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Degree-Day Requirements for Eight Economically Important Grasshoppers (Orthoptera: Acrididae) in Nebraska Using Field Data

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ABSTRACT The timing of application for the management of rangeland grasshoppers (Orthoptera: Acrididae) is critical, especially as insecticides become more specialized and the use of Insect Growth Regulators becomes more widespread. The general seasonal occurrence of adults of many grasshopper species has been well documented; however, their appearance varies widely between years. We analyzed sweep samples collected over the western two thirds of Nebraska from a 3-yr period and noted the occurrence of adults by region for eight species of rangeland grasshoppers. We analyzed occurrence based on degree-day accumulations for the region and developed estimates of degree-day requirements for these species. Because these grasshopper species are common rangeland pests, degree-day requirements to reach adulthood should improve the effectiveness of grasshopper treatment programs over a large geographic area.

KEY WORDS grasshopper development, rangeland, degree-day, phenology

Estimates of degree-day accumulation have been used widely in horticulture, agricultural production, and integrated pest management (IPM) of insects. Identification of degree-day requirements has been useful in predicting the occurrence of numerous pests (Funderburk et al. 1984, Hochberg et al. 1986, Zou et al. 2004) including those affecting human health such as mosquitoes (Madder et al. 1983, Bayoh and Lindsay 2004, Gu and Novak 2005). The minimum temperature at which a given species and/or life stage can grow and molt is estimated directly or indirectly and defined as the developmental threshold. Degree-day accumulation occurs at temperatures above this threshold to a maximum at which development is slowed because of thermal stress. Calculation of degree-day accumulation is made in a number of different ways including the rectangular, triangular, and sine wave methods (Higley et al. 1986). The most commonly used is the rectangular method (Higley et al. 1986, Pedigo, 1996) that was developed by Arnold (1959) and later modified by Bakersville and Emin (1969).

Despite their importance as pests of both crops and rangeland, the developmental thresholds of North American short-horned grasshopper (Orthoptera: Acrididae) species remain largely unknown. In fact, the estimates of total degree-day requirements for development from egg to adult have been experimentally controlled and determined for only one species: *Melanoplus sanguinipes* (F.) (Fisher et al. 1999, Pfadt 2002). Beyond the lack of measured degree-day requirements, developmental thresholds are unknown for most species and have led to estimates that may be inaccurate. For example, Kemp and Dennis (1991) estimated developmental events for six rangeland grasshopper species in Montana; however, they used a base temperature of 17.8°C (64°F), presumably relying on the work of Parker (1930). More recent work by Hao and Kang (2004) and O'Neill and Rolston (2007) suggested that developmental thresholds for most grasshoppers may be much lower than 17°C.

Re-evaluation of developmental thresholds and degree-day requirements is becoming more critical for rangeland grasshoppers as new insecticide treatments have become available. For rangeland grasshopper control, Insect Growth Regulators (IGRs) have become popular (Weiland et al. 2002). With IGRs, the timing of application is critical to control pest populations, minimize effects on nontarget fauna, and manage cost (Lockwood and Schell 1997, Foster and Reuter 1996–1999, Weiland et al. 2002) because IGRs are only effective against the immature stages of the insects, and death occurs during molting.

During studies in Nebraska between 2005 and 2007, we noted that the appearance of adults of common species varied widely between years, likely as a result of yearly climatic differences. A comparison of degree-day accumulation between years appeared to largely explain these differences in appearance of adults. Here we present estimates of degree-day requirements from winter to adult emergence for eight egg-overwintering species known to potentially pose economic threats to rangeland areas.

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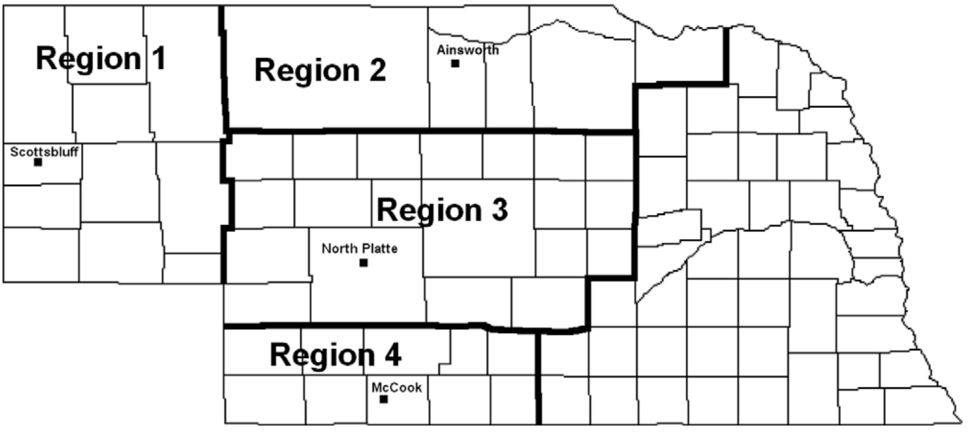

Fig. 1. Geographic location of the four regions for which weather data were obtained for this study and the location of the weather station used.

Materials and Methods

We divided the survey area consisting of the western two thirds of Nebraska into four regions. Within each region, a central weather station was selected to estimate degree-day accumulation (Fig. 1). All sampling sites for a region were located within 300 km of these weather stations.

More than 4,000 standardized sweep net samples (38-cm-diameter net, 20 sweeps per sample, one figure eight per sweep, using low and fast sweeps) were obtained by USDA–APHIS personnel in conjunction with the Rangeland Grasshopper and Mormon Cricket Suppression Program (USDA–APHIS 2007) during the summers of 2005–2007. Samples were obtained during two periods: 14 May to 7 July, targeting nymphal grasshoppers, and 14 July to 8 September, targeting adult grasshoppers. Adults from all samples were identified to species. Five USDA–APHIS field technicians visited preselected rangeland sites twice. Approximately 1,400 sites were visited per season, and each site was located ≈19 km (12 mi) apart. Surveyors sampled sites on weekdays but not on weekends.

More than 25,000 adult specimens of eight target rangeland species, *Ageneotettix deorum* (Scudder), *Melanoplus angustipennis* (Dodge), *Amphitornus coloradus* (Thomas), *Melanoplus femurrubrum* (DeGeer), *Melanoplus sanguinipes* (F.), *Orphulella speciosa* (Scudder), *Opeia obscura* (Thomas), and *Phoetaliotes nebrascensis* (Thomas), were collected during these 3 yr. From these data, the date of the first appearance of each adult species was determined by region.

Because field personnel work 40 h/wk and typically reach these hours in 3–4 d, no data were collected for several days each week (Table 1). Thus, to develop degree-day models, we used adult "first occurrence" as our biofix. The biofix was initiated as the most conservative among (1) the first occurrence of two total adult specimens per region (two total), (2) the first occurrence of two adult specimens at a single site per region (two per site), or (3) the first occurrence of five adult specimens at a single site per region (five per site). The first of these is the most conservative and would be expected to detect at least a few unusually early adults. The other two methods suggest that adults of a particular species are beginning to become at least fairly common.

Because developmental thresholds for rangeland grasshoppers are poorly known, degree-day accumulation was determined at both base-50°F (10°C) and base-60°F (15.5°C) to estimate development to the adult stage. These higher temperature is based on Parker (1930), and the lower temperature is an estimated minimum temperature for grasshopper development. For each region, degree-days above both thresholds were calculated from 1 January to first adult occurrence using the rectangular method (Arnold 1959, Bakersville and Emin 1969, Higley et al. 1986, Pedigo 1996).

In some cases, a given species was uncommon within one or two regions, and in such cases, an adjusted estimate was generated by omitting data from regions where densities were low. Regions from which

Table 1. Number of sampling days and mean ± SE no. of days between samples for each region and year from beginning of nymphal surveys (mid-May) to end of adult surveys (early Sept.)

Region	2005		2006		2007	
	No. of sample days	Mean ± SE	No. of sample days	Mean ± SE	No. of sample days	Mean ± SE
1	41	3.0 ± 0.56	60	2.0 ± 0.23	49	2.2 ± 0.31
2	33	2.8 ± 0.64	39	2.7 ± 0.48	41	2.4 ± 0.45
3	44	2.2 ± 0.45	56	1.9 ± 0.38	66	2.0 ± 0.24
4	22	5.6 ± 1.70	29	3.7 ± 0.94	29	3.2 ± 0.63

Table 2. Number of specimens used for "raw" and "adjusted" estimates of degree-day requirements

Species	Form	Specimens used
A. deorum	Raw	18,034
	Adjusted	16,225
A. coloradus	Raw	825
M. angustipennis	Raw	5,923
	Adjusted	5,085
M. femurrubrum	Raw	1,191
	Adjusted	1,140
M. asanguinipes	Raw	1,126
O. obscura	Raw	1,814
	Adjusted	1,742
O. speciosa	Raw	1,251
P. nebrascensis	Raw	1,456

<100 total specimens of a given species were collected were not used in our calculations. This was done to prevent a positive bias and resultant overestimate of degree-day requirements for a particular species in a given region (Table 2). Final estimates of degree-day requirements to reach the adult stage were obtained by averaging all four regions (raw; mean Julian date divided by number of regions) or combining all in which >100 adults were obtained (adjusted). 95% confidence intervals were calculated from the SD of mean degree-days accumulated.

Results

As anticipated, base-50 and base-60 estimates were significantly different for all species based on nonoverlapping 95% confidence intervals (Fig. 2). However, species fell into several distinct groupings based on estimated degree-day requirements, and these groupings remained constant at both base-50 and base-60.

Ageneotettix deorum, M. angustipennis, and *M. sanguinipes* (1,408–1,696 DD base-60) represent the earliest eclosing grasshoppers and differ from all other species except *A. coloradus* (1,626–1,842 DD base-60). *A. coloradus* and *O. speciosa* overlap broadly in degree-day requirements but differ from all later species. The remaining species, *M. femurrubrum, O. obscura,* and *P. nebrascensis,* form a distinct late eclosing group (1,933–2,199 DD base-60). Base-60 DD estimates produced the narrowest confidence intervals in all cases (Fig. 2).

Discussion

Our results document degree-day accumulation and appearance of adults of eight rangeland pest grasshopper species in Nebraska over a 3-yr period. Our estimates of degree-day requirements for adult emergence present consistent trends at the species level at both base-50 and base-60 levels.

Although narrower confidence intervals were found using a base-60 (15.5°C) developmental threshold, it is unknown if this represents the better estimate. The lower developmental threshold of rangeland grasshoppers was estimated by Parker (1930) to be 17°C (62.6°F). O'Neill and Rolston (2007) determined that the minimum temperature required for walking in *M. sanguinipes* to be ≈12°C (53.6°F). Hao and Kang (2004) found developmental thresholds between 11.1 (51.98°F) and 13.1°C (55.58°F) for three Mongolian grasshopper species. Thus, if these observed activity thresholds also allow development, lower threshold temperatures should be used for degree-day calculations.

Fisher et al. (1999) conducted a highly detailed study on *M. sanguinipes* and estimated not only degree-day requirements but also determined temperatures involved in egg diapause. The results given in O'Neill and Rolston (2007) suggest that the base-50 estimate might be more accurate, particularly for *M.*

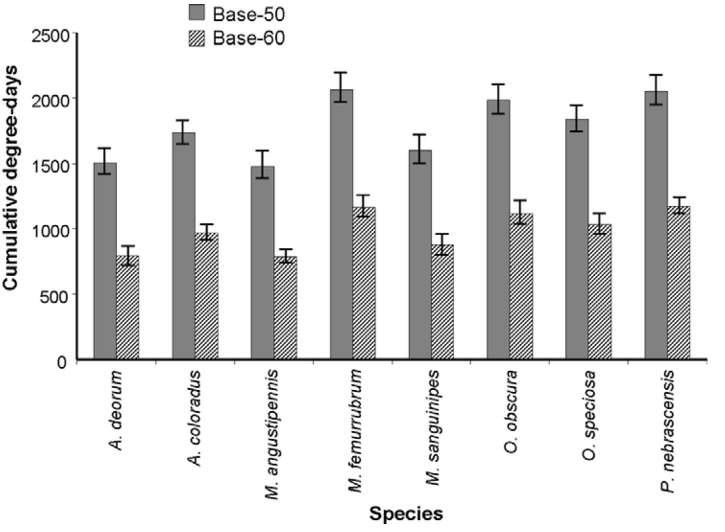

Fig. 2. Estimated mean and 95% confidence intervals of degree-day requirements for adult development from 1 January at base-50°F and base-60°F for eight Nebraska rangeland short-horned grasshopper species based on adjusted estimates.

sanguinipes. However, the minimum temperature required for activity and development in other species has not been determined and is likely to differ between species.

We recommend that, when implementing grasshopper control treatments, especially using IGRs, the most conservative estimates (earliest occurrence possible) based on 50°C be used because it would allow the fewest adults to survive treatment. The groupings noted in this study correspond closely with Pfadt (2002) in his differentiation of the early, intermediate, and late hatching groups among the acridids of the western United States. The only exception is *M. femurrubrum,* which fits the late group presented here but was classified as an intermediate hatching species by Pfadt (2002). This discrepancy might be explained by differences in nymphal development rates or the number of instars required to reach adulthood. Observations in Nebraska suggest that this species typically requires six instars in Nebraska as opposed to the five recorded by Pfadt (2002). However, because our data on first adult occurrence correspond to the hatching periods presented in Pfadt (2002), the estimates of degree-day requirements from egg to nymph may be adequate to estimate adult occurrence. Our results also correspond relatively well with Cushing et al. (1999).

Hewitt (1980) and Kemp et al. (1991) found that plant phenology was useful in determining development and timing for grasshopper control applications. As plants respond similarly to degree-day accumulation (Jordan and Haferkamp 1989, Donald 2000), degree-day accumulation may provide a good estimate for the occurrence of adults and aid in determining optimal times for control applications. Additional factors are likely to influence developmental time in grasshoppers. For example, localized geographic populations have been documented to possess traits that allow them to develop more rapidly than other populations, especially at high altitudes and latitudes (Willott and Hassal 1998, Fielding 2004). Additionally. the short-term developmental rate of immature grasshoppers is also likely to be affected by variations in local soil temperature (Pierson and Wright 1991), as well as behavioral responses to temperature (Pepper and Hastings 1952, Lactin and Johnson 1996, O'Neill and Rolston 2007) and solar radiation (Bryant et al. 1998).

The degree-day requirements needed for egg development have been recorded for several species, including several included in this study (Pfadt 2002). However, for those species studied by Pafdt, variation is generally high and ranges between 6 and >20 d (Pfadt 2002). In addition, degree-day accumulation affecting rates of development vary widely by species, latitude, and altitude, and vary from 1 yr to another (Berry et al. 1996–1999).

Although it is unknown whether a base-50 or base-60 estimate is most applicable to rangeland grasshoppers as a whole, evidence suggests that the majority of damage caused by rangeland grasshoppers occurs before the adult stage is reached. Grasshoppers are known to eat approximately one half of their body mass daily (Hewitt 1977) and approximately double their body mass with each molt (Schmidt-Nielsen 1984, Greenlee and Harrison 2004). Thus, treatment of economic numbers at earlier instars, such as second and third instars, should prevent more damage. Timing of sampling and treatment based on degree-day estimates should also allow more specific management in areas where either early- or late-emerging species more commonly reach pest status.

Among other potential limitations of this study are the distance to a weather station and the work week of field technicians. Obviously, microclimates vary across a span of 300 km and are likely to influence degree-day estimates. However, we attempted to generate conservative estimates by analyzing degree-day accumulations for each species for each region. These estimates matched closely across regions as indicated by the narrow 95% confidence intervals observed (Fig. 2).

A second limitation to our study is the fact that field employees often do not work on weekends, and thus, there are breaks in the sampling interval (Table 1). These breaks resulted in gaps of the data of 2–3 d between samples. In addition, there was an extended break between the nymphal and adult sampling periods that varyied among technicians between 5 and 20 d. The breaks in data collection can cause errors in the estimation of degree-day requirements. However, the only species that seemed to reach adulthood during this break period were *A. deorum* and *M. angustipennis.* In 2005 and 2007, these two species did not reach adulthood until after the adult surveys began. In 2006, both species reached adulthood toward the end of the nymphal survey period.

Another potential limitation of our studies is the use of sweep samples obtained by several different individuals. O'Neill et al. (2002) showed that the accuracy of sweep netting to estimate grasshopper densities varied widely among individual surveyors. Foster and Reuter (1996–1999) suggested sweep net samples do not always obtain an accurate estimate and that two different kinds of sweep sample techniques result in higher capture rates of different types of grasshoppers. These authors found that low and slow samples were more effective in capturing early instars and slow moving species, whereas high and fast sweeps were more effective for more active species. Although our samples consisted mostly of low but fast sweeps, the total number of adult grasshoppers for each species suggests that the technique was adequate for these species. Thus, although there are shortcomings, sweep net sampling remains the most commonly used and most economic means of obtaining data on grasshopper community composition (Larson et al. 1999, Skinner 2000, O'Neill et al. 2002).

Despite these limitations, our results should improve the prediction of the most opportune time period for treatment of damaging grasshopper populations, especially if the most numerous species can be determined. The best time for treatment for each species using an IGR such as diflubenzuron would be before the appearance of adults when nymphs are in the third or fourth instar. Thus, the treatment window could be conservatively set 500 DD before adult appearance at base-60 or 800 DD before adult appearance at base-50, because this would ensure treatment before adults appear but also make it unlikely that many eggs remain unhatched. Because they are conservative, our results should also be applicable for each species within all Nebraska rangelands and in other states.

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