of the parasitoid equilibrium density

$$\frac{dP^*}{dR} > \frac{P^*}{R-1}$$

revealing that stability requires parasitoid densities to increase sufficiently rapidly with increasing host growth rate. It is important to emphasise that these simplified conditions are only to be used for a host-independent escape response. When $f(RH_t, P_t)$ depends on both populations,

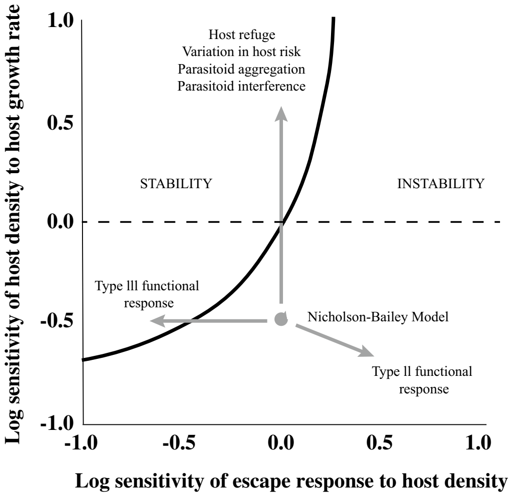


Fig. 7.14 Stability regions for the host–parasitoid model (Eq. 7.6) in terms of the sensitivity of the host density to the host growth rate $\frac{dH^*}{dR}$, and the sensitivity of the escape response to the host density $\frac{df}{dH^*}$ (Singh & Emerick, 2021). The Nicholson–Bailey model corresponds to $\frac{dH^*}{dR} < 0$ and $\frac{df}{dH^*} = 0$ and is unstable. Stability arises in two orthogonal ways: (1) an increase in $\frac{dH^*}{dR}$ to make it positive, which occurs with parasitoid interference and aggregation or host refuge; (2) a decrease in $\frac{df}{dH^*}$ which occurs with a Type III functional response in the parasitoid attack rate (Sect. 1.14). In this figure, the host growth rate is assumed to be $R = 2$ with the axes being dimensionless log sensitivities $\frac{H^*}{f}\frac{df}{dH^*}$ and $\frac{R}{H^*}\frac{dH^*}{dR}$ (modified from Singh & Emerick, 2021, with permission)

the stability conditions (Eq. 7.9) can be graphically represented in terms of two relevant quantities:

$$\frac{dH^*}{dR} \text{ and } \frac{df}{dH^*}$$

where the latter denotes the sensitivity of the escape response to the host density. Figure 7.14 shows that stability region with respect to both these quantities for a general escape response $f(RH_t, P_t)$, and stability is more likely to occur when the escape response is a decreasing function of the host density, rather than an increasing function (Singh & Emerick, 2021).

Expanding the Nicholson–Bailey Model

We next discuss expansions of the Nicholson–Bailey model, emphasising the stabilising and destabilising effects of different mechanisms.

Host and Parasitoid-Dependent Attack Rates.

The Nicholson–Bailey model assumes that parasitoids search and attack hosts with a constant rate c implying a Type I functional response (Sect. 1.14). This assumption is relaxed by considering a Type II functional response (Sect. 1.14). Prior studies have implemented it by modifying the attack rate in Eq. 7.7 to

$$c = \frac{c_1}{1 + c_1 T_h R H_t}$$

where c_1 is the attack rate at low host densities, and $T_h$is the handling time (Rogers, 1972). The net attack rate per parasitoid cRH_t increases with H_t and saturates at $1/T_h$ at high host densities. With this change, the escape response is now an increasing function of H_t and it makes the model even more unstable if we move the Nicholson–Bailey point further to the right, away from the stability boundary in Fig. 7.14. Similarly, a Type III functional response (Sect. 1.14) is incorporated by setting

$$c = \frac{c_1 (RH_t)^q}{1 + c_1 T_h (RH_t)^{q+1}} \tag{7.11}$$

with $q > 0$ capturing the acceleration of attack rate with increasing H_t at low host densities, and analysis shows that such responses fail to stabilise the population dynamics irrespective of the value of q (Hassell & Comins, 1978). The fact that a Type III response is not stabilising in the Nicholson–Bailey framework is surprising, since it is known to have a stabilising effect in the continuous-time framework of Lotka–Volterra models (Murdoch & Oaten, 1975). As discussed below, this discrepancy arises from how the Type III response is phenomenologically introduced. Indeed, modelling host mortality during the vulnerable period as a continuous-time process confirms the stabilising properties of a Type III response, removing the discrepancy between the two frameworks.

In contrast to a host-dependent attack rate, a parasitoid-dependent attack rate is stabilising. Consider the scenario where the attack rate is proportional to $c \propto P_t^{-m}$ and decreases with increasing P_t due to interference between parasitoids with $0 < m < 1$ quantifying the degree of interference. Since the escape response only depends on P_t, stability can be discerned by simply testing for host equilibrium density increasing with growth rate. Solving for the host equilibrium and applying Eq. 7.10 reveals the system to be stable for

$$\frac{R \ln R + 1 - R}{R \ln R} < m < 1$$

which corresponds to $0.28 < m < 1$ for $R = 2$, and $0.5 < m < 1$ for $R = 5$ (Hassell & Varley, 1969). In the context of Fig. 7.14, stability arises by moving the Nicholson–Bailey model ‘upwards’ via a change in the sign of $\frac{dH^*}{dR}$.

Host Refuge.

Some hosts may be in some form of a refuge that protects them from parasitoids. There may be physical refuges in which hosts are protected from parasitism or some hosts may be physiologically immune to parasitoid attack or there may be a seasonal mismatch between host and parasitoid, for instance early developing hosts may avoid searching parasitoids. Refuges may also be statistical: hosts may escape parasitism by chance more often than if parasitoid search was truly random. Host refuges can be incorporated into the Nicholson–Bailey model in two different ways: a constant host density protected from parasitism, or a constant fraction of hosts in the refuge. Both forms of the refuge stabilise host–parasitoid dynamics (Hassell, 2000a, 2000b). For example, a constant host fraction μ in the refuge leads to the following model

$$\begin{aligned} H_{t+1} &= RH_t(\mu + (1-\mu)exp(-cTP_t)) \\ P_{t+1} &= k(1-\mu)RH_t[1 - exp(-cTP_t)] \end{aligned} \quad (7.12)$$

While a weak refuge results in bounded oscillations, a moderate refuge stabilises the population dynamics (Fig. 7.13b,c). However, stability is again lost for a strong refuge with both hosts and parasitoids growing unboundedly. As before, the stability regime in terms of μ can be obtained by simply checking the criterion given by Eq. (7.10).

Variation in Risk

The stability arising from a host refuge can be generalised under the concept of variation in risk. The Nicholson–Bailey model assumes that all hosts are identical in terms of their vulnerability to parasitism. Perhaps a more realistic scenario is individual hosts differing in their risk of parasitism due to genetic factors, spatial heterogeneities, or the duration or timing of their exposure to parasitism (Bailey et al., 1962). In essence, the product cT in Eq. (7.7) represents the attack rate integrated over time, and by transforming it into a random variable x we obtain

$$H_{t+1} = RH_t \int_{x=0}^{\infty} p(x) exp(-xP_t) dx$$

$$P_{t+1} = kRH_t\left[1 - \int_{x=0}^{\infty} p(x) exp(-xP_t) dx\right]$$

where $p(x)$ is the distribution of parasitism risk across hosts (Singh et al., 2009). A key assumption in this formulation is that risk is independent of the local host density if hosts are non-uniformly distributed in space. Assuming $p(x)$ follows a Gamma distribution (a versatile distribution commonly used for capturing skewed population behaviours) with mean $\underline{c}$ and coefficient of variation CV, we obtain the following escape response

$$\int\limits_{x=0}^{\infty} p(x)exp(-xP_t)dx = \frac{1}{\left(1+\underline{c}CV^2P_t\right)^{\frac{1}{CV^2}}},$$

that yields the model

$$H_{t+1} = \frac{RH_t}{\left(1+\underline{c}CV^2P_t\right)^{\frac{1}{CV^2}}}$$

$$P_{t+1} = kRH_t\left(1-\frac{1}{\left(1+\underline{c}CV^2P_t\right)^{\frac{1}{CV^2}}}\right) \quad (7.13)$$

Stability analysis of this model leads to a classical result: $CV > 1$stabilises the population dynamics, irrespective of all other model parameters (R, k, $\underline{c}$) (May, 1978; Chesson and Murdoch, 1986; Murdoch and Stewart-Oaten, 1989; Hassell et al., 1991; Taylor, 1993). The stabilising risk distribution is shown in Fig. 7.15 where most hosts are at low risk, and stability arises from parasitoid attacks being skewed or aggregated towards a small fraction of high-risk individuals, with $1/CV^2$ representing the degree of aggregation. This stability criterion motivated several studies investigating spatial pattern of parasitism in the field, and many data sets were found to be consistent with $CV > 1$ (Pacala & Hassell, 1991).

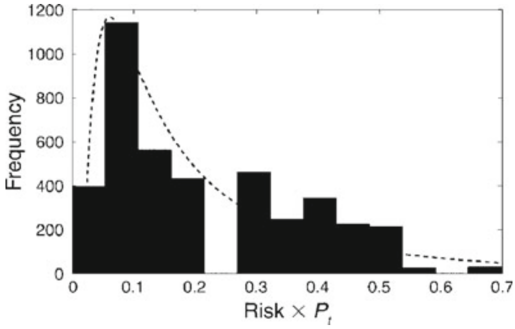


Fig. 7.15 The distribution of risk as obtained from host parasitism data across patches from Reeve et al. (1994) (see Singh et al., 2009, for details on obtaining the distribution of risk). The estimated value of CV for this distribution is 1.31 and the dashed line corresponds to an inverse Gaussian distribution with same mean and CV as the distribution of risk (Singh et al., 2009, with permission)

Recent work in this direction has relaxed the assumption of a Gamma-distributed risk. It turns out that if the host reproduction $R \approx 1$ then $CV > 1$ is the necessary and sufficient condition for stability irrespective of what form $p(x)$ takes (Singh et al., 2009; Singh, 2021b). However, if $R \gg 1$, stability requires a skewed risk distribution with the modal risk being zero (as in the Gamma distribution for $CV > 1$). We illustrate this point with the data presented in Fig. 7.15 where $p(x)$ is approximated by an inverse Gaussian distribution that has a non-zero mode. Despite having a $CV \approx 1.3$, this risk distribution is stabilising only for $1<R<2$ (Singh et al., 2009). Interestingly, if the host risk follows an inverse Gaussian distribution and $R > 5$, then the host–parasitoid equilibrium can never be stabilised irrespective of how high CV is. In summary, for host growth rates close to one, sufficient variation in host risk ($CV > 1$) is stabilising. In contrast, at high growth rates, the shape of the distribution for low-risk individuals is crucial in determining stability (Singh et al., 2009).

Semi-Discrete Hybrid Models

As illustrated above, for most host–parasitoid models the escape response is phenomenologically chosen or designed to recapitulate field observations. While these models have tremendously improved our understanding of stabilising processes, mechanistic modelling frameworks are needed to translate insect life-histories and behaviours into discrete-time models. For example, consider a scenario where the parasitoids have a density-dependent mortality from predation or food limitation. It is not obvious how to modify the Nicholson–Bailey model to reflect this density dependence. For this purpose, semi-discrete or hybrid frameworks have been proposed; these use ordinary differential equations to track population densities within the host's vulnerable period during a given year (Rohani et al., 1994; Bonsall and Hassell, 1999; Geritz & Kisdi, 2004; Pachepsky et al., 2008). The solution of the differential equations at the end of the vulnerable period predicts the population densities for the next year. We discuss this semi-discrete formulation in further detail below.

Let τ denote the time within the host vulnerable stage that varies from *0* to T corresponding to the start and end of the vulnerable stage. The density of parasitoids (P), unparasitised (L) and parasitised host larvae (I) at time τ within the vulnerable stage of year t, follows the differential equations.

$$\begin{aligned} \frac{dP(\tau,t)}{d\tau} &= -cP(\tau,t)L(\tau,t) - \gamma_P P(\tau,t) \\ \frac{dL(\tau,t)}{d\tau} &= -cP(\tau,t)L(\tau,t) - \gamma_L P(\tau,t) \\ \frac{dI(\tau,t)}{d\tau} &= cP(\tau,t)L(\tau,t) - \gamma_I P(\tau,t). \end{aligned} \tag{7.14}$$

Here c represents the parasitoid's attack rate, and γ_P, γ_L, γ_I are the mortality rates. Solving the differential equations with initial conditions at the start of the vulnerable period $\tau = 0$

$$L(0,T) = RH_t, P(0,t) = P_t, I(0,t) = 0$$

predicts the parasitised and unparasitised larval population at the end of the season $\tau = T$. This leads to a more general discrete-time model.

$$\begin{aligned} H_{t+1} &= F(H_t, P_t) \\ P_{t+1} &= G(H_t, P_t) \end{aligned}$$

where update functions are obtained by setting $F(H_t, P_t) = L(T,t)$ and $G(H_t, P_t) = kI(T,t)$. As expected, a constant attack rate c with no mortalities ($\gamma_P = \gamma_L = \gamma_I = 0$) results in the Nicholson–Bailey model. Allowing for non-zero density-independent mortalities leads to models very similar in structure to the Nicholson–Bailey models with unstable population dynamics (Singh & Emerick, 2021).

Revisiting Functional Responses

A functional response can be incorporated in the semi-discrete framework by having the attack rate take the form

$$c = \frac{c_1 L(\tau,t)^q}{1 + c_1 T_h L(\tau,t)^{q+1}} \tag{7.15}$$

where $q = 0$ corresponds to a Type II functional response, and $q > 0$ a sigmoidal Type III response (Sect. 1.14). Singh and Nisbet (2007) show that the resulting discrete-time model based on the hybrid framework is stable for $q > 1$, assuming that the handling time is significantly shorter than the vulnerable stage duration ($T_h \ll T$). With the host density $L(\tau,t)$ decreasing over time due to parasitism, the attack rate (Eq. 7.15) results in a larger fraction of hosts escaping parasitism. This seems to exert a stabilising influence on the population dynamics compared to the phenomenologically chosen attack rate (Eq. 7.11) that is set by the initial host density at the start of season. Thus, systematic consideration of continuous changes in population densities that occur within a season is critical in a discrete-time model formulation. Interestingly, the host equilibrium here is still a decreasing function of the host growth rate (as in the Nicholson–Bailey model), but a Type III functional response induces stability by making the fraction of hosts escaping parasitism a decreasing function of the host density. In the context of Fig. 7.14, this corresponds to shifting the Nicholson–Bailey model to the left in the stability region. Finally, we point out that a Type II response ($q = 0$) is destabilising in both formulations.

Density-Dependent Host Mortality

A key mechanism known to have a stabilising effect on the host–parasitoid populations is the density-dependent self-limitation in the host (May et al., 1981; Neubert and Kot, 1992; Marcinko & Kot, 2020). Density-dependent host mortality can be modelled by assuming that the death rate $\gamma_L = c_h L(\tau,t)$ is proportional to the host density. Solving the continuous dynamics (Eq. 7.14) for a constant parasitoid attack rate yields the following discrete-time model (Singh & Nisbet, 2007).

$$H_{t+1} = L(T,t) = \frac{RH_t exp(-cTP_t)}{1 + c_h RH_t \frac{1-exp(-cTP_t)}{cP_t}}$$

$$\begin{aligned} P_{t+1} &= I(T,t) \\ &= \frac{kcP_t}{c_h} ln\left[1 + c_h R H_t \frac{1 - exp(-cTP_t)}{cP_t}\right]. \end{aligned} \tag{7.16}$$

In the absence of parasitoids, the host population dynamics follows the Beverton–Holt model

$$H_{t+1} = \frac{RH_t}{1 + c_h TRH_t}$$

Gurney and Nisbet (1998). The discrete-time model (Eq. 7.16) has two non-trivial equilibrium points. The first is the no-parasitoid equilibrium that is set by the strength of the host-density dependence

$$H^* = \frac{R-1}{c_h TR}, P^* = 0$$

and this equilibrium is stable in the overall model (Eq. 7.16) for sufficiently strong density-dependent host mortality c_h verifying

$$lnR < \frac{c_h}{kc}.$$

The second equilibrium, where both host and parasitoid are present, is given by

$$H^* = \frac{exp\left(\frac{c_h}{kc}\right) - 1}{1 - \frac{exp\left(\frac{c_h}{kc}\right)}{R}} \frac{cP^*}{c_h R}, P^* = \frac{lnR - \frac{c_h}{kc}}{cT}$$

and is stable for

$$z^* < \frac{c_h}{kc} < lnR \tag{7.17}$$

where the constant z^* is the solution to

$$z^* + 1 = \frac{R(lnR - z^*)}{R - exp(z^*)}.$$

The different stability regions are summarised in Fig. 7.16, where high values of the ratio c_h/kc (the relative strength of density-dependent host mortality and parasitism) stabilise the no-parasitoid equilibrium, and moderate values stabilise the host–parasitoid interaction. Stability is again lost for low values of $c_h/kc < z^*$ with both populations exhibiting bounded oscillations.

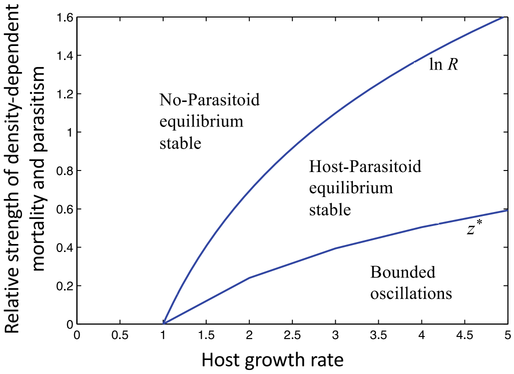


Fig. 7.16 Stability regions for the different equilibriums in the discrete-time model (Eq. 7.16) with respect to c_h/kc (relative strength of density-dependent mortality and parasitism) and host growth rate R. For this plot we assume $k = 1$. From Singh and Nisbet (2007), with permission

The quantity

$$\frac{R\left(exp\left(\frac{c_h}{kc}\right) - 1\right)\left(lnR - \frac{c_h}{kc}\right)}{(R-1)\left(R - exp\left(\frac{c_h}{kc}\right)\right)}$$

is of special interest to biological control, as it represents the ratio of the host equilibrium with parasitoids and without parasitoids. Varying c_h/kc in the stability region (Eq. 7.17) can be used to obtain the maximum level of host depression that is consistent with stable coexistence of both species. This formula predicts an approximate 66% depression of host density for $R = 2$, and 70% depression for $R = 10$ (Singh & Nisbet, 2007). While the parasitoid attack rate is assumed to be constant here, it would be interesting to see how a combination of density dependence in host mortality and other factors, such as parasitoid handling times, egg limitation, host-to-host differences in parasitism risk, shape stability and the degree of host suppression.

Density-Dependent Parasitoid Mortality

Singh and Nisbet (2007) show that density dependence in the parasitoid mortality rate modelled by taking $\gamma_P = c_P P(\tau, t)$ in Eq. 7.14 results in a model identical to the one obtained by assuming a Gamma-distributed host risk. The

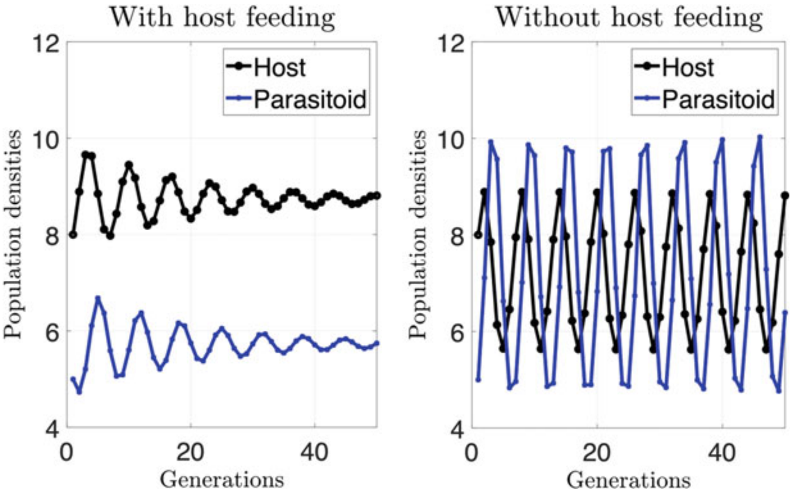


Fig. 7.17 Coupling host feeding with a quadratic parasitoid attack rate stabilises otherwise neutrally stable host–parasitoid population dynamics (from Emerick and Singh, 2016, with permission)

only difference being that $\underline{c}$ in Eq. 7.13 is replaced by c, and CV^2 by $\frac{c_P}{c}$. As discussed earlier, stability arises in the model when $CV > 1$, implying that strong density-dependent parasitoid mortality $c_P > c$ can stabilise the host–parasitoid interaction.

Host Feeding

Recent work has used the semi-discrete framework to investigate the effect of host feeding, which refers to the tendency observed in a number of species of parasitoids for adult females to use some host individuals as a food source rather than an oviposition site. Emerick and Singh (2016) considered each adult female parasitoid to be in one of two states: without eggs or with just one egg to lay. Host feeding results in the death of the host with an eggless parasitoid gaining resources to produce an egg, whereas host parasitism by an egg-carrying parasitoid results in a parasitised host and an eggless parasitoid. Analysis of such simple models using the semi-discrete framework shows that while host feeding by itself cannot stabilise the otherwise unstable Nicholson–Bailey model, it can have a stabilising effect when coupled to other stabilising mechanisms. These results complement several studies incorporating the effects of host feeding in continuous-time models, where host feeding can have stabilising effects (Yamamura & Yano, 1988; Kidd & Jervis, 1991; Murdoch et al., 1992; Briggs et al., 1995), but a delay in egg production following host feeding is destabilising (Shea et al., 1996). This point is illustrated by considering a quadratic Type III functional response $c = c_1 L(\tau, t)$ with the parasitoid attack rate (for both host feeding and parasitism) increasing linearly with the larval population density. It is important to point out that such a functional response leads to a neutrally stable host–parasitoid equilibrium in the absence of host feeding in the semi-discrete formalism (Singh & Nisbet, 2007). Interestingly, incorporation of host feeding in this model exhibits a stable host–parasitoid equilibrium for all values of R. Thus, the inclusion of host feeding converts a neutrally stable equilibrium to a stable one (Fig. 7.17).

Modelling Host–Parasitoid Communities

Most parasitoid species attack more than one species of host, and most host species are attacked by several species of parasitoids. Having presented insights from two-species host–parasitoid models, we now discuss progress towards expanding these models to more than two species. The simplest case is a three-species community, either consisting of one host species and two parasitoid species, or two host species attacked by a common parasitoid.

Two Host Species Attacked by a Common Parasitoid

We first consider the scenario where two different host species are attacked by the same parasitoid species. In this case, the overall population dynamics can be described by the model.

$$H_{t+1} = R_H H_t f_H(P_t, H_t, G_t)$$

$$G_{t+1} = R_G G_t f_G(P_t, H_t, G_t)$$

$$P_{t+1} = k_H R_H H_t[1 - f_H(P_t, H_t, G_t)] + k_G R_G G_t[1 - f_G(P_t, H_t, G_t)]$$

where H_t, G_t are the population densities of the two host species with reproduction rates R_H, R_G, escape responses f_H, f_G, and the number of parasitoids emerging from each parasitized host k_H, k_G, respectively. This indirect interaction between two hosts (due to a shared parasitoid) has been referred to as apparent competition (Holt & Lawton, 1993; McPeek, 2019). If the escape responses f_H, f_G only depend on the parasitoid density P_t, then coexistence of both hosts is not possible, and the host with the lower reproduction rate is driven to extinction. These observations have been replicated in laboratory experiments with two moth species, *Plodia interpunctella* and *Ephestia kuehniella,* that were shared by a common parasitoid, *Venturia canescens*. *P. interpunctella* and *E. kuehniella* were separated and thus could not compete with each other for resources but the shared parasitoid could access both species: either of the two hosts could persist with the parasitoid in a two-species interaction but in the three-species interaction the *Ephestia* population became extinct (Bonsall & Hassell, 1998). Thus, some form of host-density dependence in one or both of the escape responses is necessary for the stable coexistence of all three species.

Recall from Eq. (7.13) that aggregation of parasitoid attacks on a small fraction of high-risk hosts can stabilise the population dynamics. Analysis of these models in the context of apparent competition shows that while such aggregated attacks always end up excluding one of the host species, combining it with some form of host-switching by the parasitoid leads to persistence of all the three species (Bonsall & Hassell, 1999). Along the same theme, recent work has considered a Type III functional response towards just one host species. More specifically, the parasitoid attacks host G with a constant rate (as in the Nicholson–Bailey model) but attacks host H with an accelerating rate analogous to Eq. (7.15) with exponent q. Discrete-time models formulated using the hybrid framework reveal that a Type III functional response towards just one species is sufficient to stabilise the population dynamics of apparent competition, even though the interaction between the parasitoid and host G by itself is unstable (Singh, 2021c). Hence, removal of H from a stable three-species interaction will destabilise the resulting two-species interaction. For example, when $R_H = R_G = 2$ a strong acceleration of parasitoid attack rate towards H with $q > 1.15$ is sufficient for stable coexistence of both hosts. Note that this value of q is higher than that needed to stabilise the parasitoid interaction with just H, in which case $q > 1$ is required.

Two Parasitoid Species Sharing a Common Host

A complementary scenario to that presented above is when a single host species is being used as a resource by two different parasitoid species. Here the model takes the form

$$H_{t+1} = RH_t f_P(P_t) f_Q(Q_t)$$

$$P_{t+1} = k_H RH_t[1 - f_P(P_t)]$$

$$Q_{t+1} = k_Q RH_t f_P(P_t)[1 - f_Q(Q_t)]$$

where now P_t and Q_t are the population densities of the two parasitoid species and f_P, f_Q are the respective parasitoid-dependent escape responses. The implicit assumption here is that the parasitoids attack different developmental stages of the host: P attacks first and the host density escaping parasitism $RH_t f_P(P_t)$ is then exposed to attacks from Q. These models have been investigated in the context of aggregated parasitoid attacks, with f_H and f_Q taking a form like the escape response in Eq. (7.13). In this case, coexistence of parasitoids is possible when the degree of aggregation (i.e., *CV* values in Eq. 7.13) for both consumers is greater than that needed for the stability of a single parasitoid–single host interaction (May & Hassell, 1981; Kakehashi et al., 1984). It is interesting that coexistence is also possible when only one of the parasitoids exhibits aggregated attacks, and the other attacks randomly with a constant rate, but the region of parameter space permitting coexistence is significantly reduced.

Recent work has introduced a general class of models to explore multi-parasitoid dynamics

$$
\begin{aligned}
H_{t+1} &= RH_t f(P_t, Q_t) \\
P_{t+1} &= k_H RH_t[1 - f(P_t, Q_t)]g(P_t, Q_t) \\
Q_{t+1} &= k_Q RH_t[1 - f(P_t, Q_t)][1 - g(P_t, Q_t)]
\end{aligned}
$$

where the escape response $f(P_t, Q_t)$ is the fraction of hosts escaping parasitism from both parasitoids, and $0 \leq g(P_t, Q_t) \leq 1$ is the competition response representing the fraction of parasitised larvae that will develop into adult parasitoids P_{t+1} in the next generation. Similarly, *1*-$g(P_t, Q_t)$ is the fraction of parasitised larvae that will develop into adult parasitoids Q_{t+1}. To be ecologically relevant, $g(P_t, Q_t)$ is an increasing function of P_t (i.e., with increasing density P_t a larger pool of the parasitised larvae belongs to parasitoid *P*). Analysis of this general model reveals that the stable coexistence of both parasitoids depends on two remarkably simple criteria. The first criterion is the same as that for a single parasitoid–single host interaction: the adult host equilibrium density should increase with *R*, as in Eq. (7.10). The second criterion is that any increase in P_t density should not cause a large increase in $g(P_t, Q_t)$. For a symmetric interaction $k_H = k_Q$ where both parasitoids have similar equilibrium densities, the second criterion reduces to

$$
\frac{P^*}{g(P^*, Q^*)} \frac{\partial g(P_t, Q_t)}{\partial P_t}\Big|_{P_t = P^*, Q_t = Q^*} < \frac{1}{2}
$$

implying that the dimensionless log sensitivity of the competition response with respect to P_t must be less than half (Singh & Emerick, 2022). It will be interesting to expand these results to more complex communities with specialist parasitoids attacking their hosts, and generalist parasitoids sharing hosts creating both direct competition between consumers, and apparent competition between host species. However, this analytical modelling approach is likely to rapidly reach the limits of mathematical tractability as the size of the considered communities expands.

7.3.8 Confronting Models with Field Data

Introduction

The value of analytical models is to provide a framework for exploring how processes such as density dependence, and life-history traits such as search efficiency, can influence the dynamics of consumer–resource interactions. Such models are based on a minimal set of biological details but have the advantage that they are simple enough to allow analytical solutions to be found for equilibrium densities and stability properties (Sect. 7.3.7). While predictions from modified analytical models have been compared to observed changes in host and parasitoid abundance under field conditions (Hassell, 1980), in general, such models are too simplistic to capture the greater complexity associated with the dynamics of particular species under field conditions (May & Hassell, 1988). Consequently, there have been two approaches used to confront models with field data on the density of host and natural enemy populations over time: (1) comparison of simulation model predictions and observed data, and (2) time-series analyses for selecting a statistical model that best describes, or fits, the observed data. For both approaches the time frame of the observed data can vary from a single growing season for a multivoltine population in an agricultural crop to multiple years for a univoltine population in a forest stand.

Comparing Simulation Model Predictions to Observed Data

This approach requires the construction of a simulation model that can be parameterised from independent laboratory or field data and validated by graphical comparison of model predictions to observed data representing a time series of population densities. Simulation models generally include additional biological details such as temperature-driven development rates, other factors that have an important influence on either reproductive or mortality rates of the host population, and a broader set of life-history traits of the natural enemies. In addition, simulation models can differ in number of trophic levels represented, and from intermediate to extreme complexity, depending on the level of knowledge of a particular system. Although complex simulation models with extensive biological detail were developed early on in response to the availability of increased computing power, models of intermediate complexity are now favoured as they have the distinct advantage of greater clarity and generality (Godfray & Waage, 1991). Following graphical comparison of predictions and observations, it is good practice to test the robustness of a simulation model using a sensitivity analysis in which parameter values in the model are adjusted by a small amount (often ± 10%). Three examples of simulation models that evaluate the effect of parasitism on agricultural pests are considered below, representing increasing levels of complexity.

Barlow and Goldson (1993) developed a two trophic level simulation model of intermediate complexity for the lucerne weevil *Sitona discoideus*, a univoltine pasture pest in New Zealand, to evaluate the extent to which parasitism of adult weevils by an introduced multivoltine parasitoid *Microctonus aethiopoides* contributed to a 75% reduction in reproductive weevil densities in the autumn. A discrete-time simulation model for peak autumn weevil densities included variables for population growth to a larval carrying capacity and effects of parasitism, drought and larval competition. The parasitoid has four to six generations each year, but mortality from parasitism in two of these generations was identified as being of greatest importance. One generation caused mortality immediately after adult weevils return to pastures after summer aestivation, and a second caused extensive mortality among reproductive adults in the autumn. Both parasitoid generations were included in the model and parasitism was based on an analytical model for parasitoid interference (Hassell & Varley, 1969). One of the strengths of this study was that all the variables in the model could be parameterised exclusively from independent field data without the need for detailed laboratory experiments. When validated against observed data collected over a 16-year period in Darfield, New Zealand (Kean & Barlow, 2000), the model provided a close match to the field data for adult weevil densities, but slightly overestimated the extent of parasitism (Fig. 7.18).

Murdoch et al. (2005) conducted a unique field experiment which demonstrated that the abundance of California red scale, *Aonidiella aurantia*, on lemon trees in coastal California, USA, is controlled by its introduced parasitoid *Aphytis melinus* and that the interaction is locally stable on individual trees. The experiment compared scale and parasitoid populations over a period of 18 months on both caged and uncaged trees. For the caged trees, additional scale crawlers were introduced over the first three months to elevate scale abundance to levels observed during outbreaks. The results were then compared to the predictions from a simulation model. This was an extension of an analytical stage-structured parasitoid–host model by Murdoch et al. (1992) that was updated to include temperature-driven maturation of both scale and parasitoid life stages on a daily basis. Many of the known biological details of the interaction, which had been studied over a period of 20 years, were included in the model, such as the effects of host feeding, sex allocation and a type I functional response with egg limitation for the parasitoid and an invulnerable adult stage for the scale. All variables in the model were parameterised independently from both laboratory and field data. The outcome of the experiment was that parasitism by *A. melinus* reduced scale

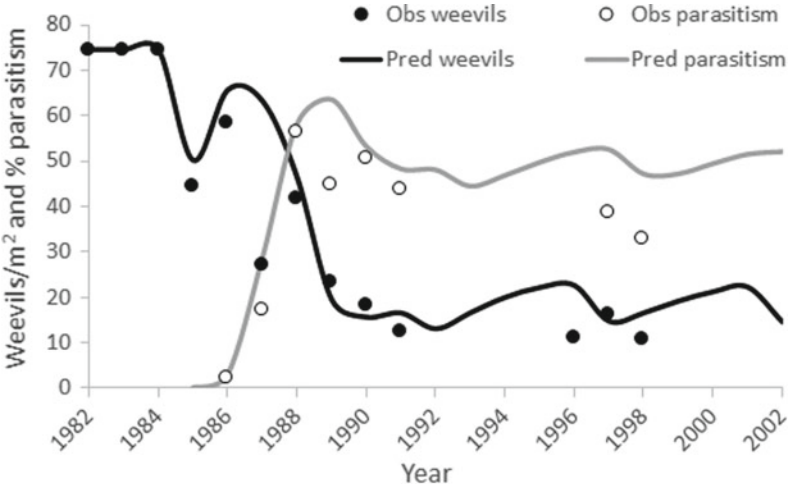


Fig. 7.18 Observed (circles) and model-predicted (lines) peak alfalfa weevil densities in the autumn (black line and solid circles) and levels of parasitism by *Microctonus aethiopoides* (grey line and open circles) in pastures in New Zealand (modified from Kean & Barlow, 2000, with permission)

densities on caged trees to the level present on open control trees within two months of the termination of scale crawler releases, and that thereafter both scale and parasitoid densities were identical on caged and open trees and showed very little variation in abundance over time. The model almost exactly predicted the pattern of change in scale and parasitoid densities in the closed cages, and the prediction proved surprisingly robust to a sensitivity analysis of each set of variables. The close match between model prediction and experimental data provided strong evidence that the model successfully captured the mechanisms by which *A. melinus* was able to both suppress and stabilise the scale population on individual trees.

Gutierrez and colleagues developed a tritrophic approach to simulation modelling in which a generalised supply–demand function is used for resource acquisition and conversion for all trophic levels from plant to predator or parasitoid (Freckleton & Gutierrez, 1996). The supply–demand function is an example of a ratio-dependent Type II functional response for resource acquisition that is driven by per unit biomass demand for resources to support growth and reproduction coupled with a numerical response for resource conversion that is based on assimilation and respiration (Gutierrez et al., 1994). The simulation model can include age structure and temperature-driven functions for maturation, reproduction, and resource acquisition and conversion, as needed for application to a specific system. This approach was used to explore the seasonal dynamics of the very successful biological control of cassava mealybug, *Phenaccocus manihoti*, by an introduced parasitoid *Anagyrus lopezi* and native coccinellids in Africa (Gutierrez et al., 1993). The model was parameterised using a combination of independent laboratory and field data and model fitting for those parameters that could not be determined independently. The model accurately predicted the growth of different components of the cassava plants over the growing season in Ibadan, Nigeria in 1983–1984 and mostly captured the seasonal fluctuations in abundance of mealybugs in the presence of the introduced parasitoid and native predators. The importance of predation and parasitism was evaluated by adding or deleting each component one at a time in a series of simulations, which showed that native coccinellids contributed little to control of the mealybug. The presence of the parasitoid could predict the extent and pattern of mealybug suppression, but only when a constant low level of parasitoid immigration was included. This suggested that the parasitoid may not be able to persist at a local scale following periods of low mealybug densities, but that it has the capacity to build populations sufficiently quickly to suppress mealybug abundance upon recolonisation.

A similar approach has been used to compare parasitoid species for the biological control of the coffee bean borer (Rodríguez et al., 2017; Cure et al., 2020; Sect. 7.4.3).

Time-Series Analysis Using Statistical Models

The time-series analysis approach to confronting statistical models with field data requires the use of longer-term data sets that typically span many generations of an herbivore and its predators and/or parasitoids. In contrast to simulation modelling, time-series analysis involves the fitting of linear, nonlinear or autoregressive statistical models to data using either a least-squares (for normal error distributions) or maximum likelihood (for non-normal error distributions) procedure. Separate models are developed for host and natural enemy populations, and the dependent variable can either be the natural log (ln) of population density at time $t + 1$ or the *per capita* rate of population change in ln population density from time t to time $t + 1$. The independent explanatory variables in a time-series model often include effects of host-density dependence (population density in previous generations), and effects of parasitism rate (proportion parasitised), predation rate (proportion predated), food quality and climatic factors. The goal is to find the simplest model that best fits the observed data, and to make sure that the fitted coefficients for the independent variables make good biological sense.

At its simplest, Münster-Swendsen and Berryman (2005) used multiple regression analysis (Chap. 9) (and the coefficient of determination as a measure of goodness of fit) to determine the best statistical model to describe the cyclic dynamics of the spruce needleminer *Epinotia tedella* in Denmark over a 19-year period based on host-density dependence and parasitism by two parasitoid species. The best-fit model was a logistic model for the *per capita* rate of population change ($R_t = \ln[N_t] - \ln[N_{t-1}]$):

$$R_t = a + bN_{t-1} + c\left(\frac{A_{t-1} + B_{t-1}}{N_{t-1}}\right) \tag{7.18}$$

where N is the density of needleminers, A the density of *Apanteles tedellae*, B the density of *Pimplopterus dubius*, and a, b and c are fitted constants. In this logistic model the effect of parasitism was represented by the ratio of parasitoids to hosts (Berryman et al., 1995) and accounted for 73% of the variation in R_t.

The analysis of time-series data is often based on autoregressive models to account not only for time lags in the effect of the independent variables (typically limited to no more than three generations to facilitate interpretation; Royama, 1992), but also for the effects of moving averages or temporal trends in the data. Time-series models are fitted to data using maximum likelihood, and the Akaike Information Criterion (AIC), which allows for maximisation of descriptive power and minimisation of the number of variables fitted, is used to select between competing models (Chap. 9). This approach has been applied to the analysis of changes in population densities of the yew gall midge *Taxomyia taxi* and its two parasitoids *Mesopolobus diffinis* and *Torymus nigritarsus* from 1967 to 2001 in the UK (Redfern & Hunter, 2005). The gall midge has a complex life-cycle which takes either one (bud galls) or two (shoot galls) years to complete and has distinct two-year generations in odd and even years. In contrast, *M. diffinis* has three generations per year and *T. nigritarsus* has a single generation each year. Separate models were fitted to log densities for the one-year and two-year life-cycles of the gall midge and to both parasitoids, and the independent variables included host-density dependence, parasitism (log density of *T. nigritarsus* and *M. diffinis*), tree vigour (width of growth rings) and climate (mean monthly precipitation, mean monthly maximum temperature and mean monthly minimum temperature). For simplicity, we consider only the best-fit models for the log densities of the two-year gall midge life-cycle (T) and its main parasitoid *T. nigritarsus* (N)

$$T_t = 0.89T_{t-2} - 0.33N_{t-2} + 0.02PREC_t - 0.57$$

$$N_t = 0.86N_{t-1} + 0.23N_{t-2} - 0.48N_{t-3} + 0.005T_{t-2} + 0.56 \quad (7.19)$$

where *PREC* denotes mean monthly precipitation and the subscript *t* denotes year. Over the 35-year period, gall midge densities were positively influenced by densities in the previous generation (*t*-2) and precipitation in the current year (*t*), and negatively influenced by *T. nigritarsus* densities in the previous generation. For the parasitoid, densities were positively influenced by gall midge densities in the previous generation, with a more complex effect of density dependence that had a positive influence for one-year and two-year time lags, but a negative influence for a three-year time lag. Further analysis from a simulation of the four time-series models (Fig. 7.19) showed (1) that *T. nigritarsus* drives cycles in the abundance of the yew gall midge, with an approximate 14-year periodicity, and (2) that stochasticity in climate variables is needed to prevent the cycles from having a constant periodicity.

While time-series analysis allows for testing of hypotheses about the role of predation or parasitism in driving the dynamics of prey or host populations, standard autoregressive models do have some limitations. For example, they do not incorporate more detailed functions for parasitism and/or predation, nor do they take the effects of measurement error in the estimation of densities from field populations or of environmental stochasticity on population processes into consideration. Although approaches have been developed to include both functional expressions of parasitism and other sources of variability into autoregressive models, complex mathematical methods are required both for model fitting and model selection. Probably as a consequence, these approaches have had limited application to date (Turchin, 2003; Kendall et al., 2005).

An alternative approach to addressing the problem of fitting statistical models of predator–prey interactions to time-series data that include observation error and process noise is through state-space or hierarchical models (de Valpine, 2003). Although state-space models are also more complex, recent developments have introduced maximum likelihood methods for parameter estimation (Chap. 9), model selection using AIC (Chap. 9), and one-step-ahead predictions to summarise model fit. This approach has been used to determine the extent to which the interaction between the woolly bear caterpillar, *Platyprepia virginalis*, and its tachinid parasitoid *Thelaira americana* (both univoltine) affects the

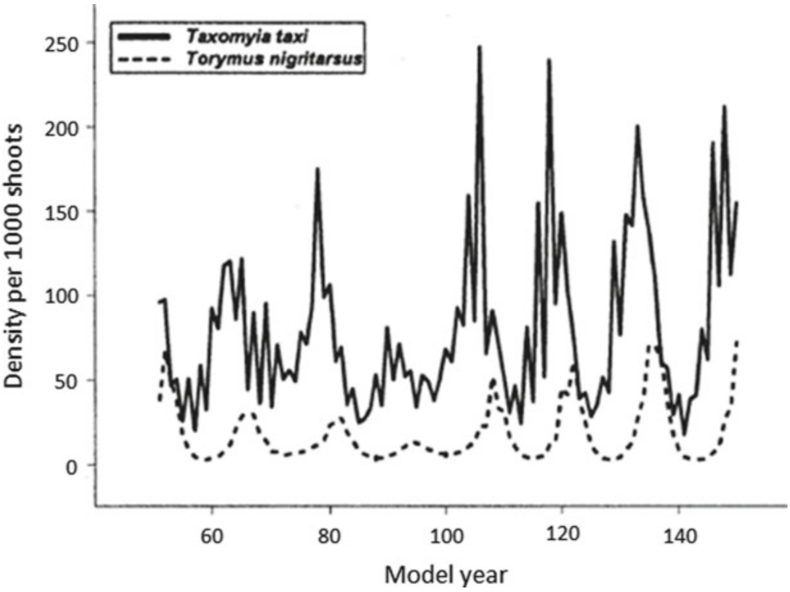


Fig. 7.19 Stochastic simulation of the coupled interaction between the 2-year life-cycle of the yew gall midge (solid line) and its main parasitoid *Torymus nigritarsus* (dashed line) based on time-series models fitted to observed data (from Redfern & Hunter, 2005, with permission)

dynamics of both species from a 21-year time series of observational data from California, USA (Karban & de Valpine, 2010). The state-space models for each species included environmental stochasticity, measurement error for both caterpillar densities and percent parasitism, Ricker and Gompertz functions for density dependence, a Nicholson–Bailey function for parasitism, and precipitation. Despite parasitism of up to 70%, both caterpillar and tachinid densities were shown to be driven by a combination of density dependence and precipitation rather than by the parasitoid–host interaction, although there was marginal evidence that tachinid abundance was driven by caterpillar abundance. State-space models have also been developed to analyse time-series data on the within-seasonal dynamics of pea aphid, *Acyrthosiphon pisum*, in alfalfa fields in Wisconsin, USA (Gross et al., 2005), and of cotton aphid *Aphis gossypii* in cotton fields in California, USA (de Valpine & Rosenheim, 2008). Although both studies found evidence for density dependence in the aphid populations, neither found a role for parasitism or predation in determining the pattern of seasonal dynamics. Nonetheless, state-space models may well offer new opportunities for the analysis of time-series data in the future and for a more rigorous approach to confronting models with field data.

7.4 Practice of Importation Biological Control

7.4.1 Overview

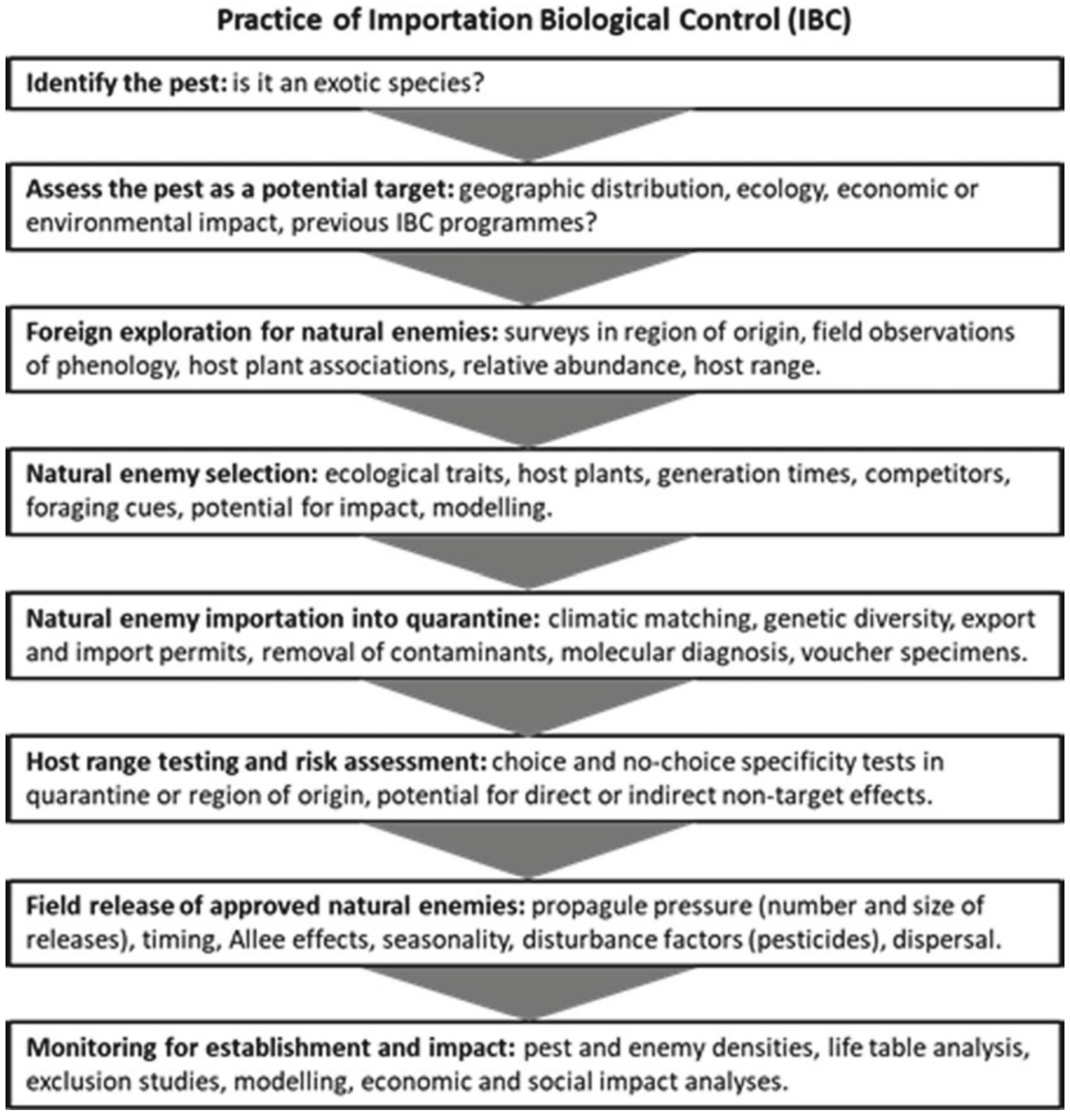
Importation biological control, also known as classical biological control, is the control of invasive pests through the deliberate introduction of specialist natural enemies from the geographic region of origin of the pest (Heimpel & Mills, 2017). Having begun as a very pragmatic and empirical approach to pest management in the late 1800s, the practice of biological control generated tremendous interest among population ecologists who sought to place it in a rigorous scientific framework that could both explain the successes achieved and provide additional guidance for the future (McEvoy, 2018). While theoretical ecology has made some important contributions to our understanding of consumer–resource interactions, our ability to predict success and to select natural enemy species with traits that are most likely to lead to success remains an elusive goal (Heimpel & Mills, 2017; Segoli et al. 2023).

The practice of importation biological control involves a complex sequence of steps that must be carefully followed to maximise the chances for success (Van Driesche & Hoddle, 2000). These steps include characterisation of the pest, foreign exploration for specialised natural enemies, selection and screening of candidate control agents, field release of approved control agents, and monitoring for establishment, spread and programme evaluation (Fig. 7.20). In this section we will explore historical patterns of success, criteria for selecting natural enemies, non-target effects, and methods for natural enemy release and programme evaluation.

7.4.2 Historical Patterns of Success

One of the earliest and perhaps the best-known examples of biological control is that of the cottony cushion scale, *Icerya purchasi*, as an invasive pest of citrus in California, USA (Caltagirone & Doutt, 1989). In this example, the vedalia beetle, *Rodolia cardinalis*, was imported from Australia in 1888 as a specialist predator and deliberately released in citrus groves where it brought about complete suppression of the pest. The degree of success of the programme was both compelling and inspiring, although the causal nature of the impact of the vedalia beetle in suppressing scale populations to very low levels of abundance was verified only more recently through unintended insecticide disruption (Grafton-Cardwell, 2015).

Cock et al. (2016) reviewed a database (BIOCAT2010) of introductions of insect biological control agents for the control of insect pests to the end of 2010. The historical record shows 6,158 introductions, using 2,384 different biological control agents against 588 pest species



Practice of Importation Biological Control (IBC)

Identify the pest: is it an exotic species?

Assess the pest as a potential target: geographic distribution, ecology, economic or environmental impact, previous IBC programmes?

Foreign exploration for natural enemies: surveys in region of origin, field observations of phenology, host plant associations, relative abundance, host range.

Natural enemy selection: ecological traits, host plants, generation times, competitors, foraging cues, potential for impact, modelling.

Natural enemy importation into quarantine: climatic matching, genetic diversity, export and import permits, removal of contaminants, molecular diagnosis, voucher specimens.

Host range testing and risk assessment: choice and no-choice specificity tests in quarantine or region of origin, potential for direct or indirect non-target effects.

Field release of approved natural enemies: propagule pressure (number and size of releases), timing, Allee effects, seasonality, disturbance factors (pesticides), dispersal.

Monitoring for establishment and impact: pest and enemy densities, life table analysis, exclusion studies, modelling, economic and social impact analyses.

Fig. 7.20 The sequence of steps in an importation biological control programme (modified from Thacker, 2002, with permission)

in 148 countries. In analysing the patterns of success, three important trends were apparent. Firstly, the number of natural enemy introductions per decade increased from the 1870s through to the 1970s, with temporary declines during the two world wars, but subsequently decreased dramatically each decade from the 1970s to the 2000s (Fig. 7.21a). Secondly, over the same period of time, the number of countries with successful introductions each decade has shown a steady increase through to the 1990s. These patterns reflect (1) the increase in unintentional introductions of exotic species via global networks of trade and transport over time (Banks et al., 2015), (2) an increased concern since the 1970s regarding the safety of biological control that has constrained the number of introductions per decade since then, and (3) an increase in both level of interest and effort devoted to biological control as an approach to

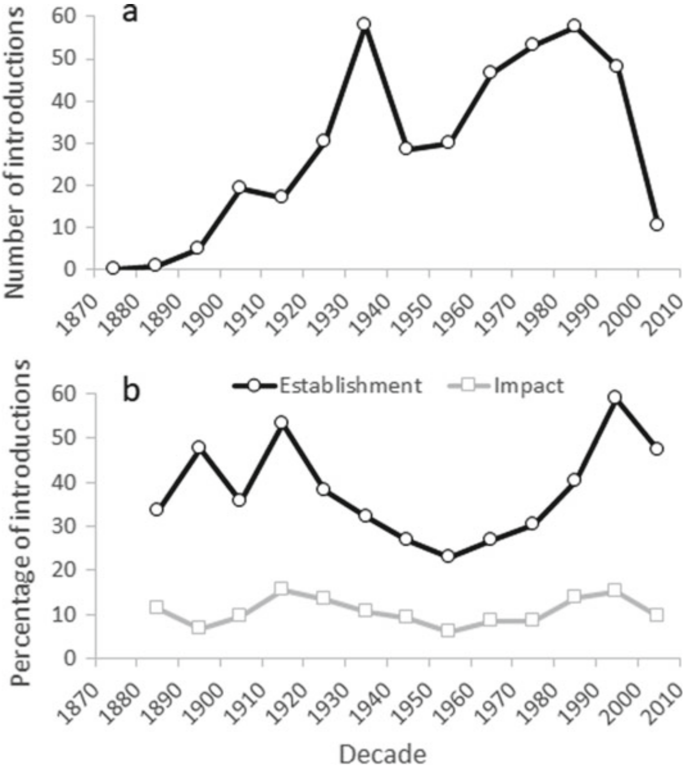


Fig. 7.21 Trends in the historical record of introductions of biological control agents, indicating, **a** the pattern in number of introductions by decade, and **b** the pattern in percentage of introductions that established (open circles, black line) and provided successful control (open squares, grey line) (modified from Cock et al., 2016)

pest management (Cock et al., 2016). Of the total introductions, 2,007 (32.6%) led to establishment, and 620 (10.1%) resulted in satisfactory control being reported against 172 (29.3%) different pest species (Fig. 7.21b). There is also some evidence that the efficiency of establishment and success have improved since the 1950s, but the improvement is moderate, from 20 to 40% for establishment and from 8 to 15% for success. Nonetheless, these positive trends reflect the greater research effort now made to optimise the chances of success and the increased confidence in importation biological control as a viable pest management strategy against a backdrop of the risk-averse culture that has developed in some key countries in recent years (Heimpel & Cock, 2018).

The historical record of importation biological control indicates that not all groups of insect pests have attracted the same level of attention or success. The Hemiptera (Homoptera), which includes scale insects, mealybugs, aphids and whiteflies, and Lepidoptera (moths and butterflies) are the two groups of insect pests that have attracted the greatest number of introductions (Waage & Mills, 1992). It is also notable that success has been consistently greater for homopteran than for lepidopteran pests (Mills, 2006a). Introductions for the control of beetle pests, such as Curculionidae and Chrysomelidae, although less well represented, have also shown high rates of establishment and success (Heimpel & Mills, 2017).

Biological control agents introduced for the control of arthropod pests include, in order of frequency of use, insect parasitoids, arthropod predators, microbial pathogens (fungi, viruses, microsporidia, bacteria and oomycetes) and insect parasitic nematodes (Hajek & Eilenberg, 2018). Among the insect parasitoids, tachinid flies and ichneumonid wasps have shown lower rates of establishment, while aphelinid, encyrtid, eulophid and scelionid wasps have had the highest rates of success, and trichogrammatid and pteromalid wasps have shown the lowest rates of success (Heimpel & Mills, 2017). In general, arthropod predators have been less successful in importation biological control than insect parasitoids (Kimberling, 2004; Heimpel & Mills, 2017). Rates of establishment have been low in most cases, with the exception of clown beetles (Histeridae) introduced for control of pests that infest livestock dung, and impacts on pest suppression have been limited, apart from ladybird beetles (Coccinellidae) introduced for the control of scale insect and mealybug pests (Heimpel & Mills, 2017).

While success rates on islands have been suggested to be greater than for mainland locations (Greathead, 1986; Stiling, 1993), due perhaps to reduced biotic resistance from resident natural enemies, the evidence so far has been inconsistent although rather more compelling for New Zealand pasture pests (Goldson et al., 2020). Similarly, although variation in success rates has been observed among continents, it remains unclear why such patterns should occur.

7.4.3 Criteria for Natural Enemy Selection

Introduction

Importation biological control began as a very pragmatic approach to pest management in the 1880s and the majority of projects were based on importations of multiple control agents to increase the likelihood that at least one effective species would establish and provide control of the pest population. Referred to as the lottery model (Denoth et al., 2002), this early empirical approach to importation made little attempt to identify and select control agents with the greatest potential for success. Nonetheless, the success of iconic projects such as the introduction of the vedalia beetle, *Rodolia cardinalis*, from Australia for control of the cottony cushion scale, *Icerya purchasi*, in citrus groves in California in 1888 did capture the attention of population ecologists who sought to explain the scientific basis for success from ecological theory (McEvoy, 2018). Consequently, criteria for selecting the most effective control agents began to be developed and applied to new importation programmes from the start of the 1970s. A reductionist approach that focused on life-history and behavioural traits of natural enemies was used initially as such traits could be incorporated into simple analytical models of parasitoid–host interactions (Sect. 7.3.7) to explore potential impacts of introduced control agents on equilibrium densities of a pest population (Waage, 1990). However, Gutierrez et al. (1994) questioned the reliance of biological control practice on theory, arguing that the latter had contributed little either to increasing the rate of success or to an understanding of the reasons for failures (see also Waage & Mills, 1992; Barlow, 1999; Heimpel & Mills, 2017; Segoli et al., 2023). Similarly, Waage (1990) argued that a more holistic approach to agent selection is needed to better integrate the specific traits of individual control agents into the population ecology of a pest. Subsequently, the safety of the traditional *ad hoc* approach to importation projects was called into question (Howarth, 1991; Simberloff & Stiling, 1996) and the need to limit the introduction of control agents to those that are sufficiently host specific so as not to put non-target species at risk was recognised (Waage & Mills, 1992; Barratt et al., 1997).

During the exploration phase of a biological control programme, a decision will need to be made as to whether the natural enemies are to be collected from the pest species or from other, taxonomically closely related, species. The theory of new associations (Hokkanen & Pimentel, 1984) states that natural enemy–pest interactions will tend to evolve towards a state of reduced natural enemy effectiveness, and that natural enemies not naturally associated with the pest (i.e., species presumed to be less coevolved with the target pest), either because they do not come from the native area of the pest or because they come from a related pest species, may prove more successful in biological control. Hokkanen and Pimentel (1984) analysed 286 successful introductions of biological control agents (insects and pathogens) against insect pests and weeds, using data from 95 programmes, and concluded that new associations were 75% more successful than old associations. However, the validity of this conclusion was called into question by a more refined analysis of the BIOCAT1992 database (Waage, 1990). The latter showed that the probability of establishment of new-association natural enemies was only half that of old-association natural enemies, and that there was no evidence that the outcome for those that did establish was any more successful. This evidence combined with the added risk of new-association natural enemies, due to a greater host range, has limited more widespread consideration of this approach for the selection of natural enemies in biological control. Nonetheless, there have been some very successful examples of natural enemy introductions using new associations (Heimpel & Mills, 2017). The tarnished plant bug, *Lygus lineolaris*, is a good example of the successful control of a native pest in North America by an exotic new-association parasitoid *Peristenus digoneutis*, with the outcome that nymph densities in alfalfa were reduced by 75% (Day, 2005). Consequently, the potential usefulness of new associations should continue to be considered (Waage & Mills, 1992).

If only a fraction of the natural enemy complex of a pest can be used for importation biological control, it is essential that the most effective and least 'risky' species can be identified and selected from among the candidates available (Waage & Mills, 1992; Mason et al., 2008). In addition, as 74% of the natural enemy species used in importation biological control have either failed to establish in the target region or failed to impact the invasiveness of the target pest (Cock et al., 2016), ecological theory still has the potential to make significant contributions to the selection of control agents for use in future programmes (Wajnberg et al., 2016; McEvoy, 2018; Mills, 2018; Segoli et al., 2023). Below we consider some of the reductionist and holistic traits that should be considered.

Behavioural and Life-history Traits in the Selection of Biological Control Agents

Introduction

We discuss below attributes of natural enemies considered to be among the most desirable for biological control, based on theoretical modelling, practical considerations and past experience. Many of these traits translate to parameters used in analytical parasitoid–host or predator–prey population models (Sect. 7.3.7). We start with reductionist traits associated with the functional response to host density, and then move on to those associated with the numerical response. Finally, we address host or prey specificity, and consideration of climatic matching and ease of rearing. We should not expect to find natural enemies that have all of the desirable attributes and we should anticipate that there will likely be trade-offs among them (Mason et al., 2008).

Traits Associated with the Functional Response

Whether or not hosts can be attacked by a natural enemy often depends on the physical accessibility of the host and the fraction of the host population that is protected from natural enemy attack within a spatial or temporal refuge (Berryman & Hawkins, 2006). Refugia can be thought of in two ways with respect to biological control. On the one hand, a refuge reduces the fraction of the pest population that is attacked, reducing pest suppression. On the other hand, a refuge facilitates stability of the natural enemy–pest interaction over time because it precludes extinction of the entire pest population. While some refuge for the pest may be needed for persistence of the interaction, if the refuge is large, most of the pests can escape from the natural enemy, and consequently the impact of the natural enemy on the pest population will be small, no matter what other attributes it may possess (Hochberg & Holt, 1999; Mills, 2001; Murdoch et al., 2003; Gutierrez et al., 2008).

In this context, Hawkins and Cornell (1994) evaluated the importance of a host refuge from parasitism as a criterion for the selection of more effective parasitoid species for use in biological control programmes. They posed the question of whether a parasitoid that achieves a high rate of parasitism in its native range could be used as a measure of the extent of the host refuge from parasitism and be used to predict the likelihood of success in importation biological control. Using the BIOCAT1992 database, they obtained a positive correlation between maximum level of parasitism in the pest's region of origin, and the degree of success in importation biological control, indicating that maximum parasitism rate can be used as a reverse measure of the fractional size of the host refuge from parasitism. In addition, they found that a cut-off exists at maximum parasitism rates of approximately 35%; below this level an introduced parasitoid very rarely achieves economic success as the outcome of importation biological control (Hochberg & Holt, 1999).

Another important feature of the functional response is the asymptotic limit to the *per capita* capacity of a natural enemy to attack prey at higher prey densities. This *per capita* limit represents the maximum rate of consumption by predators as determined by the effects of satiation, and the maximum rate of host attack as determined by the egg load (lifetime fecundity divided by mean clutch size) or attack capacity (the maximum number of hosts that a parasitoid can attack in its lifetime) of a parasitoid. These rates are sometimes referred to as the 'killing power' of a natural enemy (Mills, 2005a). Stage-specific daily consumption or parasitism rates can be obtained either from field observations for predators (van den Berg et al., 1997; Latham and Mills, 2010) or from laboratory studies for both predators and parasitoids (Ro & Long, 1998; Hallet et al., 2014) and can be used to inform the relative *per capita* capacities of natural enemy species for pest population suppression.

Other components of the functional response that have been considered of potential importance include a high search rate, the shape of the response and environmental conditions. The search rate defines the speed of approach to the asymptotic *per capita* limit and is often influenced by the strength of the response of a natural enemy to infochemical cues associated with the pest or its feeding activity. Despite the intuitive appeal of a high search rate, Kimberling (2004) found no evidence that search rate was associated with success, based on the historical record of introductions to the USA. However, Gutierrez et al. (1993) demonstrated the importance of parasitoid search rate using a simulation model to analyse the factors influencing the successful biological control of the cassava mealybug *Phenacoccus manihoti* in Africa (Sect. 7.3.8). Of the two introduced parasitoids, *Anagyrus lopezi* finds mealybug colonies five time faster than *A. diversicornis*, and its greater search rate proved to be instrumental in the suppression of mealybug population abundance in the model.

Sigmoid functional responses (Sect. 1.14) are potentially stabilising at low pest densities, which is advantageous, because they result in density-dependent parasitism or predation. Using the BIOCAT1992 database, Fernández-Arhex and Corley (2003) tested for, but were unable to detect, a relationship between the form of the functional response (Type II *versus* Type III) and success in importation biological control. Although prey and predator densities are considered the most important factors that affect *per capita* consumption rates by natural enemies (Arditi & Ginzburg, 2012; Garay et al., 2014), environmental conditions including floral resources (Lee & Heimpel, 2008) and climate (Rall et al., 2012) can also play a role. For example, temperature can influence the consumption rate of mosquito larvae by the notonectid predator *Anisops sardea* (Fig. 7.22), particularly at higher prey densities, and thus could also affect comparisons of prey kill rate among natural enemy species. Rochat and Gutierrez (2001) and Gutierrez et al. (2008) have also emphasised the importance of weather-driven physiologically based functional and

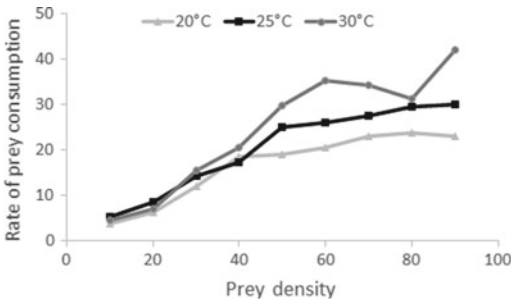


Fig. 7.22 Mean rate of consumption of mosquito larvae (*Anopheles stephensi*) by the predatory hemipteran *Anisops sardea* at increasing temperatures (modified from Mondal et al., 2017, with permission)

numerical responses in models used to explain successes and failures in importation biological control programmes.

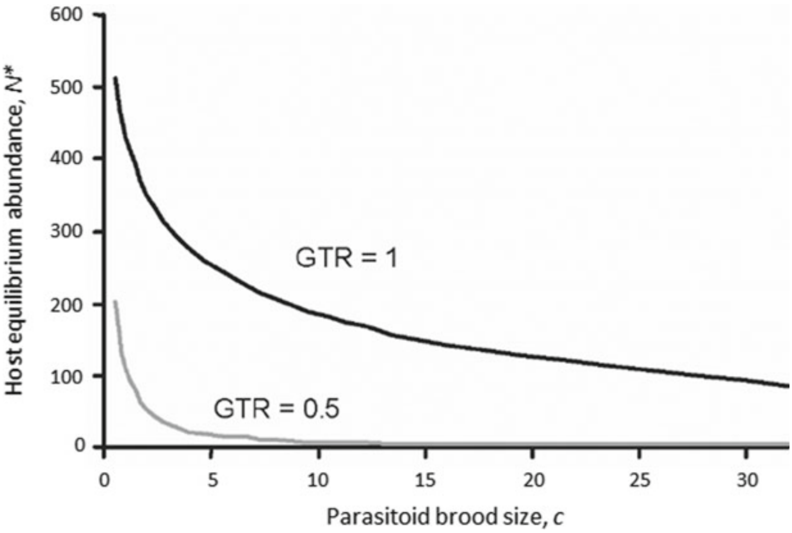
Traits Associated with the Numerical Response

The numerical response of a natural enemy represents the change in predator/parasitoid density as a function of increasing prey/host density and includes two components, a reproductive response (a change in the rate of predator/parasitoid reproduction, development or survival), and an aggregative response (a change in the number of predators/parasitoids moving into a prey patch) (Hassell, 2000a, 2000b). As one aspect of the reproductive numerical response, it has frequently been suggested that high fecundity is a necessary attribute for a natural enemy to be able to respond effectively to changes in the abundance of a pest (Beddington et al., 1978; Waage, 1990), but this has seldom been explored in the context of selection of agents for importation biological control. Lane et al. (1999) showed that in their model (which incorporated parasitoid fecundity limitation, a refuge from parasitism, and a density-dependent host population growth function), a high fecundity should provide a greater degree of host suppression and stable control of a host population over a wider range of parameter space. They also found empirical support for a correlation between high fecundity and success in biological control from the BIOCAT1992 database, which revealed a positive correlation for parasitoids introduced against Lepidoptera, although not for parasitoids introduced against Hemiptera (Homoptera). Mills (2001) noted that parasitoids may either be solitary (one offspring develops from each host) or gregarious (multiple offspring develop from a host) and through modelling, similarly identified parasitoid attack capacity as a major factor in pest suppression, irrespective of whether transient or equilibrium dynamics best represent the real dynamics of parasitoid–pest interactions, and that attack capacity was also positively correlated with the probability of success from the BIOCAT1992 database of importations for Lepidoptera. In a similar vein, modelling studies by Heimpel (2000) and Mills (2001, 2006a) have also shown that increased parasitoid brood size can lead to greater suppression of host densities. Even small increases in parasitoid brood size can lead to dramatic reductions in host abundance, and Mills (2001) again found support from the BIOCAT1992 database that gregarious parasitoids were better represented among successes than failures, particularly for Lepidoptera (Mills, 2006a).

As another aspect of the reproductive numerical response, modelling by Godfray and Hassell (1987) in relation to parasitoids, and Kindlmann and Dixon (1999) in relation to predators, has pointed to the role of natural enemy and pest generation times in determining equilibrium levels of host suppression. Godfray and Hassell's (1987) simulations indicate a slight raising of pest equilibrium density when the generation time ratio (GTR, the ratio of the natural enemy's generation time to that of its host or prey) is greater than one, while Kindlmann and Dixon's (1999) simulations reveal that the suppressive effect of a predator is inversely related to the GTR (see Kindlmann & Dixon, 1999, 2001 for a functional explanation). In addition, Mills (2006a) used a simple host–parasitoid model to show that a GTR of 0.5 can reduce the equilibrium density of a pest substantially, and to a much greater extent than parasitoid brood size (Fig. 7.23). Further examination of the BIOCAT1992 database showed that a GTR < 1 was frequently associated with success for homopteran pests, but not lepidopteran pests, while the reverse was the case for parasitoid gregariousness. Thus, the historical record shows that multiple natural enemy generations per host generation is correlated with the success of importation biological control of Hemiptera (Homoptera), whereas gregarious parasitoid development is correlated with success against Lepidoptera (see Mills, 2006a, for possible explanations).

Similarly, Murdoch et al.'s (1987) stage-structured parasitoid-host model (in which either the adults or the juveniles of the pest can be specified as invulnerable to attack from the parasitoid) incorporates a developmental delay in both the host and the parasitoid. The stability of

Fig. 7.23 The influence of generation time ratio (GTR) in comparison with parasitoid brood size (c) on the equilibrium density of the host population (N*) assuming a broad window of parasitoid attack (after Mills, 2006a)



this model depends on the length of the parasitoid time lag, relative to the duration of the invulnerable stage. The parasitoid's time lag is destabilising: the longer the developmental period of the parasitoid is relative to that of the host, the more difficult it is to obtain stability. A longer parasitoid development time also leads to exponential increases in the pest equilibrium. Therefore, Murdoch (1990) and Murdoch et al. (2003) considered a short parasitoid development time to be a desirable attribute of a parasitoid species for biological control.

As a final component of the reproductive numerical response, Stouthamer (1993) considered the merits of arrhenotoky (unfertilised eggs develop into males) and thelytoky (unfertilised eggs develop into females) in parasitoids on both genetic and ecological aspects of their success in importation biological control. Some of his conclusions were that: (1) arrhenotokous species, or 'strains', will be able to adapt more rapidly to global change. If environmental conditions in the area of introduction are different from those in the native range, arrhenotokous parasitoids may have the advantage; (2) assuming that a thelytokous strain and an arrhenotokous strain produce the same number of progeny, the thelytokous strain will (all else being equal) have a higher rate of population increase, and suppress pest populations to a lower level of abundance; and (3) arrhenotokous species, or strains, must mate to produce female offspring; therefore, in situations where parasitoid densities are very low, mating success may be compromised (an Allee effect, a positive relationship between individual fitness and population size at low densities; Kramer et al., 2018). Thelytokous parasitoids should therefore be better colonisers.

In support of the first of these conclusions, the declining effectiveness of *Microctonus hyperodae*, a parasitoid of Argentine stem weevil, *Listronotus bonariensis*, in New Zealand pastures, provides evidence that thelytoky may limit the capacity of an introduced parasitoid to co-evolve with its host, which appears to have allowed the pest to evolve resistance through enhanced evasive behaviour (Tomasetto et al., 2018). In addition, modelling revealed that when hosts and parasitoids have divergent reproductive strategies that do not generate equal amounts of genetic variation, host resistance to parasitism can readily evolve (Casanovas et al., 2019). Similarly, in support of the third conclusion, a reaction–diffusion model comparing arrhenotokous parasitoids with sexually reproducing diploid ones predicted that haplodiploidy permits successful establishment in parasitoid populations that are 30% smaller: diploid populations suffer more from an Allee effect (Hopper & Roush, 1993).

Mills (2000) outlined a post-introduction protocol for assessing the influence of mating on parasitoid establishment (see also Hopper, 1996). It includes releasing cohorts of increasing size (released as mature pupae) in spatially replicated locations, then dissecting the resulting female parasitoids at host patches, to assess whether they have been inseminated or not (Sect. 4.4).

The aggregative numerical response is influenced by how natural enemy individuals respond to the patchy distribution of hosts in a spatially fragmented environment. The aggregative response provides a linkage between the foraging behaviour of natural enemies and the population dynamics of their hosts (Ives, 1995). It likely depends on dispersal ability, ability to respond to infochemicals associated with their host or plant damage, and a series of decisions that are made as individuals move among patches of hosts. From a theoretical perspective, Mills and Heimpel (2018) discuss how the interference ideal free distribution model (Krivan et al., 2008) provides a simple representation of the optimal distribution of natural enemies among patches based on a balance between the positive effect of host density and the negative effect of interference competition. Although the model assumes that natural enemies have ‘ideal’ knowledge of the host density and quality of each patch and are ‘free’ from any costs associated with travel between patches, predicted optimal distributions of enemies among patches seem robust to violations of these assumptions (Griffen, 2009). The optimal behaviour for natural enemies is to aggregate in patches of higher host density and density-dependent aggregation leads to greater host suppression in spatially explicit models (Murdoch et al., 2003; Bianchi et al., 2010). Mills and Heimpel (2018) discuss the similarities between spatial models of aggregation based on the ideal free distribution (Sutherland, 1983) with those of natural enemy load based on the resource concentration hypothesis (Stephens & Myers, 2012). The latter models suggest that the greatest degree of temporal host suppression may be associated with spatial distributions of natural enemies that provide an exact match to those of their hosts (producing a constant natural enemy load among patches) or slight undermatching (producing a slight decline in natural enemy load for patches with higher host densities). Despite the theoretical attention that the aggregative numerical response has received, there is very little empirical information relating to the spatial patterns of attack by natural enemies used in biological control (Mills, 2000). An exception comes from the parasitoids attacking California red scale (*Aonidiella aurantii*), as Murdoch et al. (1996b, 2006) carried out experimental manipulations of both the distribution and the abundance of the scale insect on individual citrus trees. From this study the authors concluded that the spatial heterogeneity in parasitoid attack that characterises this parasitoid-pest system did not account for either local stability or successful reduction in scale abundance. Mills and Heimpel (2018) also suggest how the foraging responses of natural enemies to the spatial distributions of their hosts can be examined experimentally for both past and future importation biological control programmes.

More generally, if a natural enemy has a high ability to disperse (either as an adult or as an immature stage within the host), then it can be expected to spread rapidly from the initial release point. Thus, fewer resources (time, money) may need to be invested in large numbers of point releases over a region to ensure that the natural enemy becomes established over a wide area. Wilson and Hassell (1997) have shown, through modelling, that demographic stochasticity increases the probability of extinction of small local populations and that, because of this, higher dispersal rates are required to ensure persistence of the metapopulation. Another reason for favouring high dispersal capability in importation biological control agents is that it can minimise a time-delay in re-invasion of areas where the enemy has, for reasons of local instability, become extinct; a significant delay can allow the pest population to reach undesirable levels. High rates of parasitoid dispersal have also been shown to be advantageous in the context of biological control where insecticide application also occurs (Keaser et al. 2023). On the other hand, Heimpel and Asplen (2011) point out that high rates of dispersal can make founder populations of natural enemies susceptible to Allee effects and decrease the probability of establishment. Using modelling, Kean and Barlow (2000) show that a high rate of dispersal can be a significant drain on the rate of increase of a local population. Goodsman and Lewis (2016) also derive an expression to estimate the minimum founding population size required to ensure local establishment in spite of dispersal and a strong Allee effect. In contrast, too low a rate of dispersal could lead to very localised establishment and the potential for inbreeding depression (Heimpel & Asplen, 2011). Consequently, Heimpel and Asplen (2011) argue that a Goldilocks hypothesis of an intermediate level of dispersal is optimal as it maximises the probability of establishment and appropriate spread of an introduced control agent. This could explain why Kimberling (2004) found no correlation between dispersal ability and the success of historical introductions in the USA. Heimpel and Asplen (2011) also suggest approaches for screening candidate agents for dispersal traits and for manipulating dispersal rates at the time of field release. In addition, techniques for studying dispersal by natural enemies are discussed in Sect. 6.2.11.

Host Specificity and Hyperparasitism

One explanation for the poor performance, overall, of predators compared with parasitoids in importation biological control is their tendency to be more polyphagous (Kimberling, 2004). Among introductions of coccinellids, success rates have been higher for monophagous species than for polyphagous ones (Dixon, 2000). It is argued that a pest cannot be maintained at low equilibrium populations by a polyphagous predator or parasitoid, as the natural enemy will concentrate on the more abundant alternative host or prey species. However, as Murdoch et al. (1985) point out, a polyphagous natural enemy can survive in the absence of the pest in the event of the latter's local extinction, and it can therefore be ready to attack the pest when it reinvades. For this reason, polyphagy may not be as undesirable an attribute in importation biological control as it is commonly assumed to be, although polyphagous natural enemies pose greater risks to non-target organisms (Kimberling, 2004; Sect. 7.4.4).

In addition to host specificity, foreign exploration studies have generally focused on identifying and excluding hyperparasitoids from consideration as biological control agents. Theoretical models remain equivocal about the role of hyperparasitism in biological control, with both the disruption or the stabilisation of host–primary parasitoid interactions being possible outcomes (Rosenheim, 1998). In addition, experimental evidence for disruptive effects of hyperparasitism on the success of biological control also remains limited (Rosenheim, 1998; Sullivan & Völkl, 1999; Schooler et al., 2011). Nonetheless, the disruptive nature of hyperparasitism remains the prevailing view and, more recently, consideration has been given to exploitation of chemical ecology for the management of hyperparasitoids (Cusumano et al., 2020) and to hyperparasitoids as potential targets for biological control (Tougeron & Tena, 2019).

Climatic Matching

The optimum range of temperatures or humidities for development, reproduction and survival of a candidate biological control agent may be different from that of the pest, and the natural enemy may either fail to establish or prove ineffective owing to the direct or indirect effects of climate in the region of introduction. The conventional wisdom is that a parasitoid species should be collected from a location in the region of origin where climatic conditions provide an optimal match to those that prevail in the region of introduction (DeBach & Rosen, 1991; Sect. 2.9.3). This view is supported by the database analysis of Stiling (1993) which showed that the climatological origin of parasitoids has a large influence on establishment rate. However, the climatic adaptation criterion should not be rigidly applied: *Anagyrus lopezi*, which successfully controlled cassava mealybug in West Africa, originated from Paraguay, where the climate is very different (Gutierrez et al., 1994;

Neuenschwander, 2001). In addition, more recently this same parasitoid has proved to be equally successful in controlling cassava mealybug across the heterogeneous cassava cropping environments of Southeast Asia (Wyckhuys et al., 2018).

Despite this anomaly, it is generally accepted that climate matching is an important consideration in maximising the potential for success of importation biological control (Hoelmer & Kirk, 2005; Robertson et al., 2008; Mills & Kean, 2010). Having determined the distribution of the target invasive pest in its native region and/or the thermal requirements of a candidate agent, climatic niche models such as CLIMEX (Kriticos et al., 2015, 2021) and MaxEnt (Phillips et al., 2006) offer a practical method for evaluating climatic effects at several of the steps in an importation programme. Based on the known distribution of the target invasive pest the climate-matching tools of CLIMEX can be used to identify locations in the region of origin for foreign exploration that are climatically most similar to those in the invaded region. More sophisticated climatic niche models based on the thermal requirements and tolerances of candidate agents can then be used not only for predicting the prospects for establishment in a target region, but also for identifying when and where to release approved biological control agents to coincide with the seasonality of the target pest and potential risks to non-target species. Tanga et al. (2021) provide an example of using climatic niche models, based on MaxEnt, to identify climatically suitable regions for foreign exploration for parasitoids of the mango mealy bug, *Rastrococcus iceryoides*, in India and suitable areas for parasitoid releases in invaded areas of Africa and Asia. Similarly, using CLIMEX, Avila and Charles (2018) provide an example of how to predict the geographic range of the exotic parasitoid *Trissolcus japonicus* in New Zealand, and its potential risk to non-target species.

Mills (2000) recommended investigating the role and importance of climatic matching experimentally, post importation, by either releasing fixed numbers of parasitoids from a single climatically characterised founder population along a climatic gradient in the target region, or using unique genetic markers (Sect. 3.2.2) to identify different geographic strains of a single parasitoid species and to release them in combination at a series of climatically different locations in the target environment. The latter method can allow the success of local establishment to be related to the degree of climatic match between original and target localities for each strain. Fischbein et al. (2019) also used MaxEnt to demonstrate the benefits of climate matching for predicting both success and failure of establishment of parasitoids introduced to South America, Africa and Oceania for biological control of the forest pest *Sirex noctilio*. Climate alone provided accurate predictions for two of its parasitoids, *Ibalia leucospoides* and *Megarhyssa nortoni*, but other factors may also limit the establishment of *Rhyssa persuasoria* in Brazil and Patagonia (Fig. 7.24).

Ease of Handling and Culturing

While not a trait for consideration in the selection of control agents, Greathead (1986) concluded, from an analysis of the BIOCAT database, that the most important factors in the selection of natural enemy species for use in importation biological control programmes have, perhaps, been ease of handling and availability of a technique for culturing the insects. The case of biological control of the mango mealybug, *Rastrococcus invadens*, is an illustration of how ease of rearing can influence selection. Two encyrtid parasitoids, *Gyranusoidea tebygi* and *Anagyrus* sp., were being considered for introduction into West Africa. Despite the latter species being the dominant parasitoid in rearings from field-collected mealybugs in India, the former species was selected as the first candidate for introduction, owing to the ease with which it could be cultured (see Waage & Mills, 1992 for a discussion). A reason given by Waage (1990) for the more extensive use of Ichneumonidae compared with Tachinidae in programmes aimed at

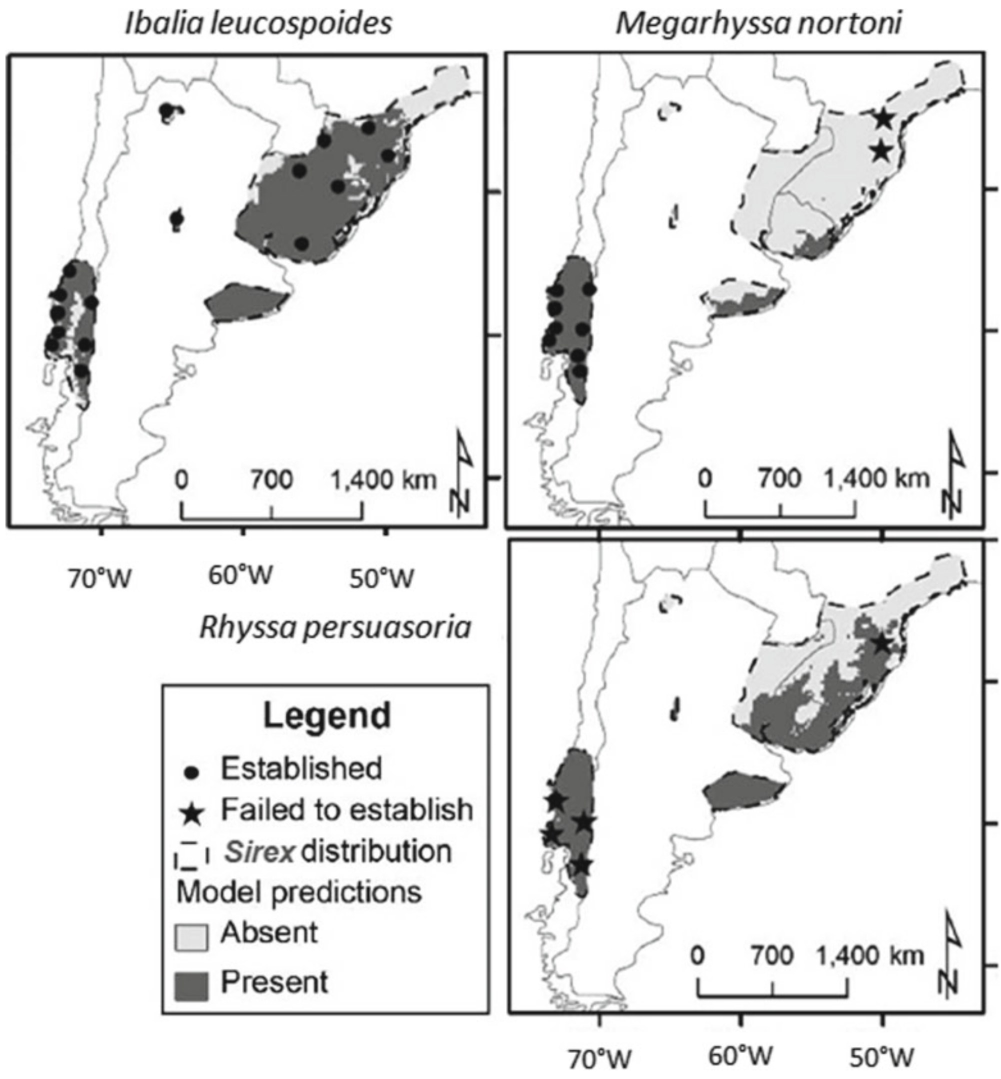


Fig. 7.24 Predicted geographic range in South America of the three parasitoid species introduced to the southern hemisphere for importation biological control of the wood wasp *Sirex noctilio* showing the distribution of the wood wasp (dashed line), model predictions for the presence (dark grey) and absence (light grey) of the parasitoids, and locations where they either established (black circles) or failed to establish (black stars) (modified from Fischbein et al., 2019, with permission)

controlling exotic Lepidoptera is the greater difficulty encountered in culturing the latter parasitoids. It is also noteworthy that the ranking of culturable agents for introduction has usually followed the sequence in which they were established in culture (Waage, 1990). In this context, it is important not to eliminate potentially effective agents from consideration just because they are difficult to handle and culture in captivity.

Population and Community Level Considerations in the Selection of Biological Control Agents

Introduction

In contrast to the focus on life-history traits of natural enemies, the holistic approach to the selection of agents addresses the dynamic nature of natural enemy–host interactions (Waage, 1990) and how demographic and genetic processes can influence the establishment and impact of introduced natural enemies (Mills, 2018). Examples of this approach are presented below.

Collecting Parasitoids from Non-outbreak Areas in the Native Range of the Pest

Selection of agents can begin during the exploration phase of a programme. If an invasive species is known to have outbreaks in its region of origin, then intuitively we would expect that the natural enemy species present during host outbreaks would not necessarily be those best suited to preventing outbreaks and maintaining the pest at low densities in an invaded region (Pschorn-Walcher, 1977; Fuester et al., 1983; Waage, 1990; Waage & Mills, 1992). In contrast, focusing exploration on low-density populations of the invasive pest in its region of origin could provide a more effective approach for selecting the 'best' natural enemy species. Waage (1990) and Waage and Mills (1992) also recommend the use of sentinel host cohorts exposed to natural enemies in the field as a more practical alternative to the challenge of conducting exploration surveys in natural, low-density host populations (see Sects. 6.2.8 and 7.2.3 for methodology).

Selection of Agents in the Context of Density-Dependent Mortality and Vulnerabilities in the Pest Life-cycle

Density-dependent mortality acting later in a pest's life-cycle can influence the contribution of mortality from natural enemies acting earlier on (May & Hassell, 1988). Indeed, if the density dependence is over-compensating, too high a level of parasitism acting early in the life-cycle can lead to increased host population densities later in the life-cycle (van Hamburg & Hassell, 1984; Suh et al., 2000).

In a discussion of augmentative releases of *Trichogramma* against stem-boring Lepidoptera, van Hamburg and Hassell (1984) concluded that the success of a programme will be largely influenced by the level of egg parasitism, the level of the subsequent larval losses, and the degree to which the latter are density dependent. Similar considerations have also been suggested for programmes in which deliberately introduced exotic natural enemies are used for the biological control of invasive pests (Goldson et al., 1994; Abram et al., 2020).

It is also often assumed that parasitism or predation at any stage in the life-cycle of a pest can contribute equally effectively to successful biological control. As indicated above, however, the timing of major density-dependent mortalities in the life-cycle of a pest can compensate for the contribution of parasitism to pest suppression. More generally, it is possible that other specific aspects of the demographic vital rates of a pest could also influence the impact of natural enemies acting at different stages in the life-cycle. One way in which the life-cycles of pests can be screened for vulnerabilities that could maximise the effect of added mortality from introduced natural enemies is through prospective or predictive modelling using stage-structured matrix models (Shea & Kelly, 1998; Mills, 2005b, 2008; Abram et al., 2020). The elements of a matrix model consist of two probabilities for each of the stages in the life-cycle of a pest: one representing the probability of survival and successful transition from one life stage to the next, and the other representing the probability of survival and stasis or remaining within the same life stage, plus the daily *per capita* offspring production during the reproductive phase of the adult stage (Caswell, 2001). The probabilities of transition and stasis are estimated from component vital rates for development and survival at each life stage and the daily offspring production from the realised fecundity, duration of the reproductive phase, and female sex ratio. Elasticity analysis of the resultant model (which estimates the effect of a proportional change in a vital rate on population growth rate) can be used to identify vulnerabilities in the life-cycle. The larger the elasticity, the greater the relative importance of the component vital rate as a contribution to population growth rate. Thus, the life stage or stages with the greatest elasticity for daily survival rate represent vulnerabilities in the life-cycle of the pest where the addition of mortality from an introduced natural enemy would have maximum impact in suppressing pest population growth.

As one of the criteria for the selection of parasitoid species for introduction from Kazakhstan to California, USA, Mills (2005b) used a simple stage-structured matrix model to assess the relative importance of adding parasitism to each of the different stages in the life-cycle of the codling moth, *Cydia pomonella*, as a pest of pome fruit and walnuts. The elasticity analysis of the model identified the cocoon stage as the most vulnerable stage in the life-cycle of this pest and *Mastrus ridens*, a specialist cocoon parasitoid, became the main focus of the biological control programme for codling moth in the western region of the USA where it has become established with parasitism rates of overwintering cocoons reaching 70% in some unsprayed orchards. Other examples of prospective analyses of life-cycle vulnerability for invasive insect pests include light brown apple moth, *Epiphyas postvittana*, and generic stink bugs (Mills, 2008; Abram et al., 2020).

Complementarity and Antagonism in the Reconstruction of Natural Enemy Communities for Invasive Pests

The outcome of interactions among species in a natural enemy community have the potential to be either null, additive, antagonistic or synergistic in their effect on the strength of pest suppression (Letourneau et al., 2009; Hajek and van Nouhuys (2016). In addition, numerous studies have shown that additive or synergistic interactions can be very beneficial in the context of conservation biological control and that complementarity can arise through a number of different mechanisms (Snyder, 2019). In contrast, in the context of importation biological control, there has been far less attention paid to complementarity in the reconstruction of natural enemy communities of invasive pests and rather more to the avoidance of antagonism (Batchelor et al., 2006; Mills, 2006b; Heimpel & Mills, 2017).

There has been an ongoing debate about the benefits of single *versus* multiple introductions and the consequences of interspecific competition among natural enemies in importation biological control (Mills, 2006b). Such competition can extend beyond insect parasitoids to include microbial pathogens with outcomes that can vary from facilitation to competitive exclusion. For example, Hajek and van Nouhuys (2016) found that among the natural enemies introduced for control of gypsy moth in the USA, facilitation can occur between the baculovirus LdMNPV and the larval parasitoid *Cotesia melanoscela*, whereas the fungal pathogen *Entomophaga maimaiga* outcompetes each of the four main larval parasitoids. From a (simple) theoretical perspective, insect parasitoids that interact through exploitative competition cannot coexist and a superior species that is able to drive resource densities to the lowest level will successfully exclude or displace others (Murdoch et al., 2003). As pointed out by Kidd and Amarasekare (2012), however, equilibrium dynamics may never be achieved under field conditions and under shorter-term transient dynamics a superior competitor may not always result in the greatest level of pest suppression. In addition, coexistence can be mediated by several factors that include enemy density dependence and either spatial or temporal niche partitioning among enemies. For example, the breaking of a host refuge from parasitism through the introduction of a second parasitoid species that has low niche overlap with the first is a compelling reason to consider multiple introductions, as theoretical models predict that it can lead to substantial reductions in pest densities (Pedersen & Mills, 2004). The historical record of biological control includes several examples of more effective control of arthropod pests from multiple natural enemies (Stiling & Cornelissen, 2005). In addition, although competitive displacement by a superior competitor has been documented for several importation biological control programmes, it has always led to greater pest suppression (Mills, 2006b). Consequently, the outcome of multiple introductions in biological control is generally considered to be either inconsequential or beneficial, particularly if there is evidence for competitive displacement

(Murdoch et al., 1996a) or niche partitioning among enemy species (Rochat & Gutierrez, 2001; Pekas et al., 2016; Duan et al., 2021).

The main concern with regard to multiple introductions is whether antagonistic interactions between natural enemy species, such as intraguild predation and facultative parasitism, could decrease the efficiency of importation biological control. As discussed earlier in the context of hyperparasitism, however, neither theoretical models nor experimental evidence provide a consistent view of the potential for a disruptive effect of these interactions on the success of biological control (Janssen et al., 2006; Rosenheim & Harmon, 2006; Evans, 2016). A range of different factors can influence the impact of both intraguild predation and facultative parasitism on the outcome of biological control. For example, host preference in a facultative parasitoid for a primary parasitoid over its insect host could tip the balance from a positive or neutral effect to a negative effect on the outcome (Moore & Kfir, 1995). In contrast, Finke and Denno (2002) showed how the structural characteristics of an herbivore's habitat can mediate the effects, upon planthoppers, of intraguild predation by wolf spiders upon mirid bugs. In contrast to structurally simple laboratory 'habitats', more complex habitats increased the combined effectiveness of the predators in suppressing planthopper populations. Finke and Denno's (2002) findings suggest that for importation biological control the dynamic significance of intraguild predation will vary according to both the type of agroecosystem involved and/or the type of habitat management practised.

A combination of facultative hyperparasitism and intraguild predation led Batchelor et al. (2006) to recommend against introduction of the parasitoid *Cephalonomia hyalinipennis* for biological control of coffee berry borer, *Hypothenemus hampei*, indiginous to Mexico, to other regions. Subsequent simulation modelling has also confirmed the likely detrimental effects that this candidate agent would have on the outcome of biological control (Rodríguez et al., 2017; Cure et al., 2020). The general perception remains that restraint should be exercised in using either facultative hyperparasitoids or intraguild predators in importation biological control, and laboratory studies can be conducted to screen for antagonistic interactions before control agents are selected for introduction (Batchelor et al., 2005, 2006; Wang et al., 2019).

Selection of Agents in Relation to Host Plant Quality

To protect themselves from insect damage, plants use both direct defence (nutritional quality, deterrence and toxicity) and indirect defence (herbivore-induced plant volatiles to attract natural enemies), and thus plant quality can play an important role in enemy–host interactions (Verkerk et al., 1998; Hunter, 2003; Peterson et al., 2016). Plant quality effects upon host suppression by natural enemies may in some cases be positive (additive, synergistic) or neutral, but in others may be antagonistic. While many plant defence traits have been lost through crop domestication (Chen et al., 2015), whether the bottom-up effects of host-plant resistance are compatible with efficient top-down biological control cannot be assumed and needs to be taken into consideration in the selection of candidate control agents for importation biological control.

Consequently, there is a strong case for employing multitrophic models in biological control (Gutierrez et al., 1994; Mills & Gutierrez, 1999), given the potential for significant bottom-up effects. For example, using linear multiple regression and marginal analysis of the data from a simulation model for the successful control of the spotted alfalfa aphid *Therioaphis maculata* in California, USA, Gutierrez and Ponti (2013) were able to estimate the relative contributions of the different factors included in the model to suppression of aphid densities. The greatest contributions came from the development of new alfalfa varieties that had greater host-plant resistance to the aphid and the action of native coccinellids. In this example, the host-plant resistance also proved to be compatible with parasitism by the three introduced parasitoids (dominated by *Trioxys complanatus*) that combined to achieve successful control of the invasive aphid.

More generally, the compatibility of host-plant resistance and importation biological control will depend on the strength of the negative effects of direct defences on the pests themselves and their suitability as hosts or prey for natural enemies, and the extent to which changes in indirect defences disrupt the signalling pathways used by natural enemies. Plant quality seems likely to affect potential control agents in different ways and thus greater emphasis on testing for the compatibility of modern crop varieties with available candidate agents should be included among the criteria considered in the selection of natural enemy species for use in importation biological control.

Selecting for Seasonal Synchrony with the Target Pest

Populations of hosts and parasitoids with discrete generations frequently show imperfect phenological synchrony, with the result that some host individuals experience a temporal refuge from parasitism. Compared with perfect synchrony, imperfect synchrony will result in reduced host suppression, although models developed by Münster-Swendsen and Nachman (1978) and Godfray et al. (1994) show that it can stabilise the parasitoid–host population interaction. For example, there is considerable variation in the synchrony of the specialist parasitoid *Cotesia melitaearum* with its host butterfly *Melitaea cinxia* that is driven by cool early spring temperatures (van Nouhuys & Lei, 2004). By basking in the sun, the dark-coloured host larvae can complete their development and escape from parasitism before adult parasitoids emerge from overwintering cocoons. The asynchrony reduces both parasitoid population size and the rate of colonisation of host patches which is likely to be important for the metapopulation dynamics of the host butterfly.

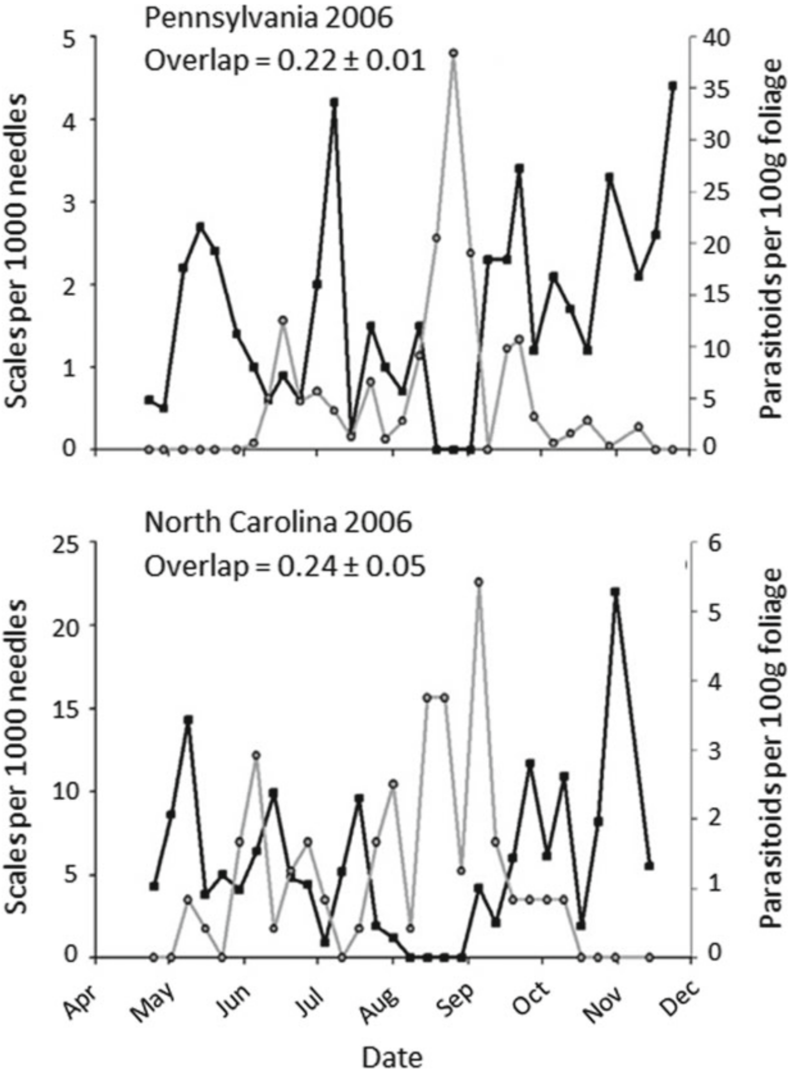
Temporal synchrony can also be lost in novel environments, as demonstrated by the case of synchronisation of the parasitoid *Encarsia citrina* with the susceptible stage of its host the elongate hemlock scale, *Fiorinia externa*. In its native Japan, the scale has two generations a year and parasitism can reach 90% (McClure, 1986). In the United States, however, the number of scale generations varies from one in the north to two in the south, and the introduced parasitoid is poorly synchronised throughout the invaded range (Abell & Van Driesche, 2012). This failure of the programme, due to poor seasonal synchrony (Fig. 7.25), could be due to differences in host-plant quality between tree species in the region of origin and invaded region, again emphasising the value of a more holistic view to the selection of candidate control agents.

Finally, it has frequently been suggested that climate change and extreme climatic events could also lead to imperfect synchrony in enemy–host interactions (Stireman et al., 2005; Hance et al., 2007; Thomson et al., 2010), and Wetherington et al. (2017) demonstrated that even relatively small changes in the severity of extreme climate events can affect emergence times and reduce both parasitism and survival by an egg parasitoid *Oobius agrili* of the emerald ash borer, *Agrilus planipennis*.

Intrinsic Rate of Natural Increase (r_m) and Pest Kill Rate (k_m)

Janssen and Sabelis(1992) were among the first to explore the use of the intrinsic rate of population increase (r_m) as a selection criterion for biological control agents, as it integrates a suite of individual natural enemy traits into a single population-level metric for population growth. In reviewing the biological control programme against cassava mealybug, Neuenschwander (2001), however, concluded that r_m was, in retrospect, a poor predictor of agent effectiveness in that particular case. Modelling by Hochberg and Holt (1999) has shown that r_m (which they estimated from a partial derivative of their host refuge model) is enhanced by a greater searching efficiency, a greater attack capacity (maximum number of hosts attacked over the parasitoid's lifetime) and a greater mean number of parasitoids emerging from a parasitised host. It was also shown that in highly productive environments (high host carrying capacity), it is parasitoid attack capacity alone that determines the conversion of hosts to parasitoids and therefore the transient impact of parasitism on the host

Fig. 7.25 Seasonal abundance of adults of the parasitoid *Encarsia citrina* and of the susceptible stage (second instar) of its host *Fiorinia externa* in Pennsylvania and North Carolina, USA in 2006 showing the limited degree of overlap in seasonal synchrony (modified from Abell & Van Driesche, 2012, with permission)



population. If the brood sex ratio is biased towards females (as is often the case for gregarious parasitoids, Sects. 1.11 and 5.4), then a gregarious species will have a higher population growth rate than a solitary species with the same fecundity (Mills, 2001).

Although r_m can be used as a comparative measure of the potential impact of many solitary parasitoids, as pointed out by van Lenteren et al. (2019), it is less applicable to predators or to parasitoids that are either gregarious or cause additional host mortality through destructive host feeding or stinging. For these latter categories of biological control agents, r_m provides only a measure of the capacity for population growth and not their capacity to kill pests. Alternatively, the pest kill rate (k_m) can be estimated by replacing age-specific fecundity with an age-specific kill rate to provide a better estimate of potential impact for a biological control programme (van Lenteren et al., 2021). A comparison of pest kill rates for six predator and seven parasitoid species as candidate control agents for the South American tomato moth, *Tuta absoluta*, identified the predator *Nesidiocoris tenuis* and the parasitoid *Trichogrammatoidea bactrae* as potentially the most effective species for importation biological control.

One important advantage of pest kill rate is that the estimated impact of parasitism can be extended to include host mortality from destructive host feeding and stinging as well as host mortality from parasitism. In addition, it effectively integrates daily host or prey kill rates with the amount of time that the natural enemy spends in each life stage. Using models and the BIOCAT1992 database, Jervis et al. (1996) questioned whether destructive host feeding is a desirable attribute for a biological control agent. Although modelling suggested no benefit with regard to establishment rate or suppression of host abundance, the historical record revealed that destructive host feeding in parasitoids does lead to a slight improvement in establishment rate and a greater success rate than for non-host feeding parasitoids (Jervis et al., 1996). Thus, as an additional source of mortality, destructive host feeding or stinging does appear to be an important attribute to consider for the selection of biological control agents. While the estimation of pest kill rate captures all of the direct effects of natural enemy impacts on a pest population, it does not include the indirect non-consumptive effects that result from prey responses to the threat of natural enemy presence (Sect. 7.2.5), which can in some cases be as strong as the direct consumptive effects (Buchanan et al., 2017). The strength of indirect effects can differ between natural enemy guilds, and also between predator species, but quantifying these effects on an age-specific, or even stage-specific, basis poses a considerable challenge and has yet to be taken into consideration in the selection of agents for use in importation biological control.

7.4.4 Non-target Effects

Introduction

There has been increasing concern over the risks posed by biological control, especially importation biological control, to natural biodiversity, and since the 1990s numerous studies and reviews of the risks of natural enemy introductions have been conducted (Heimpel & Cock, 2018). Protocols for risk assessment were developed for weed biological control in the 1970s (Wapshere, 1974; see next section below) and have proved to be remarkably successful (Hinz et al., 2014; Paynter et al., 2018). However, no such protocols for arthropod biological control were considered until the 1990s (Van Driesche & Hoddle, 1997), and further developments have continued since that time (Van Driesche & Reardon, 2004; van Lenteren et al., 2006; Heimpel and Mills, 2017; Paynter & Teulon, 2019). The risk from introduced natural enemies can be either direct, due to consumption of non-target species (Lynch et al., 2002), or indirect and mediated by complex interactions within the target community (Messing et al., 2006). Direct risks from introduced natural enemies can readily be assessed through laboratory host-specificity tests of the ability of a candidate control agent to use a non-target host or prey species (including resident natural enemies as well as herbivores). In contrast, indirect risks to food webs and ecosystems from introduced natural enemies are much more difficult to assess even though they are known to be significant in some instances (Heimpel & Cock, 2018).

The evidence for harmful ecological impacts from natural enemy introductions is variable in quality, ranging from anecdotal to relatively quantitative (Lynch et al., 2002). Although there have been some notable examples of negative effects (Van Driesche & Hoddle, 2017) many of them stem from the early period of importation biological control from 1880 to 1960, with direct non-target effects appearing to have stopped after the 1960s (Heimpel & Cock, 2018). There has also been little evidence for host range expansion by natural enemies following introduction (Wright & Bennett, 2018). While a focus on reducing the risks of importation biological control since the 1970s has resulted in a decline in the number of natural enemy introductions worldwide (Cock et al., 2016), it has proved to be beneficial in improving the practice of importation biological control, with particular emphasis on the need for careful monitoring and safety. As regulators in most countries now require risk assessment prior to approval of natural enemy introductions, here we will focus on the approaches and methods developed for assessing host specificity of arthropod biological control agents and for prediction of ecological impacts.

Host-Specificity Testing to Minimise Direct Non-target Effects

The first step is to choose which non-target species to test. The centrifugal phylogenetic testing method developed by Wapshere (1974) for natural enemies of weeds exposes a candidate biological control agent to a sequence of test plants from those that are most closely related to the target weed to those belonging to successively most distant taxa. This testing method has also been adopted for natural enemies of arthropod pests (Kuhlmann et al., 2006). Important differences, however, are that the range of non-target species available for host-specificity testing of entomophagous species can be extensive and their phylogenetic separation may not be as well understood. In addition, the phylogenetic signal can be weaker for entomophagous insects than for insect herbivores, while host habitat (e.g., leafminers) and other forms of ecological specificity can influence the host range of some species (Messing, 2001). The number of non-target species selected for host-specificity testing of entomophagous insects is fewer than for insect herbivores, can be reduced through initial field surveys to assess host ranges in the region of origin (Kuhlmann & Mason, 2003), but can still often average more than ten (Kuhlmann et al., 2006). The approach is then to expose each non-target species (on its host plant) in turn to a candidate control agent to assess (1) the proportion of hosts or prey attacked, (2) the proportion of hosts parasitised in the case of a parasitoid, and (3) the suitability of the host or prey for supporting successful development and reproduction (van Lenteren et al., 2006). In addition, Paynter and Teulon (2019) suggest that the relative performance of candidate control agents on non-target and target hosts in laboratory host-specificity tests should be considered for potential prediction of the risk of non-target effects in the field.

A number of difficulties can arise in the interpretation of host-specificity tests as no-choice laboratory tests, which are used to assess the physiological host range (the set of non-target species that support development), often overestimate the potential risks of candidate control agents (van Lenteren et al., 2006). Consequently, large arena choice tests and olfactometer studies are also recommended to assess better the ecological host range (the set of non-target species used in the field) of a candidate control agent (Wyckhuys & Heimpel, 2007; Murray et al., 2010). When using parasitoids in choice tests, however, kairomones from the target pest can often result in the non-target species being attacked even though it would not be used as a host under field conditions (van Lenteren et al., 2006).

Other methodological considerations for host-specificity tests include the physiological state of the candidate control agent and what statistical tests to use for analysing host-specificity data. With regard to physiological state, individuals that are hungry and in the case of parasitoids, those that are time limited with high egg loads, are more likely to accept low-quality hosts or prey (Withers & Browne, 2004). Although some studies have not found a significant influence of physiological state on host acceptance in host-specificity tests (e.g., Jenner et al., 2014), it is still recommended that physiological state be taken into consideration. Appropriate choices of statistical analyses for host-specificity tests are also essential for correct interpretation of the data and this has been reviewed by Withers et al. (2013).

Assessing Indirect Non-target Effects

Indirect effects of biological control agents on food webs (Sect. 6.3.12) and ecosystems have rarely been assessed due to the difficulty of quantifying complex interactions. Messing et al. (2006) provide a framework of possible indirect interactions and discuss the observational and experimental approaches that might help to define the role of a candidate biological control agent within a local ecological community. Memmott (2000) points out that quantitative food webs could be a useful tool for a retrospective analysis of indirect non-target effects in biological control and discusses approaches and methods. Although such food webs are purely observational studies, they can be used to quantify the extent of interaction between a biological control agent and the members of a native community and to generate hypotheses about potential impacts of the agent on the population dynamics of non-target members of the community. It has also been suggested that quantitative food webs could be used as a prospective tool prior to introduction of a biological control agent (López-Núñez et al., 2017). Such an approach is currently difficult to implement but is likely to become more practical in the future as next-generation sequencing technologies (Sect. 3.2.2) facilitate the study of both diet breadth and food web interactions under field conditions (Gonzalez-Chang et al., 2016). A less expensive option is to use a qualitative food web to identify direct interactions with other species in the food web and to predict which non-target species may be at indirect risk (Todd et al., 2021). The latter approach has been used to explore potential indirect non-target effects for two parasitoids in New Zealand; *Cotesia urabae* released for control of the eucalyptus defoliator *Uruba lugens*, and *Trissolcus japonicus* approved, but not yet released, for control of the brown marmorated stink bug, *Halyomorpha halys* (Todd et al., 2021).

7.4.5 Natural Enemy Release and Evaluation

Once approved for field release, a selected biological control agent must be reared, transported to the field and openly released. From studies on invasion biology, it is generally agreed that the probability of establishment increases with propagule pressure, defined as the size and number of introductions made (Simberloff, 2009). Exactly how many individuals to release at each site and how many sites are needed, however, remain open questions. In an analysis of the historical record of biological control, Hopper and Roush (1993) found that establishment from single releases has been more successful when more than 100 individual parasitoids belonging to species of Ichneumonoidea were released or more than 1,000 individuals belonging to the Chalcidoidea or the Tachinidae. Models developed to address the trade-off between conducting more small releases *versus* fewer large releases have been inconclusive, leading to a recommendation that a range of release rates be used for initial releases and that information gained from these be used to optimise later releases (Shea et al., 2002). In addition, Fauvergue et al. (2012) discuss the demographic and genetic processes that influence small founder populations and opportunities for improving the practice of importation biological control.

Once a biological control agent has been released and established, the success of the importation programme should be assessed, but unfortunately this is often neglected due either to lack of financial resources or personnel (Heimpel & Mills, 2017; Segoli et al., 2023. Monitoring the abundance and spread of introduced biological control agents can be carried out using a variety of techniques that are detailed in Sect. 7.2. One recent study compared three different sampling methods (sentinel logs, debarked logs and pan traps) to monitor the establishment and spread of two larval parasitoid species released for control of the emerald ash borer, *Agrilus planipennis* (Rutledge et al., 2021). All three methods detected both species; the use of sentinel logs was the most efficient method for detecting *Tetrastichus planipennisi*, whereas debarking the lower 2 m of ash trees was a more efficient method for detecting *Spathius galinae,* and setting out yellow pan traps was the least efficient method for both species.

In addition to monitoring establishment and spread, the goal of importation biological control is to assess the ecological success of an introduced biological control agent in suppressing pest densities and the economic value of the programme. A change in pest density can be documented through 'before and after sampling', but confirmation of the contribution of the biological control agent to pest suppression requires the use of life-table analysis (Bellows & Van

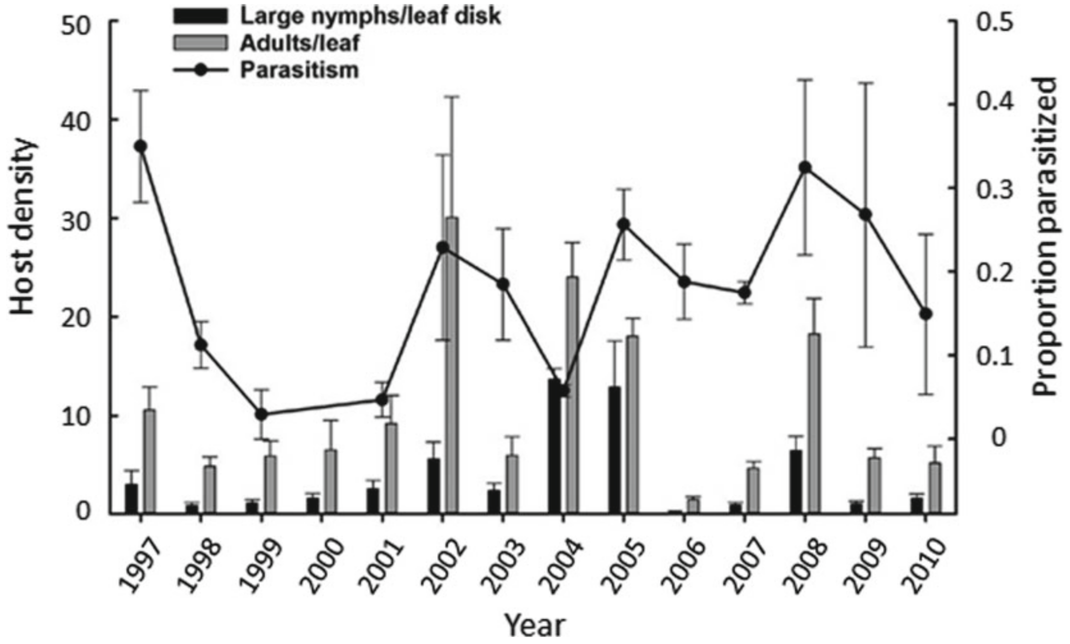


Fig. 7.26 These field data show the absence of a relationship between seasonal mean densities of *Bemisia tabaci* nymphs (black bars) and adults (grey bars) and the marginal rates of parasitism (black line) by the introduced parasitoids *Encarsia sophia* and *Eretmocerus* sp. in Arizona cotton fields. Error bars are ± 1 SE (modified from Naranjo, 2018)

Driesche, 1999; Duan et al., 2014; Sect. 7.3.4), exclusion techniques (Luck et al., 1999; Sect. 7.2.2) or the use of population models (Gutierrez et al., 1994, 2008; Murdoch et al., 2006; Sect. 7.3.7). For example, in a retrospective assessment of the importation biological control programme for *Bemisia tabaci*, Naranjo (2018) used a combination of matrix models, life tables and life-table response experiments to quantify the cause of the decline in abundance and status of this pest in Arizona cotton. This approach revealed that the use of selective insecticides promoted greater populations of native generalist predators in cotton with an associated increase in the mortality of the immature stages of *B. tabaci*. In contrast, there was no improvement in biological control from the establishment of two introduced parasitoids, *Encarsia sophia* and *Eretmocerus* sp. from Ethiopia, with no relationship between host density and marginal parasitism rate (Fig. 7.26). The two parasitoids contributed an average level of 20% parasitism, which is below the threshold found necessary for success by Hawkins and Cornell (1994). The economic value of ecological successes in importation biological control has only rarely been estimated, but Naranjo et al. (2015) summarise the information available and provide a guide to methods and analytical approaches for economic valuation of biological control outcomes for arthropod pests.

7.5 Conclusion

In this chapter we have discussed the established methods as well as recent advances made in quantifying predation and parasitism, evaluating the role played by natural enemies in the dynamics of host populations, and selecting the most appropriate control agents for use in importation biological control. Some of the most significant advances have focused on natural enemy impact assessment such as: (1) introduction of next-generation sequencing as a methodology for detection of predation and parasitism; (2) increased recognition of non-consumptive as well as consumptive effects of predators and parasitoids; (3) landscape scale assessment of the effectiveness of biological control; (4) development of semi-discrete hybrid models to improve our understanding of the dynamics of host–parasitoid interactions; (5) application of more sophisticated statistical models to analyse time-series data collected from the field; and (6) use of improved methods to predict the success and safety of introduced biological control agents. This focus on natural enemy impact assessment stems from a desire to develop a more robust ecological framework for pest management and to increase the level of confidence among managers in the reliability of biological control. Although important advances have been made, for biological control services of predators and parasitoids to be more consistently included in pest management decision-making, there remains a need for simple metrics that are easily measured in the field and sufficiently robust to accurately predict the contributions of natural enemies to pest suppression through a field season. This ongoing challenge still needs to be met to raise the level of recognition of the significant role that predators and parasitoids play in both natural and managed ecosystems.

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