Review

Evaluation of discrete host–parasitoid models for diamondback moth and *Diadegma semiclausum* field time population density series

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ABSTRACT

The performance of discrete mathematical models to describe the population dynamics of diamondback moth (DBM) (*Plutella xylostella* L.) and its parasitoid *Diadegma semiclausum* was investigated. The parameter values for several well-known models (Nicholson–Bailey, Hassell and Varley, Beddington, Free and Lawton, May, Holling type 2, 3 and Getz and Mills functional responses) were estimated. The models were tested on 20 consecutive sets of time series data collected at 14 days interval for pest and parasitoid populations obtained from a highland cabbage growing area in eastern Kenya. Model parameters were estimated from minimized squared difference between the numerical solution of the model equations and the empirical data using Powell's method. Maximum calculated DBM growth rates varied between 0.02 and 0.07. The carrying capacity determined at 16.5 DBM/plant by the Beddington et al. model was within the range of field data. However, all the estimated parameter values relating to the parasitoid, including the instantaneous searching rate (0.07–0.28), per capita searching efficiency (0.20–0.27), search time (5.20–5.33), handling time (0.77–0.90), and parasitism aggregation index (0.33), were well outside the range encountered empirically. All models evaluated for DBM under Durbin–Watson criteria, except the May model, were not autocorrelated with respect to residuals. In contrast, the criteria applied to the parasitoid residuals showed strong autocorrelations. Thus, these models failed to estimate parasitoid dynamics. We conclude that the interactions of the DBM with its parasitoid cannot be explained by any of the models tested. Two factors may be associated with this failure. First, the parasitoid in this integrated biological control system may not be playing a major role in regulating DBM population. Second, and perhaps more likely, poor correlations reflect gross inadequacies in the theoretical assumptions that underlie the existing models.

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1. Introduction

Mathematical models play a central role in elucidating host–parasitoid system interactions. They help to shed some light on mechanisms that underlie these interactions, which may not be directly observable in the field (Gertsev and Gertseva, 2004). Difference equations are widely used for the study of dynamics between insect populations in temperate regions because of the discrete nature of their generations (Royama, 1971; Hassell and May, 1973; Hassell et al., 1976; May et al., 1981; Fay and Greeff, 2006). They are less suitable for tropical insects where continuous generations and life cycles of host and parasitoid of different length are to be expected. However, Royama (1971) suggested that discrete models could be applied to populations with overlapping generations provided age structure is accounted for and the period of observation is shorter than a generation.

The diamondback moth is a major pest of cruciferous crops worldwide, and has increasingly developed resistance to all major classes of insecticides (Annamalai et al., 1988). Integrated management systems have been developed with emphasis on the use/release of parasitoids (Annamalai et al., 1988; Talekar and Shelton, 1993; Wakisaka et al., 1991; Haseeb et al., 2001). In this regard, a classical biological control programme was initiated at the International Centre of Insect Physiology and Ecology (ICIPE) in Kenya from April 2001 to July 2005. *D. semiclausum* was introduced and released first in Kenya (Löhr et al., 2007) and later in Tanzania and Uganda (Löhr et al., 2007).

A host–parasitoid system is an ecological interaction between victims (hosts) and exploiters (parasitoids) where the second species consumes biomass from the first (McCallum, 2000). Adult female parasitoids forage actively for hosts and oviposit in or near host individuals. After hatching, the larvae begin feeding on host tissues and complete their development either within or on the host. Parasitoids are abundant in almost all terrestrial ecosystems and have been identified as one of the main causes of mortality of their hosts (Godfray, 1994).

We evaluated the performance of a number of difference equation models to describe the population dynamics of the diamondback moth, *Plutella xylostella* (Lep.: Plutellidae) and its parasitoid *D. semiclausum* (Hellen) (Hym.: Icheumonidae). The main focus of population dynamics studies has traditionally been on local stability analysis, searching the equilibrium points, determining the nature of their stability and spatial synchrony in which model parameters are obtained through trial and error (Hassell and May, 1973; Hassell et al., 1976; May et al., 1981; Meng et al., 2007). In this regard, a good number of host–parasitoid models have been developed, which can be evaluated by comparing their predictive parameters with empirical time series datasets collected from the field. Mathematical models evaluated here possess rich sets of dynamical regimes. They include (i) Nicholson and Bailey (1935), (ii) Hassell and Varley (1969), (iii) Beddington et al. (1975), (iv) May (1978), (v) Holling (1959) type 2, 3 functional responses and (vi) Getz and Mills (1997) functional responses. In order to perform the models evaluation, a loss function made of the difference between model equation predictions and field time population density series was developed. The function was minimized and parameters were estimated. The estimates were finally subjected to the Durbin–Watson statistical test in the aim to evaluate the model ability in capturing field data.

2. Site description and data collection

The data were obtained from the pilot release areas in Werugha Location (03°26′16″S; 38°20′24″E) of Wundanyi Division in Taita Taveta District, Coast Province of Kenya. Werugha is located on an island mountain, Taita Hills, rising from an area of about 700 m elevation to 2200 m. The top of the mountain measures about 10 km × 25 km and stretches roughly in a north/south direction. Crucifer production is concentrated between 1600 and 1800 m elevation and mainly rain fed. Additional irrigation during the dry seasons is common using buckets to draw water from shallow wells. Much of the land is terraced and crucifer production moves up on the terraces during the rainy seasons and down to the valley bottom in dry seasons, thus ensuring year-round production. The major staple crop is maize and several species of crucifers are grown with head cabbage (*Brassica oleracea* var. *capitata*) as the main cash crop. Soils are mostly degraded, low in organic matter and sandy (Momanyi et al., 2006).

The data used were collected by ICIPE'S DBM biological control team as described in detail in Löhr et al. (2007). Fifteen farmer-managed cabbage farms were sampled at 2-week intervals starting from 2 weeks after transplanting until harvest. When one field was harvested, a recently transplanted field in the immediate vicinity was chosen as its replacement. In each field, 10 plants were selected at random and a population census for larvae (1st, 2nd, 3rd, and 4th instars), pupae and adults was undertaken. Third and 4th instar larvae and pupae were transferred to the laboratory and observed for adult moth and parasitoid emergence. The percentage parasitism was estimated for each collection and then multiplied by the total DBM population from each field. This was then divided by number of sampled plants to estimate the number of parasitoids per plant. The total number of DBM adults was divided by number of plants to establish its population density per plant. Likewise, the total number of DBM was divided by number of plants to establish its population density per plant.

3. Models evaluated

Table 1 summarises the models that were evaluated. Difference equations arising from these models were compared with empirical time series dataset collected during 3-year post-release period.

Conforming to the discrete seasonality of most arthropods, the models are phrased as finite recursive equations of the basic form:

$$N_{t+1} = \lambda N_t f(N_t, P_t)$$
$$P_{t+1} = c N_t [1 - f(N_t, P_t)] \tag{1}$$

where N_t, N_{t+1}, P_t, P_{t+1} give the host and the parasitoid population densities in successive generations, respectively; λ is the geometric growth factor for the host ($\lambda = e^r$ where r is the intrinsic rate of increase); and c is the number of parasitoids produced for each host individual attacked. The function f represents host survival with respect to parasitoid and host densities and can be varied to reflect various parasitoid foraging behaviors (May et al., 1981). Two major features of the parasitoid life cycle conform to this model structure. First, it is the adult female parasitoid that searches for hosts; and second, parasitoids normally oviposit in or on or near hosts, making reproduction closely dependent on the number of host parasitized.

4. Assumptions

The following assumptions were made:

(a) In Kenya, there are two seasons with favourable and unfavourable weather conditions each year associated with bimodal rainfall distributions (Sutherst et al., 1999). This leads to the seasonality of some species such as DBM, which