

# Can population modelling predict potential impacts of biocontrol? A case study using *Cleopus japonicus* on *Buddleja davidii*

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## Summary

As weed biological control comes under much closer scrutiny from legislators and risk managers, increasingly we are asked to provide evidence on the potential impacts a biological control agent will exert on the weed we want to control. Invariably this evidence is required well before the potential biocontrol agent can be released from quarantine. When quantitative data cannot be readily accessed from the country of origin, tools such as population modelling become invaluable. From laboratory studies, the biology of *Cleopus japonicus* (Curculionidae) had already been ascertained in relation to temperature and day length. Additional studies were undertaken on the leaf area consumption by larvae and adults. Using these data, we simulated the population dynamics of the weed biocontrol agent as if it was being released in a non-limiting monoculture of its host plant, the weed buddleia (*Buddleja davidii*; Buddlejaceae), in the central North Island of New Zealand. The results are useful for predicting the potential impacts on the weed, the rate of population build-up, and how many generations can be expected per annum in the likely distribution of the agent. The model predicts that only two generations of *Cleopus japonicus* can be expected per year and that overwintering survival is critical to population build-up. Experiments that ascertained the consumption of leaf area by larvae and adults showed that the leaf area index (LAI) for buddleia will be significantly reduced only from mid-summer until mid-winter, leaving the spring flush undamaged. The extent to which population modelling such as this will be utilized and accepted as a predictive tool before the release of weed biological control agents will depend upon the verification of predictions such as these.

**Keywords:** *Cleopus japonicus*, *Buddleja davidii*, functional relationships, leaf consumption, modelling impact on plant, population dynamics.

## Introduction

There are unique challenges faced when undertaking weed management in plantation forests. Managed forests tend to require intensive weed control during the establishment phase. Often in the first few years following harvest, with its attendant disturbance, and during replanting, rapid weed growth is most problematic. At this time, weeds will compete with young plantation trees for nutrients, water and, in the central North

Island forests, especially light (Richardson *et al.* 1996). Biological control provides one good option for sustainable weed suppression.

Numerous examples exist where biological control using insects has resulted in excellent suppression of the target weed. Unfortunately, there are also many examples where introductions have failed to affect the weed status or management requirements of the target plant (Cullen 1990, McFadyen 1998). With increased costs and stricter legislation concerning the introduction of exotic agents, we can no longer afford the luxury of a trial-and-error approach. Kriticos *et al.* (1999) recommend that studies on the population dynamics of the target weed be carried out before the implementation of biological control programs. In this way, critical

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life stages could be targeted for attack by specific biological control agents in order to maximize the likelihood of success. Additionally, population models of the proposed biological control agent, incorporating the effects of feeding damage on the plant, could also be a useful tool to predict the impact they will have on suppression of weed populations. This in turn has the potential to predict the beneficial impact of biological control upon the growth of pine plantations where weed competition is known to reduce growth (Zabkiewicz *et al.* 1998).

In this paper, we examine, before implementation of a biological control program, whether a population dynamics model of a proposed agent (*Cleopus japonicus* Wingelmüller, Curculionidae) could be used to predict its effectiveness against populations of buddleia (*Buddleja davidii*; Buddlejaceae) in New Zealand. There are two stages to the project. The first requires development of a model that describes the development of insect and weed populations and their interactions (i.e. the effect of the insect on weed population development). The second stage is model validation, which can only be accomplished if *C. japonicus* is eventually released in New Zealand.

Previously published data were utilized on the development and survival of different life stages of *C. japonicus* at the range of temperatures representative of New Zealand's central North Island region, where buddleia is prevalent (Zhang *et al.* 1993). We also know that the higher the number of larvae per plant, the more leaf area they consume (Brockerhoff *et al.* 1999). However, in order to model leaf area consumption, we needed to calculate how daily leaf consumption of both larvae and adults was influenced by temperature and larvae or adult age. This paper describes how leaf area consumption was measured and incorporated into a model to predict the impact *C. japonicus* would have on buddleia. Specific details of all the parameters based on that data and used to run a population dynamics model of *C. japonicus* are not included.

## Materials and methods

### Laboratory experiments

Offspring of a New Zealand laboratory colony of *Cleopus japonicus*, imported into Forest Research Invertebrate Quarantine in 1992 from Hunan province in China, were used for all experiments. *C. japonicus* is a multivoltine external leaf-feeding weevil (Zhang *et*

*al.* 1993) with two damaging life stages, the larva and the adult. The adult female also causes minute damage when depositing the eggs singly within the leaf, but this was not taken into account. The amount of leaf area consumed per larva from when it exits the leaf as a neonate to when it ceases feeding at pupation, and the daily rate of leaf area consumed per adult from eclosion and for 30 days of the pre-oviposition period, were gathered at 10°, 15°, 20°, and 25°C in Contherm environmental chambers set with a 14:10 light:dark cycle. Photoperiod is reported to have no significant impact on *C. japonicus* growth and development (Zhang *et al.* 1993).

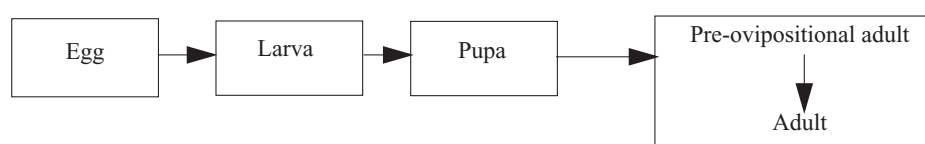
Individual newly emerged larvae or adults were caged on a sprig of *B. davidii* foliage whose base was resting in water. Twice a week the sprig of foliage was replaced and the area of leaf area consumed during the previous few days was calculated by tracing the outline of the feeding track onto square millimetre grid paper under a 20× microscope. At the conclusion of the experiment (30 days), all weevils (replicated 20 times for both adults and larvae) were sexed by dissection.

### Model description

The *Cleopus japonicus* model was implemented using SAS macros (SAS Institute, Raleigh, NC) and used climatic information to predict the survival and development of cohorts on a daily time-step.

The model identifies five discrete life stages of *C. japonicus*: egg, larva, pupa, pre-ovipositional adult and adult (Fig. 1). Movement between life stages is based on cumulative development of physiological age, which is calculated by the average daily temperature cycle. In this way, development is cumulative and all individuals move to the next life stage when their physiological development reaches one. The other function for which there were some data available was the rate of mortality in the adult stage. The one exception to this is post-oviposition adult mortality, which, due to a lack of data, was set as a gradual linear daily rate of adult mortality with a maximum adult lifespan of 500 days.

Three functions in the current model are not based entirely on the data in Zhang *et al.* (1993). The first is low temperature-induced egg mortality. The linear relationship described by 24% survival at 16°C and 91% survival at 20°C produced excessively high egg mortality at temperatures less than 20°C. Therefore the linear relationship was attenuated by also assuming 24% survival at 12°C. Mortality is calculated similarly,



**Figure 1.** Schematic representation of the lifecycle module of *Cleopus japonicus* weevil used in the population dynamics model.

based on equations of increasing rates of mortality at temperatures significantly above or below the optimum. Consequently, we ran the model using one of two constants to describe daily mortality rates (proportion of the population dying each day). These were 0.007 (derived from 75% survival of pre-ovipositing adults over 36 days at 16°C (Zhang *et al.* 1993) and 0.012 (derived from 75% survival of pre-ovipositing adults over 22 days at 20°C (Zhang *et al.* 1993). These mortalities were applied to both pre-ovipositional and ovipositing adults. Thirdly, fecundity was based on an assumed sex ratio of 50:50 and daily rates were obtained from total fecundity of 8–12 pairs monitored for one month, calculated from four different temperatures (T. Withers & D. Jones, unpublished data). These were compared to total lifetime fecundity figures in Zhang *et al.* (1993) to obtain a best approximation for a temperature-driven daily rate of egg laying that ranged from 0.4 eggs per day (at 10°C) to 2.6 eggs per day (at 20°C).

The model is driven by a meteorological data set based on daily minimum and maximum temperatures which is calculated from the daily minimum and the daily maximum using a 12 segment sine curve and then used to drive the growth and mortality processes. In this case, an eight-year sequence of maximum and minimum temperatures was obtained from the national climate database for the Rotorua Airport climate station. Rotorua is considered close to the centre to the major New Zealand buddleia infestation, where a release of *C. japonicus* is most likely to occur in the future.

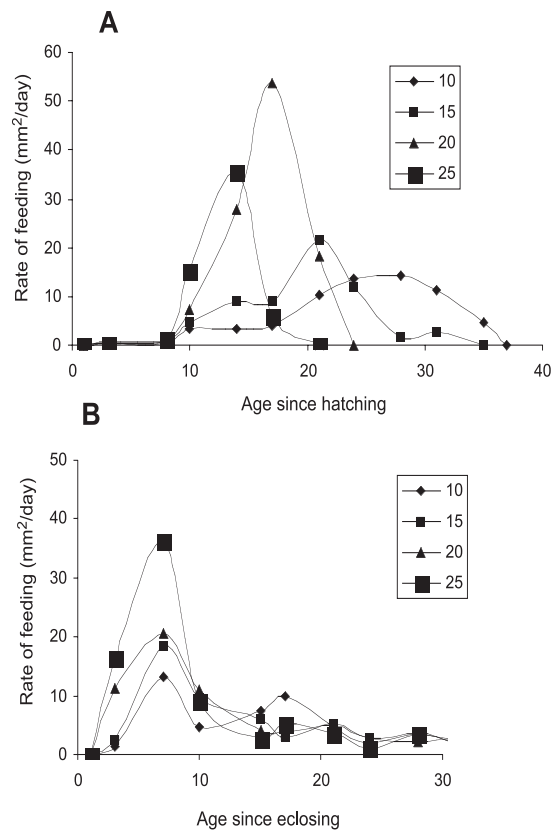
## Results

### Leaf area

Data on the rate of leaf area consumption by *C. japonicus* larvae under four different temperature regimes were analyzed by normalizing them with respect to both daily leaf consumption and age for each temperature. This relationship was found to be independent of temperature and was modelled using a modified version of the equation describing a beta probability density function. Parameter estimates were obtained using nonlinear least squares regression. Leaf area consumption by larvae increases with age, rapidly tailing off to zero when approximately 0.75 of the total larval period is reached (Fig. 2a), while that of newly emerged adults increases rapidly over the first week and then tails off to a steady rate per day (Fig. 2b). The relationship between temperature and maximum daily consumption rate was nonlinear, increasing with increasing temperature up to a maximum at approximately 21°C then decreasing with any further increases in temperature above this point (Fig. 2). There was also no significant difference in mean leaf area consumption according to the sex of the larval *C. japonicus* (two-way ANOVA;  $F = 0.17$ ;  $df = 1$ ;  $P = 0.7$ ), but there was a

highly significant impact of temperature (two-way ANOVA;  $F = 3.9$ ;  $df = 3$ ;  $P < 0.014$ ).

In the simulation model, by combining the models described above, consumption was calculated on a two-hourly step based on temperature and the predicted age and size of each cohort for larvae and adults (only these life stages consume buddleia leaves). This was then summed to give total daily consumption.



**Figure 2.** Daily rate of buddleia leaf consumption by (A) larval and (B) adult *Cleopos japonicus* at a range of temperatures (in °C).

### Model of population dynamics

We initiated the simulations of the population dynamics of *C. japonicus* with 100 eggs “released” per day during January 1990. The simulation was then run for eight years using the actual daily temperatures recorded at Rotorua Airport for those years. Due to a lack of data on the expected rates of mortality of adult *C. japonicus*, we ran the model using estimates of adult daily mortality rates (proportion of the population dying each day) of both 0.007 and 0.012. These mortality rates were independent of temperature.

Significantly different results were obtained for each mortality rate. With the higher adult mortality rate (1.2% mortality per day) the population did not expand, but instead died out within three seasons. Most adults produced from the second, late-summer generation die by the following spring, meaning there are less adults

surviving to contribute to egg-laying. In this case, the model predicts that the agent will fail to establish (Fig. 3).

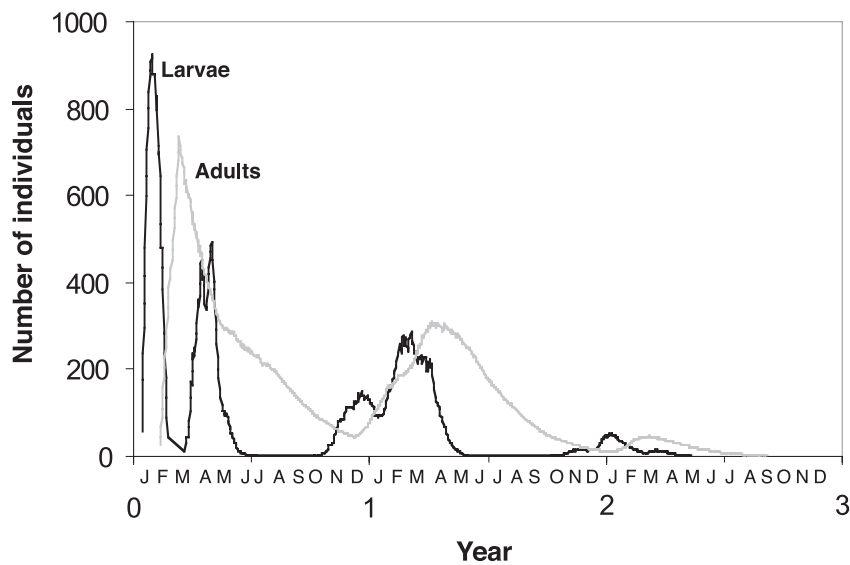
Assuming the lower adult mortality rate of 0.7% mortality per day, the model predicted the population gradually increases every year (Fig. 4). Sufficient adults from the second generation over-winter to initiate significant egg-laying in the spring.

Under the lower adult mortality scenario we were able to calculate the leaf consumption. As expected, leaf consumption is related to larval and adult numbers. Predicted daily leaf area of buddleia eaten by *C. japonicus* larvae and adults during the third year of the simulation (1993) peaked at a mere 0.04 m<sup>2</sup> at the end of February (late summer). Total leaf area consumed by the population over this calendar year was a modest 4.4 m<sup>2</sup>. However, the leaf area eaten over the entire simulation is shown in Figure 5 and, by the eighth season, is

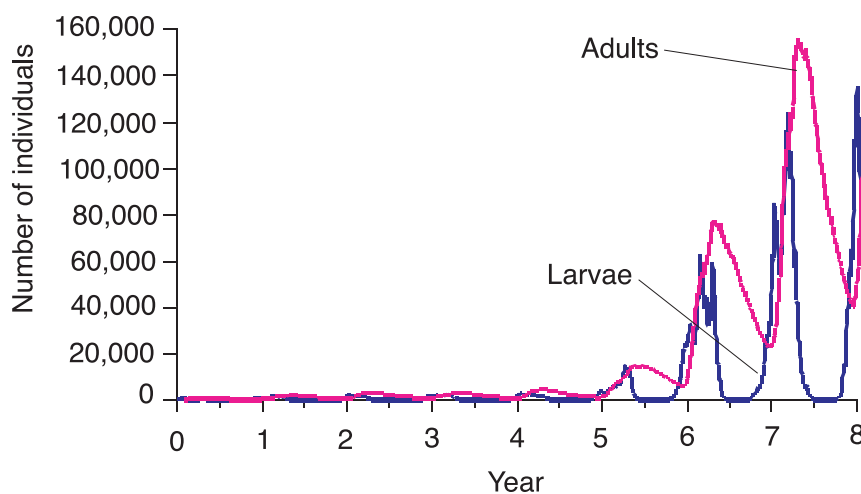
peaking in late summer at 2.3 m<sup>2</sup> of buddleia leaf area eaten per day (Fig. 5). The total leaf area removed by both larvae and adults in the final year was predicted to be 25,000 m<sup>2</sup> (2.5 ha).

## Discussion

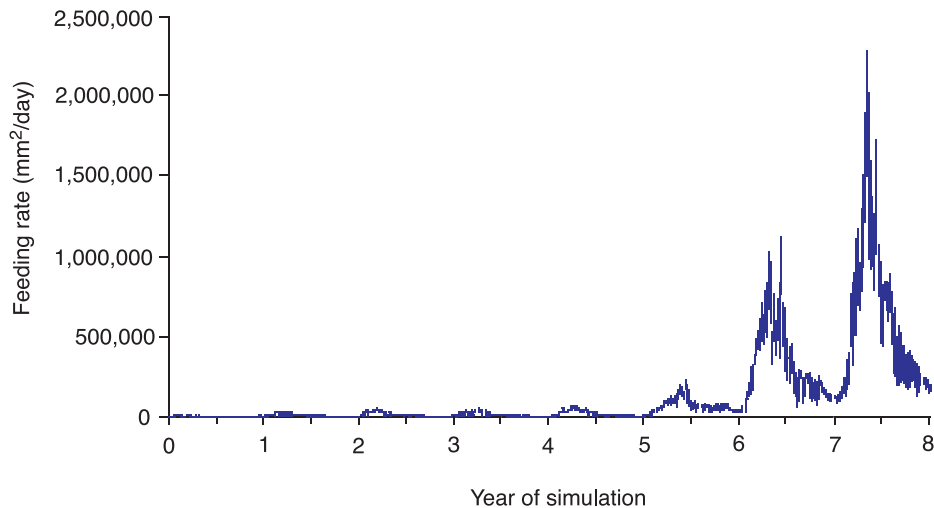
Simulation models of the population dynamics of insects are only as good as the data that have been used to construct them. We were fortunate that the insect under study already had many experiments undertaken on its biology under controlled conditions (Zhang *et al.* 1993; Brockerhoff *et al.* 1999). Therefore, we believe that *C. japonicus*, the potential biocontrol agent for buddleia, has been modelled using more reliable data than have many other insects. Despite this, we must acknowledge that there are at least three functions within the model



**Figure 3.** The predicted *Cleopus japonicus* population dynamics (only larvae and adults are shown) under a 1% daily adult mortality regime.



**Figure 4.** The predicted *Cleopus japonicus* population dynamics (only larvae and adults are shown) under a low 0.7% daily adult mortality regime.



**Figure 5.** The predicted area of *Buddleja davidii* leaf consumed daily by larval and adult *Cleopus japonicus* under a low 0.7% daily adult mortality regime.

that have a considerable degree of uncertainty associated with them. These include egg mortality and adult mortality. When we ran multiple simulations, it was immediately obvious that adult mortality, and the associated measure of maximum longevity of adults, is crucial to the success of this insect as a biocontrol agent in New Zealand. Indeed the data suggest that only two generations will occur per annum, which is at least one less than that predicted by Zhang *et al.* (1993). The discrepancy here may be as simple as the choice of meteorological data file used to run this set of simulations. However, the sensitivity of the predicted outcome to the two assumed mortality rates emphasizes the need to collect more data to improve our confidence around the mortality functions. Additionally, there is considerable room for improvements to our model, e.g. by including a stochastic component.

Adult longevity is particularly crucial, as adults comprise the life stage that leads to spring egg laying as soon as temperatures allow. However, the possibility that the overwintering survival of pupae may have been underestimated should not be ignored. If the main life stage to successfully overwinter without mortality is pupae, then adults arising from these may assume the role of ovipositing the next generation of eggs in spring. Longer-term laboratory experiments at a range of temperature regimes are required to improve our understanding of mortality factors and to improve the model.

The aim of this research is to evaluate whether we can predict the effectiveness of a biological control agent before its release. In this case, we have been able to predict that a population arising from 3100 eggs could lead to the equivalent of 2.5 ha of green buddleia leaf area being removed each season, eight years later. While this is encouraging, we are not yet at a stage where figures such as this can be related to individual *B. davidii* leaf-area indexes. This is because no population density functions have been built into the model. We do not know how many individual weevils remain

feeding on a plant before density dependent factors come into play, prompting adults to move to fresh plants. Adults are likely to move between plants as they are capable fliers, though larvae are not quite as mobile and are likely to only move when all fresh leaf tissue has been removed from the plant on which they emerged. These kinds of data are always going to be difficult or nearly impossible to collect within the confines of quarantine laboratories.

Other important considerations in being able to predict the impact of populations of an agent on populations of a weed are the type of damage, its timing, and the plant's response to that herbivory. For instance, this model predicts that *C. japonicus* leaf feeding will peak in late summer, while being minimal throughout springtime. This has important implications for whether or not this particular agent will be effective on seedlings. To the best of our current knowledge, seedlings germinate throughout the year, so it is possible that those present in springtime will temporarily escape feeding damage (Miller 1984). We will not know whether the peak periods of *C. japonicus* leaf consumption equate to peak periods of plant growth until the insect is established in New Zealand. In the meantime, we have field research under way to model buddleia growth in response to different levels and timings of defoliation.

Ultimately, many of the predictions made in this paper can only be tested when permission is given for the weevil *C. japonicus* to be released from quarantine in New Zealand. At the time of writing, official approval had not yet been sought, but it was likely to be under way by the end of 2003.

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