

## Toward a General Model of Rangeland Grasshopper (Orthoptera: Acrididae) Phenology in the Steppe Region of Montana

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**ABSTRACT** A 4-yr study was conducted to examine the phenology of rangeland grasshoppers at 12 sites throughout Montana. A six-species complex of common and economically important rangeland grasshoppers was selected to facilitate comparisons between sites in this environmentally heterogeneous state. Results showed that a published phenology model (developed by Dennis, B., W. P. Kemp & R. C. Beckwith, 1986. A stochastic model of insect phenology: estimation and testing *Environ. Entomol.* 15: 540-546, and Dennis, B. & W. P. Kemp, 1988. Further statistical inference methods for a stochastic model of insect phenology. *Environ. Entomol.* 17: 887-893) provided good estimates of "general" grasshopper phenology for each site and year. Comparisons of developmental "signposts" (75% first instar, peak second to fifth instars, and 75% adults) for grasshoppers between sites and years indicated that they can be used by resource managers for estimating when development stages of rangeland grasshoppers are likely to occur. The developmental signposts were separated, on average, by 8-12 d. Implications of these results for rangeland insect pest management are discussed.

**KEY WORDS** Insecta, integrated pest management, insect development, phenology

RANGELAND GRASSHOPPER (Orthoptera: Acrididae) development has important implications for integrated pest management efforts in much of the western United States and Canada. Recent work has suggested that the general progression of assessment and, if necessary, control activities should follow and be linked to the occurrence patterns of the various phenological stages of rangeland grasshoppers. For example, Onsager (1987a) suggested that assessment of rangeland grasshopper communities (a collection of co-occurring populations of individual species) should be conducted at "peak third instar" to determine whether or not a problem exists and to allow for mobilization of resources for control activities, if warranted. The term "peak third instar" refers to the point in time when the proportion of grasshoppers in that development stage reaches a maximum (Dennis & Kemp 1988). Other important development "signposts" (peak fourth and fifth instars, 75% adult) of rangeland grasshoppers have been identified as appropriate times for applying different biological and chemical controls (Onsager 1987a,b). However, in general, there has been very little research on rangeland grasshopper phenology that would allow rangeland pest managers to use the management guidelines described by Onsager (1987a,b).

One serious problem facing rangeland pest managers is the fact that grasshoppers comprise a complex of nearly 200 species in the western United States and Canada. It is common to find anywhere from 30 to 40 species of grasshoppers on a 10-ha site over the course of the year (Onsager 1987b). Furthermore, the rangeland grasshopper community at a site is influenced by plant community characteristics (e.g., Kemp et al. 1990a,b). The rangeland resource manager is therefore faced with a complex of species that vary in space and time, unlike many other pest management situations with only one or a few clearly defined pest species. Fortunately, only  $\approx 15$  rangeland grasshopper species are responsible for most forage losses and, frequently, 3-5 species comprise between 75 and 95% of the overall local community abundance (Onsager 1987b), especially during outbreak years.

In spite of the obvious economic importance of rangeland grasshoppers and the importance of phenology to pest management, surprisingly little work has been conducted on quantifying phenological patterns. Newton et al. (1954) described the general patterns of hatching, adult presence, and oviposition for 46 rangeland grasshopper species at an unspecified number of sites in Montana and Wyoming over a 2-yr period. Other studies have reported on general trends for hatching or phenological points similar to the work of Newton et al. (1954) (Shotwell 1941, Hewitt 1979). However, none of these studies provides information on rangeland grasshopper developmental signposts for communities that can be used in a pest management context.

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Most of the work on phenology prediction for rangeland grasshoppers has been conducted in Canada. Mukerji & Randell (1975) developed an embryonic development model for *Melanoplus sanguinipes* (F.) eggs in the fall, and Randell & Mukerji (1974) reported on a springtime hatching model for the same species, which was driven by air temperatures. Also, Gage et al. (1976) developed a predictive model for the seasonal occurrence of a group of three grasshoppers, two of which (*Camnula pellucida* (Scudder) and *M. bivittatus* (Say)) are more commonly associated with crops in Montana.

Kemp & Onsager (1986) reanalyzed data collected by Hewitt (1979) and compared the phenological patterns of six individual rangeland grasshopper species. The data were collected during 1975–1976 at Roundup, Mont. The analyses showed that in spite of significant differences in phenology parameter estimates (for methods, see Dennis et al. 1986, Dennis & Kemp 1988) among the individual species, sufficient similarities existed so that it was reasonable to treat these species as a group in terms of phenology for pest management purposes (Kemp 1987). As noted by Onsager (1987a,b), rangeland grasshopper pest management activities, at present, do not generally distinguish among individual species. Rather, management activities (assessment and control) are generally directed toward the heterogeneous mix of springtime-emerging grasshopper species.

Based on the results of previous investigations (Kemp & Onsager 1986, Kemp 1987), we established a study to investigate the statewide variation of rangeland grasshopper communities in Montana. The major goal of this research was to provide rangeland resource managers with a straightforward method for estimating the timing of assessment and control activities for grasshopper populations in Montana.

#### Materials and Methods

**Sentinel Sites.** In 1986, 10 sentinel sites were established throughout Montana for the purpose of monitoring yearly phenology of rangeland grasshoppers. The number of sentinel sites was expanded to 12 in 1987 and thereafter remained constant through 1989 (Fig. 1). Sites were located over a range of long-term plant phenological zones (see Kemp 1987, 365, fig. 24.6) in an attempt to include the range of climatic conditions characteristic of sites within either the *Agropyron spicatum* or the *Bouteloua gracilis* provinces of the steppe region of Montana (Daubenmire 1978). All but one of the sites were located within 3.20 km of a National Oceanic and Atmospheric Administration (NOAA) weather station. On-site temperatures were recorded at the Three Forks site because there was no nearby NOAA station. Four of the sentinel sites (Broadus, Jordan, Great Falls, and Glasgow) were moved locally before sampling in 1987 to ensure

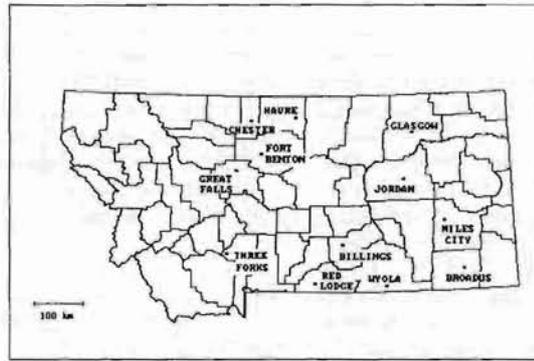


Fig. 1. Sentinel sites used for collection of rangeland grasshopper phenology data 1986–1989, Montana.

long-term access (<2 km away on similar vegetation).

Weather permitting, weekly sweep net samples (each sweep consisting of an area of 180° through the vegetation [Evans et al. 1983, Evans 1988]) were collected each year at all sites during the interval between mid-April and October. The number of net sweeps at a site in 1986–1987 was variable, although a minimum of 100 grasshoppers were collected at each sample date during the nymphal period. This was standardized to 100 sweeps in 1988–1989. Grasshoppers collected via sweep net were placed in plastic bags, put on ice, and taken to the laboratory for identification to species and determination of development stages.

As described previously, we expected the species composition of grasshopper communities to differ with site and to some extent with year (Kemp et al. 1990a,b). Therefore, we selected six major species for comparisons among sites. The six species chosen were *Ageneotettix deorum* (Scudder), *Amphitornus coloradus* (Thomas), *Aulocara elliotti* (Thomas), *M. infantilis* Scudder, *M. packardii* Scudder, and *M. sanguinipes* (F.) and were the same species that were used in previous studies (Kemp & Onsager 1986, Kemp 1987). Because of extremely low densities at Chester (1986–1988), Red Lodge (1986–1988), Wyola (1986–1988), and Jordan (1988) during this study, phenology data from these sites could not be used in analyses.

**Modeling Phenology.** The methods described by Dennis et al. (1986) and Dennis & Kemp (1988) were used to describe the phenology of the six-species community complex of rangeland grasshoppers. Data from 1986–1988 were used in analyses and data from 1989 were used for model evaluation. The reader should refer to Dennis et al. (1986) and Dennis & Kemp (1988) for complete details of the technical aspects of model development; however, we briefly summarize below the methods and steps followed.

At each site, a series of samples of size  $n_1, n_2, \dots, n_q$  was collected from the grasshopper community at times  $t_1, t_2, \dots, t_q$ . If there are  $r$  development stages (in grasshoppers, first to fifth instars

and adult;  $r = 6$ ), then the  $j$ th sample would consist of the counts  $x_{1j}, x_{2j}, \dots, x_{rj}$ , where  $x_{ij}$  is the number of sampled insects in development stage  $i$  at time  $t_j$  and where  $n_j = \sum_i x_{ij}$ . In this case,  $t_j$  is measured in degree-days (DD) computed in °F (above a threshold of 17.8°C) with a starting date of 1 January (Allen 1976). Because year-round weather recording at the Three Forks site was not established until 1989, the starting Julian dates (JD) for temperature collections were 59, 64, and 57 for 1986–1988, respectively. Given that degree-days do not generally begin to accumulate until after JD 90 at the Three Forks site, we were confident that the later starting dates for this site did not influence our results.

The counts  $x_{1j}, x_{2j}, \dots, x_{rj}$  can be described as having a multinomial distribution conditional on the sample size  $n_j$ . The underlying proportion of the community in each development stage would be expected to change with time as the individual population members develop.

Let  $Y(t)$  be the stage of a randomly sampled member of the community at time  $t$ ; possible values for  $Y(t)$  are  $[1, 2, \dots, r]$ . The phenology model of Dennis et al. (1986) assumes that an insect's development is really a continuous stochastic process consisting of accumulated small development increments. However,  $Y(t)$  is the fundamental observed random variable because a sampled insect is recorded as having reached a discrete development stage. We define  $p_i(t) = \text{Pr}[Y(t) = i]$  as the proportion of the population in development stage  $i$  at time  $t$ ,  $i = 1, \dots, r$ .

The model of Dennis et al. (1986) takes the proportion  $p_i(t)$  to be

$$p_i(t) = \begin{cases} \{1 + \exp[-(a_1 - t)/\sqrt{vt}]\}^{-1}, & i = 1; \\ \{1 + \exp[-(a_i - t)/\sqrt{vt}]\}^{-1} \\ \quad - \{1 + \exp[-(a_{i-1} - t)/\sqrt{vt}]\}^{-1}, & i = 2, \dots, r-1; \\ 1 - \{1 + \exp[-(a_{r-1} - t)/\sqrt{vt}]\}^{-1}, & i = r. \end{cases} \quad (1)$$

This expression arises from assuming that an insect's underlying continuous development level, denoted by  $X(t)$ , has a logistic probability distribution with mean  $t$  and variance ( $=\pi^2 vt/3$ ) proportional to  $t$ . Then  $\text{Pr}[Y(t) \leq i] = \text{Pr}[X(t) \leq a_i]$  is the cumulative distribution function of a logistic distribution:

$$\text{Pr}[Y(t) \leq i] = \begin{cases} 0, & i = 0 \ (a_0 \equiv -\infty); \\ \{1 + \exp[-(a_i - t)/\sqrt{vt}]\}^{-1}, & i = 1, \dots, r-1; \\ 1, & i = r \ (a_r \equiv +\infty). \end{cases} \quad (2)$$

The proportion  $p_i(t)$  is obtained from equation 2 as  $\text{Pr}[Y(t) \leq i] - \text{Pr}[Y(t) \leq i-1]$ . The quantity  $a_i$ ,  $i = 1, \dots, r-1$  can be interpreted as the time  $t$  at which half of the community is in stage  $i$  or

below:  $\text{Pr}[Y(a_i) \leq i] = \text{Pr}[Y(a_i) > i] = 1/2$  (fig. 1 of Dennis & Kemp 1988). The quantity  $v$  is a measure of the variability of development rates among insects in the community. In applications,  $t$  is usually measured in degree-days.

If there are  $r$  development stages, then the model has  $r$  unknown parameters. The unknown parameters can be written as a column vector,  $\theta$ :

$$\theta = [a_1, a_2, \dots, a_{r-1}, v]'$$

Also, the proportions  $p_i(t)$  defined in equation 1 can be written as  $p_i(t; \theta)$  to emphasize their dependence on  $\theta$ .

These parameters can be estimated from data using the maximum likelihood (ML) method. Non-linear regression packages can be used to perform the ML calculations as explained by Dennis et al. (1986) and Dennis & Kemp (1988).

**Model Evaluation.** The complexity of a data set is reflected by the number of parameters required to describe its structure (Bishop et al. 1975). Any model that describes the structure of the data with fewer parameters than the number of cells ( $x_{ij}$ 's) is unsaturated. The saturated model, because it describes the data set structure completely with one parameter per cell, is used for comparison with other models containing fewer parameters. In our case, we were interested in describing a grasshopper phenology data set with the fewest parameters necessary.

With a data set that spans three years (1986–1988) and nine sites (12 original sites minus Chester 1986–1988, Jordan 1988, Red Lodge 1986–1988, and Wyola 1986–1988) (Fig. 1), parameters could be estimated according to several alternative hypotheses. First, data could be pooled over sites (nine) and years (three or two in the case of Jordan), and a single set of six parameters ( $\hat{a}_1, \dots, \hat{a}_5, \hat{v}$ ) could describe the general development trends. Alternatively, either a set of six parameters could be estimated for each of 3 yr over all sites for a total of 18 parameters (3 yr  $\times$  6 parameters each year), or a set of six parameters could be estimated for each of nine sites over all years for a total of 54 parameters (9 sites  $\times$  6 parameters for each site). If it were necessary to keep sites and years separate, a total of 156 parameters would be needed. Thus, the complexity of the data will determine which alternative model we select.

In this study, we used the Akaike Information Criterion (AIC) (Sakamoto et al. 1986) to compare alternative models. We refer the reader to Sakamoto et al. (1986) for a detailed description of the AIC. In summary, however, the AIC has advantages over simply using the log likelihood (Dennis et al. 1986, Dennis & Kemp 1988) because the log likelihood is a biased estimator of the mean expected log likelihood. The somewhat awkward term "mean expected log likelihood" refers to the fact that the quantity results from taking the expected value of the log likelihood twice: first, with respect to the underlying "true" model, and second, with respect to the underlying "true" distribution of the

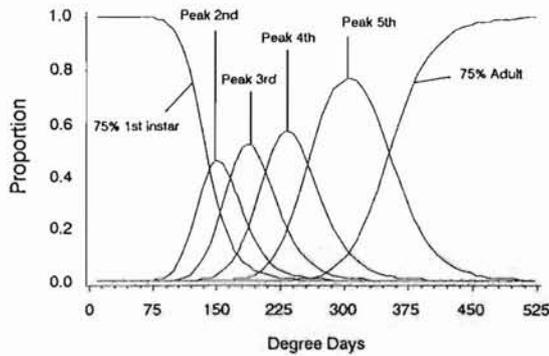


Fig. 2. Six phenological "signposts" for rangeland grasshoppers in Montana, as estimated by the Dennis-Kemp model (Dennis et al. 1986, Dennis & Kemp 1988).

ML estimate of  $\theta$ . The mean expected log likelihood is a measure of the goodness of fit of a model; the larger the mean expected log likelihood, the better the fit of the model (Sakamoto et al. 1986), that is, the closer the hypothesized model is to the underlying "true" model. Sakamoto et al. (1986) show that the maximum log likelihood tends to overestimate the mean expected log likelihood, particularly when models have unnecessarily large numbers of free parameters. The AIC is computed as

$$AIC = -2(\text{maximum log likelihood of the model}) + 2(\text{number of free parameters}),$$

and is an unbiased estimate of (minus two times) the mean expected log likelihood. Because the model that minimizes the AIC is considered to be the most appropriate, it is clear that the "+ 2(number of free parameters)" term is a penalty for overparameterization. The AIC has many useful applications in comparing models within the entomological literature outside of the specific purposes of this study.

Table 1. Percentage of rangeland grasshopper populations comprising six selected species, nine locations and three years, Montana<sup>a</sup>

Location	% Population in six species <sup>b</sup>				$\bar{x}$	SD
	1986	1987	1988			
Glasgow	91	77	85	84.3cd	7.0	
Havre	55	57	74	62.0d	10.4	
Miles City	88	76	84	82.6cd	6.1	
Jordan	72	86	— <sup>c</sup>	79.0cd	9.8	
Fort Benton	95	83	86	88.0c	6.2	
Broadus	93	87	91	90.3c	3.1	
Billings	79	82	84	82.7cd	2.5	
Great Falls	89	69	57	71.7cd	16.2	
Three Forks	96	95	96	95.3c	0.6	

Like letters indicate no significant difference (df = 17,  $\alpha = 0.05$ ; ANOVA, Tukey's studentized range test [SAS Institute 1988]).

<sup>a</sup> Data from Kemp et al. (1992).

<sup>b</sup> Six selected species used by Kemp & Onsager (1986): *Agrotettix deorum* (Scudder), *Amphitornus coloradus* (Thomas), *Aulocara elliotii* (Thomas), *Melanoplus infantilis* Scudder, *M. packardii* Scudder, *M. sanguinipes* (F.).

<sup>c</sup> Densities too low to make accurate estimates.

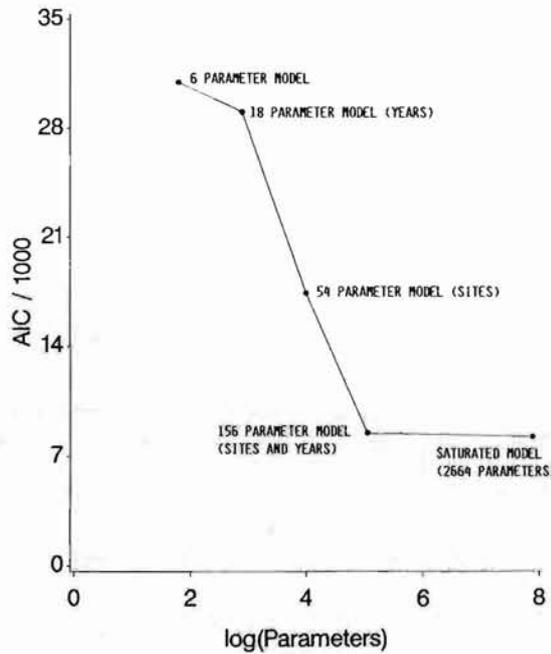


Fig. 3. Akaike Information Criterion (AIC) values computed for various parameterization options for the Dennis-Kemp model (Dennis et al. 1986, Dennis & Kemp 1988) for a rangeland grasshopper data set consisting of nine sites and 3 yr (except Jordan, which had only 2 yr of data), Montana.

**Comparisons Between Sites.** Once parameters for a community at a given site and year were estimated, two additional estimates for the Dennis-Kemp model were computed (Dennis & Kemp 1988). First, the peak time of  $p_i(t)$  and the associated confidence interval was computed for each of the second to fifth instars for each site and year (Fig. 2) (see equations 16–22 of Dennis & Kemp 1988). Second, the estimated time and confidence interval for  $\tau$  was computed for 75% first instar and 75% adult (see below). All estimates were produced in terms of degree-days as well as Julian date for site-to-site comparisons.

**Estimating the Time at Which 100· $\xi$ % of the Population is in Stage  $i$  or Less.** This section describes statistical methods for estimating the time at which 100· $\xi$ % of the population is in stage  $i$  or less, where  $0 < \xi < 1$ . For instance, the time at which 75% of the population is adult (i.e., 25% is fifth instar or less) is one of the "signposts" used in this paper, along with the time at which 75% is first instar. The remaining signposts used are peak second to fifth instars; statistical methods for peak instars have been described elsewhere (Dennis & Kemp 1988).

The probability that an insect is in stage  $i$  or less is given by equation 2 under the model of Dennis et al. (1986). As a function of  $t$ , the quantity  $Pr[Y(t) \leq i]$  is a declining sigmoid curve (e.g., stage 1, Fig. 2). We obtain the value of  $t$  at which this curve

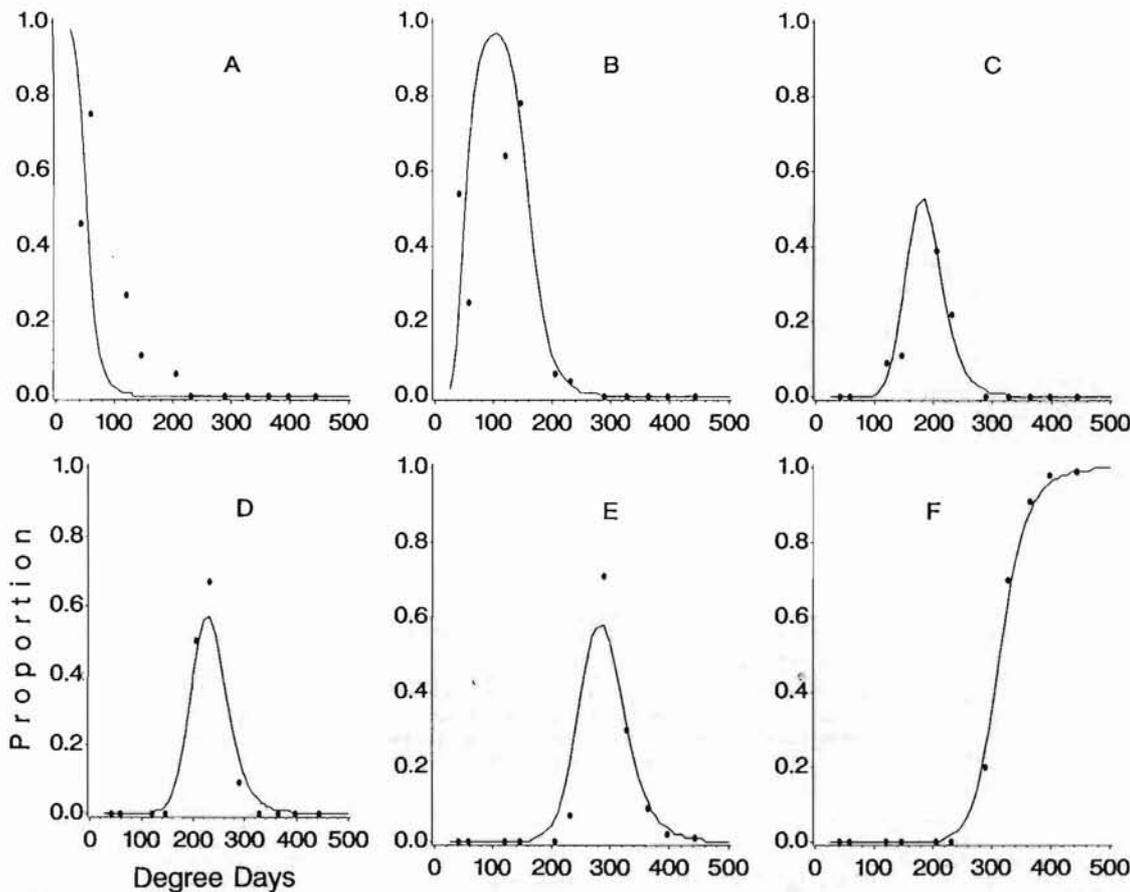


Fig. 4. Comparison of raw data (plotted points) and model results (solid line) for the proportion of the grasshopper community in each developmental state as a function of accumulated degree-days, Havre, Montana, 1986 (log likelihood = -52.63). (A) First instar. (B) Second instar. (C) Third instar. (D) Fourth instar. (E) Fifth instar. (F) Adult.

attains the value  $\xi$  as follows. Let  $\tau$  be the time (i.e., value of  $t$ ) at which  $Pr[Y(t) \leq i] = \xi$  for some given stage  $i$ . Thus  $\tau$  and  $\xi$  are related by

$$\xi = \left\{ 1 + \exp \left[ - \left( \frac{a_i - \tau}{\sqrt{v\tau}} \right) \right]^2 \right\}^{-1}$$

This expression can be solved for  $\tau$ :

$$\begin{aligned} \tau = a_i + \frac{v}{2} \left[ \log \left( \frac{\xi}{1 - \xi} \right) \right]^2 \\ - \frac{1}{2} \log \left( \frac{\xi}{1 - \xi} \right) \\ \times \sqrt{v \left\{ 4a_i + v \left[ \log \left( \frac{\xi}{1 - \xi} \right) \right]^2 \right\}} \end{aligned} \quad (3)$$

The resulting expression (equation 3) defines  $\tau$  as a function of  $\xi$  (selected by the investigator) and two model parameters,  $a_i$  and  $v$ .

Once ML estimates,  $\hat{a}_i$  and  $\hat{v}$ , have been obtained, the ML estimate of  $\tau$ , denoted  $\hat{\tau}$ , is just equation 3

evaluated at  $\hat{a}_i$  and  $\hat{v}$ . The approximate variance of  $\hat{\tau}$ , and a  $100(1 - \alpha)\%$  confidence interval for  $\tau$ , can be derived with the  $\delta$  method (see Dennis & Kemp 1988 for a discussion of the  $\delta$  method). The  $\delta$  method requires the following derivatives of  $\tau$  with respect to  $a_i$  and  $v$ :

$$\frac{\partial \tau}{\partial a_i} = 1,$$

$$\frac{\partial \tau}{\partial v} = \frac{1}{2} \rho^2 + \rho \left( a_i + \frac{1}{2} v \rho^2 \right) [v(4a_i + v\rho^2)]^{-1/2},$$

where  $\rho = \log[\xi/(1 - \xi)]$ . Let  $\beta$  be a column vector of these derivatives,

$$\beta = [\partial \tau / \partial a_i, \partial \tau / \partial v],$$

and let  $S$  be the  $2 \times 2$  large-sample variance-covariance matrix for the ML estimates  $\hat{a}_i$  and  $\hat{v}$ . The  $\delta$  method is essentially a theorem from mathematical statistics stating that the large-sample distribution of  $\hat{\tau}$  is normal with a mean of  $\tau$  and a variance of  $\beta' S \beta$ . The variance can be estimated by picking  $\hat{S}$  out of the estimated variance-co-

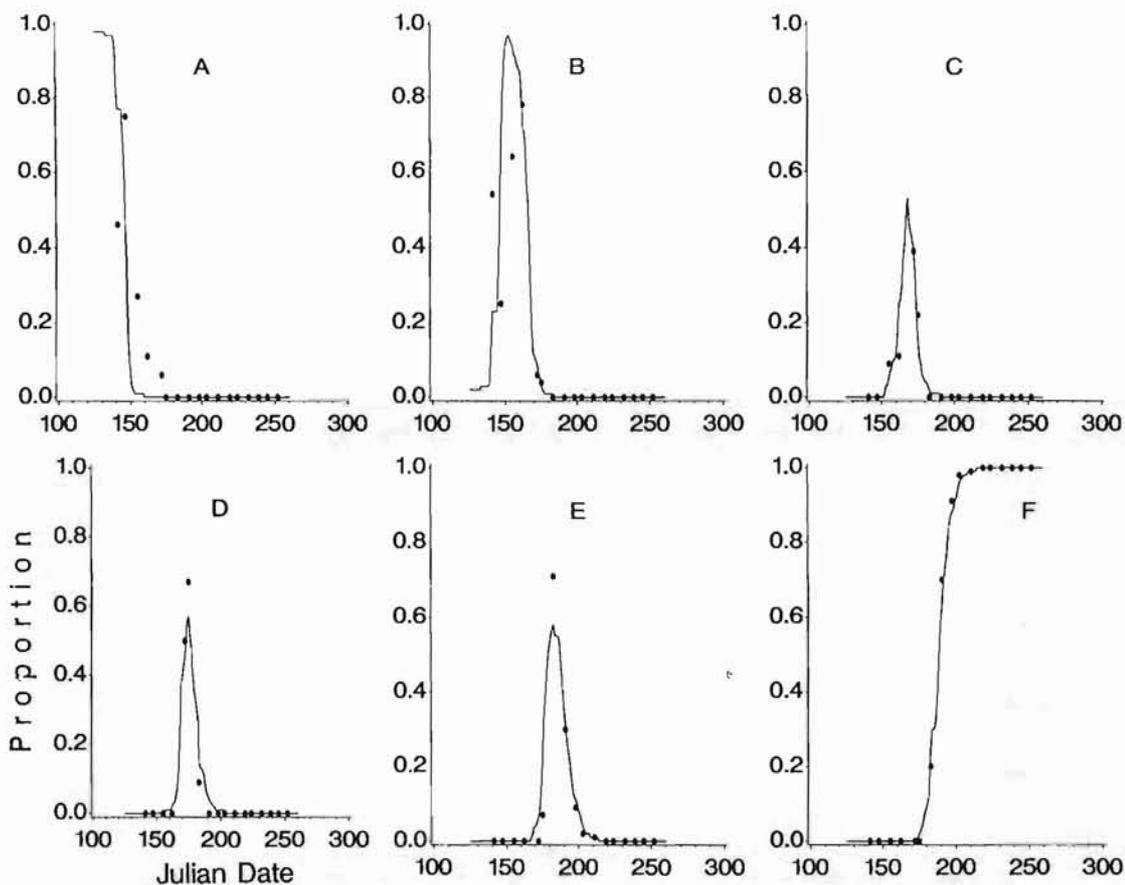


Fig. 5. Comparison of raw data (plotted points) and model results (solid line) for the proportion of the grasshopper community in each developmental state as a function of Julian date, Havre, Montana, 1986 (log likelihood = -52.63). (A) First instar. (B) Second instar. (C) Third instar. (D) Fourth instar. (E) Fifth instar. (F) Adult.

variance matrix obtained from fitting the model to data (see Dennis & Kemp 1988) and by substituting  $\hat{a}_i$  and  $\hat{v}$  in  $\beta$ . Then

$$\hat{\tau} \pm z_{\alpha/2} \sqrt{\hat{\beta}' S \hat{\beta}}$$

is an approximate  $100(1 - \alpha)\%$  confidence interval for  $\tau$ . Here  $z_{\alpha/2}$  is the  $100[1 - (\alpha/2)]$ th percentile of the standard normal distribution.

Standard ANOVA and regression methods were used to compare species percentages among grasshopper communities and the timing of rangeland grasshopper phenological signposts (estimated from the model). Where appropriate, multiple comparisons were made with Tukey's studentized range test (SAS Institute 1988).

### Results and Discussion

**Communities.** The six selected species constituted >50% of the communities at the nine sites during 1986-1988 (Table 1). The proportion of the communities made up of the six species at Three Forks was consistently high. Although there were significant differences among the 3-yr proportion

means among sites, there was considerable overlap (Table 1). Based on these results, it appeared reasonable to use the six-species complex for further comparisons of phenology among communities from the nine sites.

**Model Comparisons.** The AIC was used to determine the number of parameters necessary to describe the data for nine sites over 3 yr (Fig. 3). Results showed that the most appropriate way to describe the data was with the Dennis et al. (1986) model fit to data from each site each year because this method had the lowest AIC (Fig. 3). For comparison, the AIC was computed for the saturated model (the "saturated model" estimates  $r$  parameters, that is,  $r$  stage proportions, for every sample, subject to the constraint that the parameters add to 1) with 2,664 parameters. Fig. 3 shows that there is little improvement in the AIC with the addition of >10 times as many parameters when compared with the sites and years model. Therefore, the model that describes the data with 156 parameters (i.e., the Dennis et al. (1986) model fit to data sets from individual sites and years) was the most appropriate for our purposes. Fig. 4-7 show the range of log

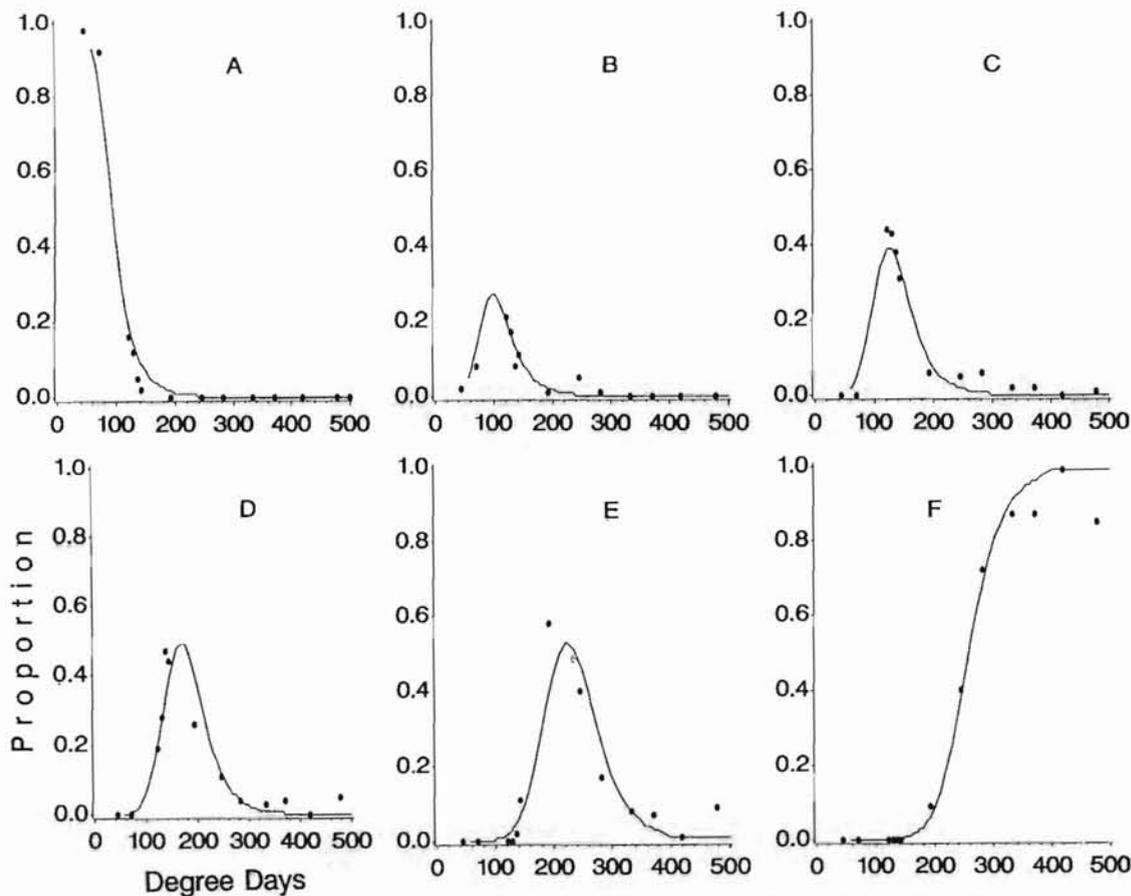


Fig. 6. Comparison of raw data (plotted points) and model results (solid line) for the proportion of the grasshopper community in each developmental state as a function of accumulated degree-days, Three Forks, Montana, 1987 (log likelihood = -497.94). (A) First instar. (B) Second instar. (C) Third instar. (D) Fourth instar. (E) Fifth instar. (F) Adult.

likelihoods encountered and provide a contrast between results expressed in Julian date and degree-days.

Although describing the data by parameterizing the Dennis et al. (1986) model for each year and site is appropriate (Table 2), this poses problems for the pest manager. It suggests that every site and year is different, even when trying to estimate phenology for the six-species complex. Although this is true to some degree, we examined the results further to consider the variation in estimates of specific developmental signposts that are important to resource managers involved in grasshopper pest management.

**Population Signposts.** Julian date and degree-day estimates for the six rangeland grasshopper signposts at each of the sentinel sites are contained in Table 3. For each signpost, comparisons of Julian date means among the sites showed there were no significant differences. Further, although significant differences were found among sites for the mean number of degree-days across sites for sign-

posts peak third instar through 75% adult, there was considerable overlap and no clear patterns emerged. In all cases where there were significant differences in degree-days, it was the result of contrasts between Three Forks and Jordan or Broadus. Overall, the average occurrence dates (nonleap year) for the six phenological signposts are JD 138 (May 18) for 75% first instar, JD 146 (May 26) for peak second instar, JD 158 (June 7) for peak third instar, JD 167 (June 16) for peak fourth instar, JD 177 (June 26) for peak fifth instar, and JD 188 (July 7) for 75% adult (Table 3).

With the same data used to construct Table 3, we computed the Julian date and degree-day differences between each of the major grasshopper development signposts (Table 4). In all cases, sites were not significant (Table 4). This suggests that once hatching occurs, there is a fairly orderly progression in the phenological sequence for the six-species complex over the period of study. The mean Julian date and degree-days separating developmental signposts are similar to those used by On-

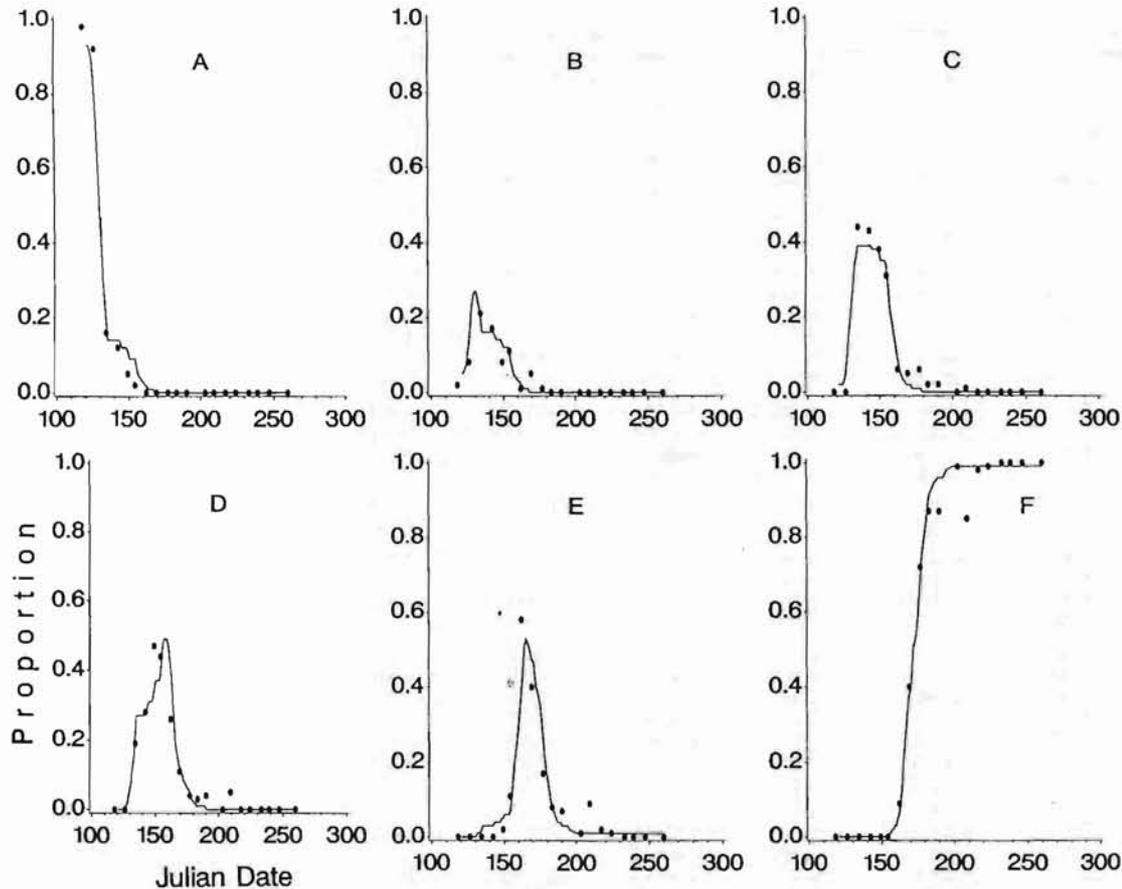


Fig. 7. Comparison of raw data (plotted points) and model results (solid line) for the proportion of the grasshopper community in each developmental state as a function of Julian date, Three Forks, Montana, 1987 (log likelihood = -497.94). (A) First instar. (B) Second instar. (C) Third instar. (D) Fourth instar. (E) Fifth instar. (F) Adult.

sager (1983) in simulation studies of rangeland grasshopper growth, survival, and forage consumption.

Grasshopper populations drastically declined throughout Montana between 1988 and 1989. Therefore, we were able to compare only the general results collected from 1986 to 1988 with data from three sites collected during 1989 (Table 5). The term "observed," in this case, refers to the estimate for this stage computed by fitting the Dennis et al. (1986) model to 1989 data, then calculating the signpost estimates (Dennis & Kemp 1988 and as above).

Given the "observed" date of peak second instar, the average differences between signposts (Table 4) were then used to "forecast" occurrence dates of the peak third instar through 75% adult signposts in 1989 (Table 5, forecasted Julian date). We had hoped to start with the observed date of 75% first instar at each of the three sites as a given and then use the average differences between signposts found in Table 4 for forecasting. However, low densities and poor weather conditions (that prevent sam-

pling) prevented us from obtaining precise observed estimates of the timing of 75% first instar during 1989 (estimates had very large confidence intervals). Therefore, forecasts (Table 5) were initiated with the observed dates for peak second instar at each of the three sites. Comparisons between observed and forecasted signposts shown in Table 5 suggest that the average Julian date differences between the phenological signposts for the 26 site-years reported in Table 4 have value in forecasting the phenological progression of populations over a wide range of conditions in Montana. However, this result must be tempered by the understanding that the use of Table 4 depends on a reasonable knowledge of the timing of peak second instar and, ultimately, of hatching.

Further work will be required before we are able to estimate the differences among sites in grasshopper hatching dates in an environmentally heterogeneous state like Montana (Hewitt 1979). However, Kemp et al. (1992) found that the begin-bloom phenophase of purple common lilac, *Syringa vulgaris* (L.) (a commonly grown ornamental

Table 2. Parameter estimates and asymptotic standard errors ( ) for nine sites during 1986–1988 in Montana for a model (Dennis et al. 1986) describing a six-species population complex of rangeland grasshopper phenology<sup>a</sup>

Site	Year	$a_1$	$a_2$	$a_3$	$a_4$	$a_5$	$v$
Glasgow	1986	102.527 (2.771)	146.707 (3.091)	188.260 (3.485)	265.072 (4.058)	372.493 (3.917)	7.451 (0.405)
	1987	125.625 (3.992)	176.433 (3.908)	249.366 (4.794)	316.813 (4.457)	395.998 (5.138)	3.535 (0.306)
	1988	65.718 (3.792)	123.654 (4.755)	267.839 (7.452)	364.896 (6.498)	488.741 (7.646)	4.694 (0.449)
Havre	1986	51.278 (4.898)	161.178 (7.782)	203.346 (6.001)	255.151 (5.633)	314.051 (4.779)	1.715 (0.256)
	1987	95.712 (2.832)	138.876 (2.644)	200.381 (3.542)	270.098 (3.403)	325.370 (3.967)	4.359 (0.320)
	1988	71.138 (2.859)	129.873 (2.724)	231.597 (3.789)	323.193 (4.190)	448.043 (6.176)	3.095 (0.230)
Miles City	1986	69.793 (4.745)	124.577 (3.453)	196.425 (3.660)	290.312 (5.701)	400.393 (5.289)	5.570 (0.416)
	1987	107.939 (4.714)	154.760 (3.825)	218.864 (4.467)	275.745 (5.618)	372.614 (5.252)	5.771 (0.493)
	1988	13.666 (7.197)	67.972 (7.560)	241.412 (14.355)	357.321 (10.565)	500.989 (12.010)	9.069 (1.196)
Jordan	1986	143.102 (5.199)	207.028 (5.155)	304.504 (5.790)	397.850 (4.254)	521.794 (3.707)	4.799 (0.310)
	1987	158.269 (4.100)	242.051 (3.323)	318.701 (3.323)	398.571 (3.896)	512.547 (5.499)	5.722 (0.336)
Fort Benton	1986	139.843 (3.148)	196.310 (2.342)	264.308 (2.407)	344.171 (2.577)	434.007 (2.830)	4.272 (0.189)
	1987	175.744 (2.039)	208.703 (2.329)	268.045 (2.631)	332.567 (2.854)	418.284 (3.762)	3.027 (0.171)
	1988	62.858 (1.749)	122.546 (2.791)	212.462 (3.184)	297.464 (4.323)	431.538 (5.457)	5.238 (0.307)
Broadus	1986	157.184 (2.205)	211.294 (2.636)	271.708 (3.715)	356.782 (4.702)	474.503 (3.779)	4.856 (0.257)
	1987	150.015 (1.977)	223.315 (2.661)	305.336 (3.635)	336.837 (3.696)	427.881 (4.720)	6.543 (0.374)
	1988	94.702 (2.197)	150.150 (2.813)	229.577 (3.539)	348.428 (4.245)	521.072 (7.458)	7.834 (0.439)
Billings	1986	94.197 (2.816)	127.214 (3.811)	233.954 (8.756)	301.769 (6.472)	390.719 (3.859)	3.780 (0.325)
	1987	137.081 (1.846)	169.015 (1.437)	209.679 (1.673)	260.499 (2.766)	353.234 (3.866)	1.654 (0.118)
	1988	57.957 (2.814)	112.905 (3.305)	196.915 (3.960)	283.165 (4.456)	408.574 (6.319)	6.884 (0.469)
Great Falls	1986	126.817 (2.552)	167.605 (2.175)	221.926 (1.894)	272.984 (2.558)	333.563 (2.486)	2.202 (0.134)
	1987	164.162 (6.467)	231.130 (4.497)	305.619 (3.421)	370.631 (3.609)	428.101 (4.298)	4.834 (0.367)
	1988	56.892 (5.354)	112.451 (4.097)	176.534 (3.755)	262.853 (5.518)	372.283 (7.117)	6.504 (0.596)
Three Forks	1986	91.606 (1.215)	121.316 (1.107)	169.940 (1.268)	220.141 (1.463)	297.670 (1.745)	3.540 (0.117)
	1987	92.040 (0.954)	111.868 (0.868)	145.184 (0.896)	195.567 (1.477)	258.721 (1.893)	3.215 (0.111)
	1988	97.670 (0.902)	151.460 (1.001)	189.215 (1.141)	255.945 (1.564)	354.496 (2.714)	2.069 (0.083)

<sup>a</sup> Estimates are in degree-days starting 1 January, 17.8°C base (Allen 1976).

shrub), preceded the estimated hatch (date of 75% first instar) of this six-species complex of grasshoppers by  $\approx 10$  d (24 site-years). Therefore, it seems that the use of a plant phenological indicator like the begin-bloom phenophase of purple common lilac is appropriate for estimating an initial reference date for this six-species complex of rangeland grasshoppers. Given an estimated hatch date, resource managers can then use differences between

the phenological signposts (Table 4) to forecast the occurrence of the remaining signposts in a given year. Because the timing of the begin-bloom phase of purple common lilac is a good indicator of accumulated heat (if not water-stressed [Caprio et al. 1970]) and was significantly related to hatch ( $y = 30.36 + 0.84x$ , where  $y =$  JD 75% first instar [spring hatch] and  $x =$  JD of the begin-bloom phase of purple common lilac;  $P = 0.0001$ ,  $r^2 = 0.51$ ), it is

Table 3. Mean estimated developmental signposts (average of *n* years) for rangeland grasshoppers in Montana (1986–1988) in Julian and degree-days

Site	Hatch (75% 1st instar)			Peak 2nd instar			Peak 3rd instar		Peak 4th instar		Peak 5th instar		75% adult	
	n	JD	DD	n	JD	DD	JD	DD	JD	DD	JD	DD	JD	DD
		(SD)	(SD)		(SD)	(SD)								
Glasgow	3	137 (9.5)	76.7 (28.0)	3	148 (4.6)	117.7 (29.0)	158 (3.2)	186.0 (24.6)	165 (4.2)	269.7 (46.7)	175 (3.8)	361.7 (55.5)	187 (9.5)	472.7 (61.8)
Havre	3	136 (8.6)	58.3 (17.0)	3	144 (8.5)	104.3 (8.1)	161 (6.4)	174.0 (7.9)	170 (4.7)	243.7 (26.3)	179 (3.8)	319.3 (54.5)	189 (4.5)	400.7 (81.5)
Miles City	1	125 (-)	84.0 (-)	3	133 (13.2)	82.3 (47.6)	148 (5.0)	159.0 (20.0)	161 (5.3)	255.7 (28.9)	171 (5.0)	358.7 (53.3)	182 (6.1)	488.0 (81.2)
Jordan	2	141 (13.4)	123.0 (8.5)	2	152 (2.8)	182.0 (17.0)	165 (2.1)	262.0 (17.0)	172 (4.2)	349.5 (4.9)	183 (2.1)	451.5 (3.5)	199 (4.2)	578.0 (2.8)
Fort Benton	3	137 (12.2)	104.3 (53.8)	3	148 (10.1)	146.3 (53.0)	157 (8.6)	207.3 (40.4)	166 (7.5)	282 (28.6)	178 (5.5)	371.3 (13.0)	189 (10.5)	476.7 (15.4)
Broadus	3	138 (12.5)	106.0 (32.5)	3	145 (10.8)	157.7 (37.8)	159 (8.3)	224.7 (39.2)	166 (7.5)	301.3 (18.7)	175 (6.0)	403.7 (26.1)	187 (8.2)	538.7 (53.5)
Billings	3	137 (9.9)	79.3 (41.1)	3	143 (8.5)	112.0 (36.8)	156 (6.8)	170.3 (21.1)	165 (8.1)	243.3 (17.9)	173 (7.4)	328.3 (20.3)	182 (8.4)	429.0 (45.3)
Great Falls	3	146 (10.6)	95.0 (50.2)	3	157 (10.4)	138.3 (57.3)	166 (7.6)	197.7 (62.7)	177 (6.5)	264.7 (62.1)	187 (9.5)	335.0 (51.3)	201 (8.5)	425.3 (58.1)
Three Forks	3	139 (11.1)	77.3 (4.9)	3	143 (10.8)	108.0 (12.3)	151 (14.3)	145.0 (21.7)	162 (6.1)	192.7 (26.5)	171 (5.6)	260.7 (39.8)	182 (7.4)	338.0 (47.0)
Significant differences among sites ( $\alpha = 0.05$ )		No	No		No	No	No	Yes	No	Yes	No	Yes	No	Yes
All sites/years	24	138 (9.8)	88.4 (34.0)	26	146 (10.3)	125.5 (42.2)	158 (8.5)	189.1 (42.2)	167 (7.0)	263.7 (47.9)	177 (7.1)	350.7 (59.6)	188 (9.3)	456.3 (81.6)

**Table 4.** Differences between predicted occurrence dates for populations of rangeland grasshoppers in Montana, 1986-1988

Interval	n	Sites	
		Julian date (SD)	Degree-days (SD)
75% 1st instar-peak 2nd instar	24	8.5 (4.9)	42.5 (10.6)
Peak 2nd instar-peak 3rd instar	26	12.1 (5.9)	63.5 (19.3)
Peak 3rd instar-peak 4th instar	26	9.2 (3.9)	74.6 (24.5)
Peak 4th instar-peak 5th instar	26	9.7 (1.8)	87.1 (23.9)
Peak 5th instar-75% adults	26	11.9 (3.4)	105.5 (28.5)

Values are not significantly different ( $df = 8$ ,  $\alpha = 0.05$ ; ANOVA [SAS Institute 1988]).

reasonable to consider the use of this indicator (Kemp et al. 1992) pending the development of more sophisticated models for the prediction of springtime hatch of rangeland grasshoppers. The use of a plant that is a good indicator of accumulated heat to initiate grasshopper forecasts has merit in that year-to-year differences in accumulated heat before hatch will result in the earlier or later occurrence of the plant phenological stage. By observing lilac plants, land managers can determine whether conditions of a given year vary substantially from individual site means for hatching or for hatching in general (Table 3) and make appropriate adjustments in forecasting the occurrence of the remaining signposts.

In summary, the AIC showed that the Dennis et al. (1986) model provided good estimates of rangeland grasshopper phenology on an individual site-year basis, based on accumulated heat. Further, average Julian date differences between grasshop-

per phenological signposts provided reasonable forecasts of grasshopper development. These results, combined with a separate but related study linking spring hatch with the begin-bloom phenophase of purple common lilac, provide a reasonable general model of rangeland grasshopper phenology in Montana.

**Implications for Pest Management.** Until this study was conducted, there was little specific information on the phenological progression of grasshoppers that could be used in a pest management context (Shotwell 1941; Newton et al. 1954; Hewitt 1979, 1980). The results of our study can be used by resource managers as they attempt to implement the recommendations of Onsager (1986, 1987a,b) for the timing of rangeland grasshopper assessment and control activities.

Predicting the phenological progression of species assemblages will continue to challenge both researchers and land managers interested in pest management. At present, however, predicting the phenological progression of the six-species complex appears reasonable in view of the variation found (Tables 3 and 4) and the occurrence patterns of these species at each site throughout the study (Table 1). Depending on their location, resource managers may find that local conditions more closely resemble the observed differences between signposts at an individual site (Table 3) rather than the overall mean differences shown in Table 4. Future work with environmental covariates (Kemp et al. 1990a,b) may offer a way of improving forecast accuracy and, at the same time, help us understand this extremely complex grassland-herbivore system. Furthermore, the establishment of the USDA-APHIS-PPQ sentinel site system (for grasshoppers) is a very important first step in understanding the large-scale variability that must be addressed if future rangeland pest management programs are to be successful.

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**Table 5.** Comparison of "observed" 1989 versus forecasted occurrence dates for major phenological events of a six-species complex of grasshoppers at three sites in Montana

Stage	Observed Julian date for site/year	Forecasted Julian date from general differences
Fort Benton <sup>a</sup>		
Peak 2nd instar	159	—
Peak 3rd instar	174	171
Peak 4th instar	185	180
Peak 5th instar	194	190
75% adult	205	202
Havre <sup>b</sup>		
Peak 2nd instar	162	—
Peak 3rd instar	170	174
Peak 4th instar	181	183
Peak 5th instar	188	193
75% adult	202	205
Three Forks <sup>c</sup>		
Peak 2nd instar	155	—
Peak 3rd instar	173	167
Peak 4th instar	183	176
Peak 5th instar	188	186
75% adult	197	198

<sup>a</sup> Six species, 85% of population.

<sup>b</sup> Six species, 77% of population.

<sup>c</sup> Six species, 98% of population.

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