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Use of life table statistics and degree-day values to predict the invasion success of *Gonatocerus ashmeadi* (Hymenoptera: Mymaridae), an egg parasitoid of *Homalodisca coagulata* (Hemiptera: Cicadellidae), in California

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Abstract

Life table statistics and degree-day requirements for *Gonatocerus ashmeadi* Girault, a parasitoid of the glassy-winged sharpshooter *Homalodisca coagulata* (Say), were used to estimate the number of expected parasitoid generations in California (USA). Between two to 51 and one to 37 generations per year were estimated across different climatic regions in California, using life table and degree-day models, respectively. Temperature-based values for net reproductive rate, R_o, were estimated in California using a laboratory-derived equation and ranged from zero to approximately 48 and analyses indicate that a minimum of eight generations are required each year to sustain a population increase of *G. ashmeadi*. Long-term weather data from 381 weather stations across California were used with an Inverse-Distance Weighting algorithm to map temperature-based estimations for the entire state of California. This Geographic Information Systems model was used to determine number of *G. ashmeadi* generations based on day-degree accumulation, T_c, and R_o. GIS mapping indicated that Californian counties in the north, central west coast, central west and Sierra Nevada regions may be climatic conditions unfavorable for supporting the permanent establishment of invading populations of *G. ashmeadi* should *H. coagulata* successfully establish year-round populations in these areas. Southern counties in California that experience warmer year round temperatures and support year round populations of *H. coagulata*, appear to be conducive to the establishment of permanent populations of *G. ashmeadi*. The mechanisms facilitating *G. ashmeadi* invasion and the implications of these temperature-based estimates for biological control of *H. coagulata* are discussed.

Keywords: Degree-days; Demographics; Biological control; GIS mapping; *Gonatocerus ashmeadi*; *Homalodisca coagulata*; Invasion; Net reproductive rate; Life table statistics

1. Introduction

Homalodisca coagulata (Say), the glassy-winged sharpshooter, a xylophagous insect, is a serious pest that has experienced a high rate of population growth following successful invasion into California USA (ca. 1990), French Polynesia (ca. 1999), Hawaii USA (ca. 2004), and Easter Island Chile (ca. 2005) (Pilkington et al., 2005). In California, invasion success has been facilitated, in part, by a lack of effective natural enemies in the receiving range, no competitors, and climatic conditions favorable for establishment, proliferation, and spread (Hoddle, 2004). Many areas with varying biogeographical attributes in California appear to be vulnerable to invasion by *H. coagulata* (Hoddle, 2004) and this pest has been observed feeding and reproducing in agricultural, urban, and natural areas that range from the relatively cool California coast to much hotter and arid desert interior regions that are irrigated.

There is a large economic cost associated with the invasion of *H. coagulata* and the subsequent vectoring of the

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bacterial pathogen *Xylella fastidiosa* (Pilkington et al., 2005). Invasion by *H. coagulata* has been facilitated, in part, via infested ornamental plants that are translocated to new regions. These plants will most likely enter an urban environment where stochastic events that could cause extinction of incipient populations (e.g., drought or lack of suitable host plants) are either eliminated or severely reduced because of anthropogenic influences such as irrigation and high abundance of other host plants in gardens, and warmer temperatures due to heat retention by buildings, concrete sidewalks, and asphalt road surfaces (Imhoff et al., 2004). One potentially effective mechanism for area-wide suppression of *H. coagulata* involves effective and host-specific natural enemies that have the potential to track *H. coagulata* spread into new agricultural, urban, and natural areas and attacking this pest on a wide variety of host plants thereby preventing development of high population densities.

Gonatocerus ashmeadi Girault, a solitary endoparasitoid of proconiine sharpshooter eggs, is a self-introduced resident of California and Hawaii and is currently the major biological control agent of *H. coagulata* (Bautista et al., 2005; Vickerman et al., 2004). Release of *G. ashmeadi* in French Polynesia for biological control of *H. coagulata* is imminent, and little is known of environmental factors that facilitate successful invasion by this parasitoid either when introduced accidentally or deliberately into new areas. Temperature can have a major influence on the establishment, proliferation, spread, and impact of an organism in a new area (Baker, 2002). To this end, we have studied the reproductive and developmental biology of *G. ashmeadi* in the laboratory at constant temperatures to better determine the effects of temperature on basic biological parameters such as development times, degree-day requirements, longevity, fecundity, and sex ratio (Pilkington and Hoddle, 2006).

Degree-days, the acquisition of thermal units over time above a critical minimum for which development is required, have been used to predict many aspects of insect life history. For example, degree-day calculations allow the estimation of life stage duration for an insect given accumulation of degree-days above the critical minimum temperature threshold. This physiological approach can assist in the calculation of the theoretical number of generations that an insect could be expected to have over a specific time period (Purcell and Welter, 1990). The ability to accumulate sufficient degree-days to complete development and begin reproduction in a new area may indicate how vulnerable that region is to invasion by an exotic organism (Baker, 2002; Sutherst, 2000), and whether incursion will be transient due to unfavorable conditions for prolonged periods (Hatherly et al., 2005; Jarvis and Baker, 2001) or potentially permanent due to year-round conditions favorable for growth and reproduction (Baker, 2002; Sutherst, 2000).

Many factors within a receiving ecosystem will influence invasion success, perhaps making accurate forecasts pertaining to successful incursion impossible (Williamson, 1996). In many instances, a priori determination of ecosystem and regional vulnerability to invasion will be assessed in terms of top down effects mediated primarily by climatic conditions (Sutherst, 2000). Using laboratory estimations of degree-day requirements and net reproductive rate, a calculation that is dependent on fecundity and the number of daughters produced per female across a range of experimental temperatures, can be used to determine what temperatures are suitable for sustained population growth (Pilkington and Hoddle, 2006). An understanding of how temperature ranges affect estimates of population growth of an invading or deliberately introduced biological control agent can assist with the prediction of invasion success by indicating geographical areas where unfavorable temperature regimens may prevent permanent populations establishing (Hoelmer and Kirk, 2005). Similar studies have looked at cold tolerances of biological control agents in the laboratory as an indication of field survivability (Hatherly et al., 2005) and evaluation of climatic conditions in the home range of proposed biological control agents for comparison to climates at introduced areas has provided ecologically based criteria for rationalizing the selection of the most appropriate agents for expensive evaluations in quarantine and potential release (Goolsby et al., 2005).

Using laboratory-derived demographic data and long-term climate records it should be possible to assess the establishment and invasion potential of *G. ashmeadi* as it either follows the continued spread of *H. coagulata* in California, after accidental (e.g., as in Hawaii) or deliberate introduction into other countries (i.e., as planned for French Polynesia) as part of a classical biological control program against this pest. A better understanding of abiotic factors affecting incursion success by *G. ashmeadi* will greatly aid comprehension of potential *H. coagulata* control, parasitoid spread within invaded ranges, and establishment success in new areas where inoculative releases of *G. ashmeadi* against *H. coagulata* are being considered. The objectives of the present study were to use developmental and life table statistics to predict the invasion potential of *G. ashmeadi* throughout California in response to expected range expansion by *H. coagulata*. To assess invasion potential, laboratory-derived demographic data (Pilkington and Hoddle, 2006) were used to develop models predicting the number of *G. ashmeadi* generations and subsequent net reproductive rates for this parasitoid across a range of temperatures. These models were used in a Geographic Information Systems (GIS) analysis to ascertain where *G. ashmeadi* could possibly establish permanent populations in California. An interpolation approach using GIS to estimate invasion likelihood is considered more robust than using data from sparsely distributed weather stations that may be unrepresentative of general prevailing conditions due to topography, proximity to urban areas, or water bodies (Baker, 2002).

2. Materials and methods

2.1. Collection of California weather data for use in GIS analyses

Daily maximum and minimum temperatures were collected from 121 weather stations maintained by the California Irrigation Management Information System (CIMIS, http://wwwcimis.water.ca.gov, last accessed December 30, 2005) and 260 weather stations maintained by the Western Regional Climate Center (WRCC, http://www.wrcc.dri.edu/, last accessed December 30, 2005). Weather stations for which data were downloaded are all located in California. Daily maximum and minimum temperatures were averaged over five to 10 years of complete weather data between January 1, 1995 and December 31, 2004.

2.2. Calculation of accumulated degree-days for GIS mapping

Degree-day accumulation for *G. ashmeadi* was calculated using a Microsoft Excel spreadsheet application (http://biomet.ucdavis.edu, last accessed December 30, 2005) from temperature data downloaded for each of the 381 accessed weather stations. Daily maximum and minimum temperatures, averaged for each weather station, were used to calculate accumulated degree-days for *G. ashmeadi* using the single sine method (UC IPM, 2005). The lower developmental threshold value, calculated from the linear portion of the developmental data (Pilkington and Hoddle, 2006), was 7.16 °C and upper lethal threshold used was 36.7 °C.

2.3. Calculation of the number of G. ashmeadi generations by location for GIS mapping

Two measures of the number of *G. ashmeadi* generations in a given year were calculated for each weather station. The number of generations based on degree-days accumulation above a thermal minimum of 7.16 °C, the point at which the linear portion of the modified Logan model converged on the *x*-axis, was calculated by dividing each weather station's accumulated degree-days by the number of degree-days, 222, that *G. ashmeadi* requires for development (Pilkington and Hoddle, 2006). This returned the number of expected generations at that weather station for the entire year. The second estimation for the yearly number of generations, T_{num}, was calculated by using an adaptation of the fitted model equation for generation time (T_c):

$$T_c = 0.1323\chi^2 - 8.0892\chi + 135.643 \quad \text{(Pilkington and Hoddle, 2006)},$$

where χ is equal to the daily average temperature at each weather station.

The value for T_{num}, the proportion of a generation that was completed at the prevailing average temperature for each weather station, was calculated for each 24 h period by taking the reciprocal of that day's value for generation time calculated from the daily mean temperature at that weather station. If, for example, the daily mean temperature returned a generation time of 10 days in that 24 h period, then it follows that 10%, or 0.1, of a generational cohort will have completed development in that day (i.e., 1 day being 10% of the total required time, ten days, for the individual to develop to an adult). Consequently, as a result of that day's temperature, in that 24 h period the individual will have completed 10% of the time required for development. The sum of the inverse of generational proportions over 365 days is equal to the total generation turnover in that region for the year. This daily calculation of the generational development was only undertaken when the average temperature for that 24 h period was over the minimum developmental threshold of 7.16 °C. Temperatures below 7.16 °C were considered too cold and parasitoid development would temporarily cease thereby returning a value of zero at that weather station at that specific time. The formula for calculating the total number of yearly generations, T_{num}, for *G. ashmeadi* was

$$T_{\text{num}} = \sum_{\chi\ \text{day1...365}} (1 \div (0.1323\chi^2 - 8.0892\chi + 135.643)) \times [\text{derived from Pilkington and Hoddle (2006) Fig. 3}, T_c],$$

where χ is equal to the daily average temperature at each weather station.

2.4. Calculation of net reproductive rates (R_o) for GIS mapping

Estimates of the number of generations for each weather station site in California may not reflect an accurate value for generation turnover as this calculation does not take into account the impact of daughters produced by each reproductively competent adult female on the growth of the parasitoid population. The demographic statistic for net reproductive rate, R_o, estimates the per generation growth rate of the population based on the number of daughters produced and is a robust indication of the capacity for a population to sustain itself or increase in size. When the value for R_o is greater than 1.0 the population increases in size. In contrast, when R_o is less than 1.0 then the population is contracting; R_o of one indicates a stable population (Deevey, 1947). The success that an invading population of *G. ashmeadi* may experience in a given area was estimated by calculating the average R_o, for each weather station from daily maximum and minimum temperature values. The model estimating R_o across a range of temperatures is (Pilkington and Hoddle, 2006):

$$R_o = -0.5534\chi^2 + 27.0954\chi - 277.054,$$

where χ is equal to the daily average temperature at each weather station. Daily estimates for R_o were averaged over the entire year to estimate R_o for *G. ashmeadi* populations in specific locations. It was assumed that any area where the calculation of the yearly value for R_o resulted in a negative value would preclude the possibility of *G. ashmeadi* populations permanently establishing. This result was observed in some areas of California over winter when cold temperatures were predicted to prevent individuals persisting in specific area because of low reproductive output.

2.5. Construction of GIS maps to assess invasion potential of Gonatocerus ashmeadi in California

The number of generations estimated by degree-day accumulation and generational turnover using the R_o model as calculated for *G. ashmeadi* from all weather stations were compiled into a spreadsheet along with the location of the station in decimal degrees of latitude and longitude. The spreadsheet was then imported into ArcGIS 8.3 (ESRI, Redlands, USA). The estimates of number of generations, and of R_o for *G. ashmeadi* for each weather station were converted into an ArcGIS shapefile and latitude–longitude coordinates were used to perform a Teale Albers projection.

The ArcGIS Extension Geostatistical Analyst (ESRI, Redlands, USA) was used to generate interpolated grids for estimated values of number of generations using degree-days, and R_o using an Inverse-Distance Weighting (IDW) algorithm that covered the entire state of California. The input parameters for the IDW analysis were

(1) For each interpolation, 15 weather station sites were used. The default value of 15/10 was used; meaning that in the event that 15 sites are unavailable, the minimum number accepted was 10, a default function that was not required with this dataset as 15 weather stations were always available for analyses.
(2) The spatial shape for including neighboring weather stations was designated to be circular as a directional influence in the data cannot be assumed a priori in these analyses.
(3) The default Power Optimization in the Geostatistical Analyst was chosen. The "Power Value" is the distance weight given to a station used in the interpolation. The "Power Value" is inversely weighted so that the contribution of more distant input stations to the interpolation of the data at any given location is less with increasing distance.

3. Results

3.1. GIS mapping of estimated life table statistics

Maps delineating *H. coagulata* establishment status (total, partial or no establishment) in Californian counties (Fig. 1A), number of generations of *G. ashmeadi* calculated by degree-day accumulation (Fig. 1B), number of generations of *G. ashmeadi* calculated from the modified life table statistic T_{num} (Fig. 1C), and R_o (Fig. 1D) were produced reflecting estimated demographic values across California based on averaged annual temperature data.

Current establishment of *H. coagulata* in California (Fig. 1A) shows that the initial invasion of the pest is in areas where climatic conditions most favor the populations. The estimates for the yearly number of generations based on degree-day calculations (Fig. 1B) indicated that *G. ashmeadi* would be capable of completing between two and 51 generations a year in all areas of California. The possible number of generations produced by *G. ashmeadi* is severely reduced in the northern parts of the state where winter temperatures are significantly lower than in southern counties. These estimates indicate that in winter months, populations of *G. ashmeadi* may continue to reproduce in southern California but at a much lower rate than observed over summer.

The estimated number of generations per year based on the equation for T_{num} indicates that *G. ashmeadi* can be expected to range from almost 1 to over 36 generations (Fig. 1C). This produces a smaller range of generation estimates but is verified by degree-day calculations in that the distribution of generation activity is similar to other estimates. These two estimates of generation numbers, calculated by degree-day accumulation and the equation for T_{num}, do not take into account the number of daughters produced per reproductively active female or the effects of cold temperatures on reproductive output in which populations can maintain themselves thereby preventing a decline that leads to extinction when $R_o < 1.0$.

The value of $R_o = 1$ (i.e., *G. ashmeadi* population growth is static) occurs when the average temperature is approximately 14.6 °C (this can be either for one day, week, or an entire year). By substituting this temperature into the equation for T_{num}, a value of approximately eight generations is returned. This suggests that when eight or more generations of *G. ashmeadi* are produced yearly, the population will maintain itself, less than eight generations and the population will not be able to persist in an area for an entire year, and if more than eight generations result then parasitoid densities should increase. The coastal counties north of Monterrey exhibit temperatures that are on the threshold of this critical generation number and populations in this area of California, according to R_o estimates, may be stable year round at best but not provide an environment suitable for rapid and sustained establishment of *G. ashmeadi*. Extreme cold weather events could easily extirpate tenuous populations.

The values returned for R_o (Fig. 1D) range from 0 to approximately 48 indicating that many of the northern counties of California may be unsuitable for *G. ashmeadi* due to low winter temperatures. These estimates validate the suggestion that generation production in the coast north of Monterrey is insufficient for *G. ashmeadi* population increases with R_o ranging from 0 to 1.25. The basic shape of the darker colors shown in Fig. 1D broadly mirrors the shape seen in both of the generation estimate maps

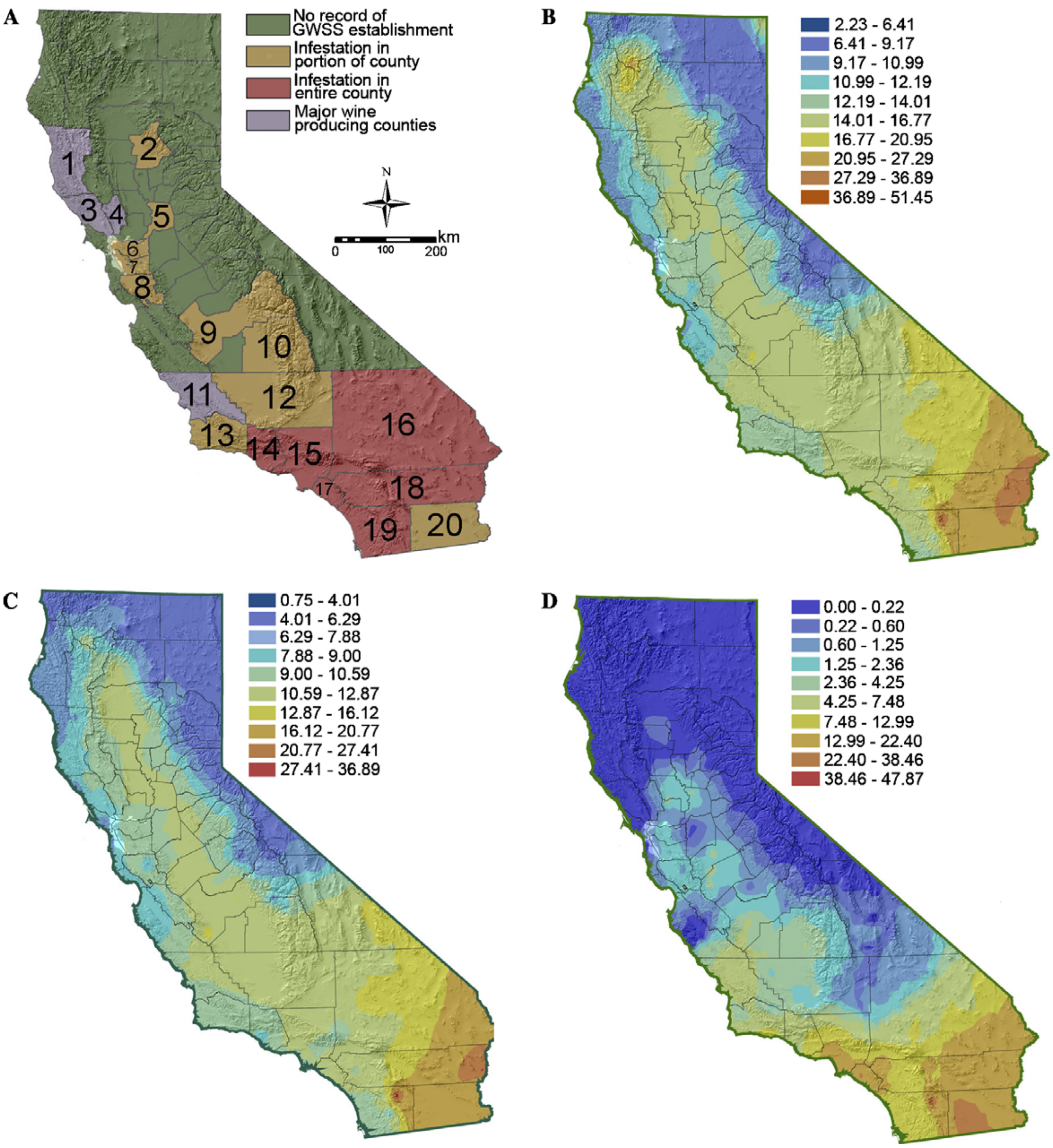

Fig. 1. Geographical information systems mapping of estimated life table statistics for the parasitoid *Gonatocerus ashmeadi* in California, USA; (A) Counties in California and the status of *Homalodisca coagulata* populations in each area 1, Mendocino; 2, Butte; 3, Sonoma; 4, Napa; 5, Sacramento; 6, Contra Costa; 7, Alameda; 8, Santa Clara; 9, Fresno; 10, Tulare; 11, San Luis Obispo; 12, Kern; 13, Santa Barbara; 14, Ventura; 15, Los Angeles; 16, San Bernardino; 17, Orange; 18, Riverside; 19, San Diego; and 20, Imperial. (B) estimated number of generations populations of *G. ashmeadi* may experience in each area calculated by dividing the year's accumulated degree-days by the total degree-days required by *G. ashmeadi* for development; (C) estimated number of generations that hypothetical populations of *G. ashmeadi* may experience in each area calculated by applying historical weather data to the formula for yearly generations, T_{num}, derived from the life table statistic for generation time, T_c. and; (D) estimation of the yearly value for net reproductive rate, R_o, derived by applying historical weather data to the formula for R_o. (B–D) Colored legend indicates the value of the particular statistic of interest for an entire year.

and indicates that the central eastern counties of California may be unsuitable for permanent establishment of *G. ashmeadi* populations.

These estimates of generation turnover and use of the temperature life table statistic R_o indicate that counties in the central coast, north and north east California may be unable to sustain invading populations of *G. ashmeadi* should *H. coagulata* establish in these regions. Based on the results of this work, southern counties such as Riverside, San Diego and Imperial appear to be well suited to supporting *G. ashmeadi* and long-term persistence of robust parasitoid populations in these counties supports this finding.

4. Discussion

The ability of an insect population to invade and establish in an area outside its native range can be significantly affected by weather, especially inclement conditions (Crawley, 1987). The length of time the population is subjected to deleterious temperatures (too low or high) affects the population's ability to recover from adverse climate effects and continue development (Jarvis and Baker, 2001). Modeling of demographic statistics as influenced by temperature from long-term weather data records for the receiving area may provide an indication of the potential success or failure for an invading insect species to establish itself permanently in a new area, and for the population growth of that incipient population.

In this study, the invasion success by *G. ashmeadi* into uncolonized areas of California has been estimated by calculating the number of generations from degree-day accumulation, the use of the derived equation for T_{num}, and the average net reproductive rate (R_{o} as calculated from laboratory studies) for this parasitoid in a given area based on long-term weather data from 381 weather stations across California. Results of these temperature-based calculations provided data that were used to graphically represent the relative potential invasion success of *G. ashmeadi* in California in response to the probable continued spread of its host, *H. coagulata*. Host availability will obviously have a major impact on parasitoid spread in California. The results of these analyses indicate where *G. ashmeadi* could be expected to spread based on climatic conditions only. Consequently, these estimations need to be viewed cautiously and used as a comparative tool between regions rather than a definitive number of expected parasitoid generational turnover in any area. A major short-coming with managing *H. coagulata* in California (and elsewhere) and accurately predicting its invasion potential is the severe paucity of demographic data for this pest and the influence of temperature on its development.

Calculating the number of generations completed in an area is useful for evaluating the efficacy of a biological control agent in one geographic location compared to another (Mills, 2005). The number of degree-days required to move from one generation to the next is a valuable tool in estimating the establishment success of an insect (Tullett et al., 2004) and the calculation of the number of generations from this estimation is an accurate estimate of the potential success of an invading organism in that area (Hart et al., 2002). Developmental data experimentally derived under varying temperatures will allow for diagnostic mapping of areas based on degree-day requirements when estimates of reproductive output across a range of temperatures are not available.

Another method to estimate an invading population's ability to colonize a new area is the use of demographic statistics derived under varying temperatures such as the net reproductive rate, R_{o}. Use of R_{o} to estimate invasion success indicates the effects of temperature on the growth rate of the population as opposed to the number of generations a particular area will support as indicated by degree-day accumulation. While populations may experience generational turnover in a given area, this may not be sufficient to drive significant population growth that could tolerate catastrophic stochastic events, overcome Allee effects, or provide sufficient propagule pressure for sustained incursion (Morse and Hoddle, 2006). For example, differences in the degree-day requirements for a biological control agent of toadflax was considered to be responsible for the success of insects originating from one specific climatic area when compared to the same species sourced from a different climatic area (McClay and Hughes, 1995). Even with generational turnover, the size of the following generation may be inadequate to drive population numbers higher and ultimately cause a reduction in the population density of the target (Lockett and Palmer, 2003).

Results presented here using R_{o} estimates indicate that counties in southern California (i.e., all those to the south of Kern County) are, host availability notwithstanding, favorable for *G. ashmeadi* and this correlates well with the current known distribution of *G. ashmeadi* in California. *Gonatocerus ashmeadi* has been recovered from the counties of Riverside, Ventura, Orange and Kern in California (de León and Jones, 2005; Luvisi, 2002; Triapitsyn et al., 1998) and has, in addition, been released as part of the California Department of Food and Agriculture's release program in the counties of Los Angeles, San Bernardino and San Diego (Anon, 2002). All these counties fall within areas of California where *G. ashmeadi* is predicted to have high potential for reproductive and development success based on laboratory-derived estimates of its climatic requirements.

All counties that have a R_{o} value < 1.0, indicating negative or declining population growth, occur predominantly in northern California, above Fresno County. These areas are probably incapable of supporting invading populations of *G. ashmeadi* that result in perennial populations. Winter temperatures in these northern areas would appear to be deleterious to parasitoid populations and *G. ashmeadi* would be expected to have trouble recovering to fully infiltrate these areas each year regardless of host availability. The effect of temperatures experienced in these areas on *H. coagulata* are unknown, but inferential modeling suggests areas in the extreme north of California and southern Oregon will be too cold for this pest to persist (Hoddle, 2004). Of particular concern are the counties highlighted as important wine growing regions in California as these northern wine growing districts appear to have environmental conditions that are inhospitable for year-round persistence of *G. ashmeadi*. Equivalent information on the influence of temperature on the developmental and reproductive biology of *H. coagulata* is lacking and studies are urgently needed to address this important knowledge gap. However, inferential modeling suggests that California's premier wine-growing counties in northern California may be vulnerable to invasion by *H. coagulata* (Hoddle, 2004).

While egg to adult degree-day requirements have not been calculated for *H. coagulata*, the degree-day requirements for embryonic development are 113.8 degree-days over a minimum threshold of 11.9 °C (Al-Wahaibi and Morse, 2003). Nymphal stages of *H. coagulata* reared at a constant laboratory temperature of 27 °C require between 50 and 60 days to develop to adult stages (Sétamou and Jones, 2005). Rough estimates of degree-day requirements for development by *H. coagulata* motiles therefore suggest that approximately seven degree-days need to be accumulated in each 24 h period to complete development. If this rough degree-day estimate is used, *H. coagulata* may require up to approximately 530 degree-days to complete development from egg to adult. In contrast, *G. ashmeadi* requires 222 degree-days for development from oviposition to emergence of adult stages (Pilkington and Hoddle, 2006). This parasitoid could potentially experience generational turnover of more than double that of *H. coagulata*. This information suggests that when the local climate allows *G. ashmeadi* to successfully establish a population and maintain that population perennially, it will potentially be an extremely efficient control agent of *H. coagulata* populations. This may be evidenced by the low numbers of *H. coagulata* populations in its home range of southeastern USA and northeastern Mexico (Pilkington et al., 2005). Anecdotal evidence from Hawaii suggests that populations of *H. coagulata* are effectively controlled by *G. ashmeadi*. This is possibly due to stable and moderate year-round temperatures in Hawaii that promote year round production of host eggs and high reproductive turnover of the parasitoid in relation to its host.

In conclusion, the results of this work indicate that a potential limiting factor affecting invasion success in California by *G. ashmeadi* may be the climate in the receiving area. Where climatic conditions are favorable and *H. coagulata* is present, high generational turnover by the parasitoid would be anticipated to provide significant suppression of the pest. Areas in which *H. coagulata* can invade and establish viable year round populations but in which temperatures are not suitable for year round persistence of *G. ashmeadi* may allow this pest to escape from adequate regulation by natural enemies. Understanding the relationship between reproductive biology and temperature is crucial to interpreting invasion success of natural enemies and understanding the outcomes of biological control programs.

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