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E. Matthew Hansen

Barbara J. Bentz

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Temperature-based model for predicting univoltine brood proportions in spruce beetle (Coleoptera: Scolytidae)

E Matthew Hansen,¹ Barbara J Bentz, David L Turner

USDA Forest Service, Rocky Mountain Research Station, 860 N 1200 E, Logan, Utah, United States 84321

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Abstract—The spruce beetle, *Dendroctonus rufipennis* (Kirby), has possible life cycles of 1 or 2 years. Empirical and experimental evidence suggest that temperature is the primary regulator of these life-history pathways. These different life cycles potentially result in substantial differences in population dynamics and subsequent spruce mortality. A multiyear field study was conducted in Utah, Colorado, and Alaska, to monitor spruce beetle development under a variety of field conditions with concurrent air temperature measurements. This information was used to model the tree- or stand-level proportion of univoltine beetles as a function of air temperature. Temperatures were summarized as averages, cumulative time, and accumulated heat units above specified thresholds over various seasonal intervals. Sampled proportions of univoltine insects were regressed against the summarized temperature values in logistic models. The best predictive variable, as evaluated by Akaike's Information Criterion, was found to be cumulative hours above a threshold of 17°C elapsed from 40 to 90 days following peak adult funnel-trap captures. Because the model can be used to forecast trends in spruce beetle populations and associated spruce mortality, it is a tool for forest planning.

Hansen EM, Bentz BJ, Turner DL. 2001. Modèle basé sur la température pour prédire la proportion des individus d'une couvée qui aura un cycle univoltin chez le Dendroctone de l'épinette (Coleoptera : Scolytidae). *The Canadian Entomologist* 133 : 827–841.

Résumé—Le Dendroctone de l'épinette, *Dendroctonus rufipennis* (Kirby), a un cycle biologique de 1 ou 2 ans. Des données empiriques et des résultats d'expériences laissent croire que la température est le principal facteur de contrôle du développement. Ces cycles différents peuvent donner lieu à des différences importantes dans la dynamique des populations et éventuellement dans la mortalité des épinettes. Une étude de plusieurs années en nature, en Utah, au Colorado et en Alaska, a permis de suivre le développement de l'insecte dans des conditions diverses; la température de l'air a été relevée en même temps que les données. Cette information a été utilisée pour créer un modèle pour évaluer la proportion des individus univoltins à l'échelle d'un arbre ou d'un boisé en fonction de la température de l'air. Les températures sont exprimées par des moyennes, des durées cumulatives et des unités de chaleur accumulées au-dessus de seuils spécifiques au cours de divers intervalles saisonniers. Des droites de régression mettent en relation les pourcentages d'insectes univoltins dans les échantillons et les températures résumées dans les modèles logistiques. La variable la plus prédictive, d'après le critère d'information d'Akaike, s'est avérée être le nombre cumulatif d'heures au-dessus d'un seuil de 17°C, de 40 à 90 jours après la capture maximale d'adultes dans des pièges à entonnoirs. Comme le modèle permet de prédire les tendances des populations de dendroctones et la mortalité des épinettes qui en dépend, il peut s'avérer utile en aménagement des forêts.

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¹ Author to whom all correspondence should be addressed (E-mail: matthansen@fs.fed.us).

Introduction

The spruce beetle, *Dendroctonus rufipennis* (Kirby) (Coleoptera: Scolytidae), is an important mortality agent of spruces, *Picea* spp. (Pinaceae), throughout its hosts' range in North America. In northwest Colorado, for example, spruce beetle outbreaks were found to be more important than other disturbances, including fire, in influencing the ecology of spruce forests (Veblen *et al.* 1994). Dramatic outbreaks have periodically killed extensive areas of mature spruce, including an event in Colorado from 1939 to 1951 that killed 3.8 billion board-feet of Engelmann spruce (Massey and Wygant 1954). Spruce forests in portions of Alaska and Utah were similarly affected during the 1990s (Holsten *et al.* 1999) and the potential exists for continued large outbreaks in other areas such as the Routt National Forest in Colorado (Schaupp *et al.* 1999).

Though a semivoltine life cycle is considered predominant throughout most of its range (Schmid and Frye 1977), the spruce beetle can also complete a generation in a single year if local conditions are relatively warm (Massey and Wygant 1954; Dyer 1969; Werner and Holsten 1985). These fluctuations have significant implications with respect to population dynamics and subsequent disturbance of spruce forests. Although the impact of univoltine brood on spruce forests remains to be quantified, exclusively univoltine populations can expand exponentially relative to semivoltine populations, assuming equivalent fecundity and brood survival. The course of spruce disturbance, however, can be altered even within a single beetle generation if a portion of the brood complete development in 1 year. For example, the extent of infestation can be magnified when beetles maturing in 1 year combine with beetles maturing in 2 years to infest new hosts (Dyer 1969). During the endemic population phase, such an occurrence could facilitate a population, which had previously only infested downed trees, to begin colonizing living trees, thereby dramatically increasing population numbers to the outbreak phase. Furthermore, an atypically warm summer or a warming climate could cause a shift from a predominantly 2- to a 1-year life cycle, again resulting in increased likelihood of epidemic-level beetle populations and accelerated spruce mortality. Anecdotal evidence suggests this to be the case on the Kenai peninsula in Alaska, where over 1 million hectares of spruce were recently infested (Holsten *et al.* 1999).

Temperature has repeatedly been shown to be highly correlated with spruce beetle voltinism (Massey and Wygant 1954; Dyer 1969, 1970; Dyer and Hall 1977; Werner and Holsten 1985). Werner and Holsten (1985) inferred that temperatures above a threshold of 16.5°C during the first and second instars are required for the univoltine cycle, although the required duration, if any, of such temperatures was not determined. Dyer and Hall (1977) hypothesized that temperatures below about 15°C during the third instar can induce hibernial diapause during instar IV, resulting in life cycles longer than 1 year. More recent evidence suggests that diapause is induced late in the growing season and that the effect of summer temperatures on early instar development, rather than diapause induction, determines life-cycle duration (Hansen *et al.* 2001). We hypothesize that spruce beetle voltinism can be satisfactorily modeled by quantifying the summer-temperature regime experienced by a given population.

The objective of this research was to characterize field temperatures associated with 1- versus 2-year life cycles. We present an air temperature-based model developed to forecast the proportion of univoltine beetles within our sampling areas. These predictions can potentially be used to forecast trends in beetle populations and spruce mortality, and to appropriately time suppression methods, such as sanitation harvesting. The proportion of beetles not predicted to be univoltine are assumed to be semivoltine. Although 3-year generations have been reported from high-elevation, north-aspect spruce stands (McCambridge and Knight 1972), we did not consider this cycle, because it

occurs infrequently, if ever (Schmid and Frye 1977), and 3-year beetles are unlikely to strongly influence population dynamics.

Materials and methods

Study areas

Eight sampling areas were established in 1997, 1998, and 1999 on the Dixie and Wasatch-Cache National Forests, Utah (Table 1). Because of the low proportions of univoltine beetles sampled at these areas, two areas were installed on Alaska's Kenai Peninsula in the year 2000, where, during the recent epidemic, 1-year broods predominated (E Holsten, USDA Forest Service, Pacific Northwest Station, Anchorage, Alaska, personal communication). Additionally, two areas on the Routt National Forest, Colorado, and one on the Dixie National Forest were included after it became apparent that the summer of 2000 was exceptionally warm in the central and southern Rocky Mountain regions.

Sampling areas were selected over a range of aspects and elevations, to potentially result in beetles of 1- or 2-year life cycles [*i.e.*, low elevation and (or) south aspect stands should have a higher proportion of univoltine beetles, owing to warmer temperatures]. The Utah and Colorado areas were composed of Engelmann spruce, *Picea engelmannii* Parry ex. Engelm., whereas one Alaska area was composed of Sitka spruce, *P. sitchensis* (Bong.) Carr., and the other of the Sitka – white spruce hybrid (*Picea* × *lutzii* Little).

Data collection

Ambient air temperatures were measured at 1.4 m above the ground, using a radiation-shielded temperature probe connected to a data micrologger (Campbell Scientific, Inc, Logan, Utah; Onset Corp, Bourne, Massachusetts). Radiation shields were placed on the north side of a tree, one per area. Temperatures were automatically measured every 2 min, then averaged and recorded hourly. Other factors determined at each area were physiographic class (draws/bottoms or ridges/slopes) and basal area (a surrogate for shading on bole surfaces).

Most sampling areas were established before or within 1 week of infestation, as determined from weekly inspections of trees in each area or gallery development. Consequently, these areas have a complete temperature record from June or July through October. Tippits, Floyd, and North Lake, however, were not established until August 2000, about 2 months after peak adult flight in these areas. To derive predictions for the missing intervals at Floyd and North Lake, post-installation measurements were compared with temperature records from the two closest SNOTEL stations (a network of mountain weather stations, SNOWpack TELelemetry is operated by the USDA Natural Resources Conservation Service at <http://www.wcc.nrcs.usda.gov/snotel>). Predictions for Tippits were derived from a combination of a SNOTEL station and a nearby data logger (Sunset). Because hourly recordings were incomplete for the SNOTEL stations selected, we fit a sine-wave curve to the daily maxima and minima, to estimate hourly readings at each SNOTEL station. Predictions were made using mixed models with repeated measures (PROC MIXED; SAS, version 8.1, SAS Institute Inc, Cary, North Carolina), and predictor variables included the hourly SNOTEL temperature estimates, hour of day, and the two-way interactions. An autoregressive, AR(1), covariance structure was specified to account for autocorrelation of the residuals (Littell *et al.* 1996). Although the resulting model predictions for the overlapping intervals closely match the observed values (Fig. 1), we acknowledge that there are unknown errors for the

TABLE 1. Description of sampling areas.

| Area name | Year | Location | Latitude (°N) | Longitude (°W) | Elevation (m) | Basal area (m ² /ha) | Aspect* | Trees sampled |
|------------|------|---------------------------------|------------------|-------------------|------------------|------------------------------------|---------|------------------|
| Archery | 1997 | Dixie National Forest, Utah | 37.583 | 112.900 | 2860 | 65 | NW | 5 |
| Northview | 1997 | Dixie National Forest, Utah | 37.667 | 112.867 | 3170 | 80 | Level | 6 |
| Roundup | 1997 | Cache National Forest, Utah | 41.583 | 111.450 | 2650 | 60 | North | 5 |
| Pond | 1997 | Cache National Forest, Utah | 41.617 | 111.467 | 2560 | 45 | South | 5 |
| Kearl | 1998 | Cache National Forest, Utah | 41.617 | 111.450 | 2590 | 40 | Level | 2 |
| Roundup | 1998 | Cache National Forest, Utah | 41.583 | 111.450 | 2620 | 50 | SW | 3 |
| Hancock | 1999 | Dixie National Forest, Utah | 37.633 | 112.750 | 2930 | 35 | Level | 1 |
| Quarry | 1999 | Dixie National Forest, Utah | 37.667 | 112.733 | 2900 | 70 | Level | 3 |
| Tippits | 2000 | Dixie National Forest, Utah | 37.567 | 112.800 | 2960 | 35 | Level | 3 |
| Sunset | 2000 | Dixie National Forest, Utah | 37.617 | 112.850 | 3140 | 65 | Level | 2 |
| Primrose | 2000 | Dixie National Forest, Alaska | 60.500 | 149.333 | 210 | 30 | Level | 4 |
| Centennial | 2000 | Kenai Wildlife Refuge, Alaska | 60.373 | 151.150 | 60 | 30 | Level | 4 |
| North Lake | 2000 | Routt National Forest, Colorado | 40.750 | 106.600 | 2530 | 40 | Level | 4 |
| Floyd | 2000 | Routt National Forest, Colorado | 40.667 | 106.667 | 2740 | 50 | West | 4 |

* Aspect was considered level if the slope was less than 10%.

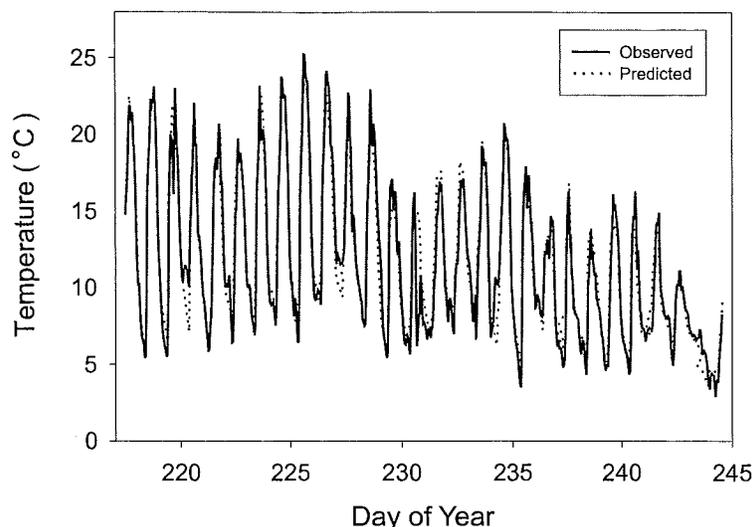


FIGURE 1. Comparison of hourly temperature observations and predictions at Tippits (prediction only interval, before installation of data logger, not shown). Model fit is comparable for North Lake and Floyd.

prediction intervals. The temperature records used in the model for these three areas are a composite of the predicted values and actual measurements. Records for all other areas are actual measurements, not predictions.

All infested spruce within 25 m of the air probe were sampled. The response variable, proportion of univoltine beetles, was determined from samples taken at the end of the growing season: late September for the Alaska areas and October for the Utah and Colorado areas (biweekly sampling from shortly after infestation through late October in 1997 and 1998 revealed no detectable development after this time). To capture aspect and height differences due to solar radiation and potential temperature inversions, trees were sampled at six locations: the north and south bole sides at ground level and at 1.8 and 4.6 m above ground level. Samples consisted of extracting a 100-cm² circular bark section at each of the six height-by-aspect combinations and removing all spruce beetle life stages therein. Any brood advancing to the teneral adult stage by fall were considered to have a 1-year life cycle, whereas larval-stage brood were considered to have a 2-year life cycle. The proportion of univoltine beetles in a sample was derived by dividing the number of teneral adults by the total brood. Sampling at one of the Alaska areas, Centennial, was partially confounded, because our late September samples missed a portion of the univoltine brood that had emerged from the upper bole to hibernate (univoltine hibernators did not significantly bias the Utah and Colorado samples, where less than 1% of univoltine beetles have been observed to hibernate; M Hansen, unpublished data). For some samples at Centennial, we counted pupal chambers with exit holes as representing univoltine individuals, and three samples were deleted where we could not confidently ascertain the univoltine proportion.

We also needed a standard for initializing brood development at each sampling area. Date of peak flight was used as a starting point for examining the temperature record for each area. This was determined from baited funnel trap (Pherotech, Inc, Delta, British Columbia) captures observed weekly at or near each area. Field observations indicate about 1–2 weeks of gallery establishment before oviposition begins; therefore, we allowed 10 days following date of peak trap captures before analyzing temperatures.

Model development

Air-temperature data from each area were summarized as accumulated degree hours and cumulative hours above various thresholds. Also, averages of the hourly recordings were calculated. These summaries were computed over different intervals, ranging from 10 to 90 days after peak-flight date in 10-day increments. Among the summaries examined were values approximating previously described temperature thresholds for univoltine spruce beetles (see Dyer 1969; Dyer and Hall 1977; Werner and Holsten 1985). About 120 sets of summarized values were evaluated graphically against the proportion of univoltine beetles per area. From these, 34 variables were further tested for strength of correlation with the response variable, transformed to logit scale, in a linear regression model (Table 2). Each observation was adjusted by the fixed effects of sample height and aspect on the bole, to determine the partial correlation coefficient of the summarized temperature variable. Other factors evaluated for univoltine predictive value included (1) basal area of the sampling area, (2) day of year peak flight, and (3) physiographic class.

Next, we used GLIMMIX (a SAS macro for fitting generalized linear mixed models; 20 September 2000 release; SAS Institute Inc), to accommodate the random effects (blocks) of area and tree within area in a logistic regression model. Error distribution was specified as binomial (univoltine brood in the numerator; total brood in the denominator). The covariance structure for tree within area was specified as heterogenous compound symmetric (Littell *et al.* 1996). Nine temperature summaries were selected from the linear regressions described above based on the partial correlation coefficients, previously published threshold values, or ease of summary calculation. Each model run used the summarized air temperature as a continuous variable, whereas sample height and aspect were included as fixed effects. These mixed effects plus the two-way interactions were included in the full model for each air-temperature variable tested:

$$\text{Logit}_{ij} = \text{Temp} + \text{Ht} + \text{Aspect} + (\text{Temp} \times \text{Ht}) + (\text{Temp} \times \text{Aspect}) \\ + (\text{Ht} \times \text{Aspect}) \quad [1]$$

where Logit is the logit scale proportion of univoltine beetles (logit, or log odds, is calculated as $\log_e[\pi/(1 - \pi)]$ for each aspect (*i*) by height (*j*) combination; π is the proportion of univoltine beetles); Temp is the summarized air-temperature variable; Aspect is the tree-bole aspect; and Ht is the tree bole sample height. Backward elimination was used to simplify the models [significance-level-to-stay: $\alpha = 0.05$]. Three- and four-way interactions were tested but were either not significant or models with these terms did not converge after 50 iterations. Further backward elimination was done using Akaike's Information Criterion (AIC), which balances the trade-off between under- and over-fitted models by adding a penalty for the number of model parameters to the loglikelihood value, with smaller values indicating better fit (Burnham and Anderson 1998). The lowest AIC value, indicating an optimal compromise between model parsimony and fit, was used to select the final model. Finally, bootstrap methods were used to evaluate the stability and bias of the parameter estimates (Efron and Tibshirani 1993). Over 5500 bootstrap samples were taken, to calculate the 90% confidence limits of the coefficients.

Voltinism estimates for a population

The above model predicts univoltine proportions specific to a single aspect-by-height bole-sample location. Estimation of voltinism at the tree (or stand) population level was accomplished by weighting the height by aspect-specific predictions according to the amount of habitat represented by each location. North- and south-aspect

TABLE 2. Summarized air-temperature variables tested in regression models predicting the proportion (logit scale) of univoltine *Dendroctonus rufipennis*.

| Variable name | Variable definition | Partial correlation coefficient |
|-------------------------------|---|---------------------------------|
| H₁₇[40-80] | Hours above 17°C, 40-80 days after peak flight | 0.7439 |
| H₁₇[40-90] | Hours above 17°C, 40-90 days after peak flight | 0.7383 |
| DH₁₁[40-80] | Degree hours above 11°C, 40-80 days after peak flight | 0.7379 |
| H₁₆[40-80] | Hours above 16°C, 40-80 d days after peak flight | 0.7375 |
| DH₁₀[40-80] | Degree hours above 10°C, 40-80 days after peak flight | 0.7340 |
| H₁₆[40-90] | Hours above 16°C, 40-90 days after peak flight | 0.7339 |
| H₁₅[30-90] | Hours above 15°C, 30-90 days after peak flight | 0.7311 |
| DH ₁₁ [40-90] | Degree hours above 11°C, 40-90 days after peak flight | 0.7291 |
| H ₁₅ [30-80] | Hours above 15°C, 30-80 days after peak flight | 0.7289 |
| DH ₁₂ [40-90] | Degree hours above 12°C, 40-90 days after peak flight | 0.7287 |
| DH ₁₁ [30-90] | Degree hours above 11°C, 30-90 days after peak flight | 0.7274 |
| DH ₉ [40-80] | Degree hours above 9°C, 40-80 days after peak flight | 0.7272 |
| DH ₁₀ [40-90] | Degree hours above 10°C, 40-90 days after peak flight | 0.7260 |
| DH ₁₂ [30-90] | Degree hours above 12°C, 30-90 days after peak flight | 0.7257 |
| H ₁₅ [40-90] | Hours above 15°C, 40-90 days after peak flight | 0.7253 |
| DH ₁₀ [30-90] | Degree hours above 10°C, 30-90 days after peak flight | 0.7252 |
| DH ₁₄ [40-90] | Degree hours above 14°C, 40-90 days after peak flight | 0.7208 |
| DH ₉ [40-90] | Degree hours above 9°C, 40-90 days after peak flight | 0.7198 |
| DH ₉ [30-90] | Degree hours above 9°C, 30-90 days after peak flight | 0.7191 |
| H ₁₄ [30-90] | Hours above 14°C, 30-90 days after peak flight | 0.7161 |
| DH ₁₂ [20-80] | Degree hours above 12°C, 20-80 days after peak flight | 0.7137 |
| DH ₆ [40-90] | Degree hours above 6°C, 40 to 90 days after peak flight | 0.6924 |
| DH₆[30-90] | Degree hours above 6°C, 30 to 90 days after peak flight | 0.6875 |
| AVG₄₀₋₈₀ | Average temperature, 40-80 days after peak flight | 0.6841 |
| DH ₅ [30-90] | Degree hours above 5°C, 30-90 days after peak flight | 0.6797 |
| AVG ₃₀₋₈₀ | Average temperature, 30-80 days after peak flight | 0.6673 |
| AVG ₄₀₋₉₀ | Average temperature, 40-90 days after peak flight | 0.6657 |
| AVG ₃₀₋₉₀ | Average temperature, 30-90 days after peak flight | 0.6602 |
| AVG ₄₀₋₇₀ | Average temperature, 40 to 70 days after peak flight | 0.6532 |
| H ₁₂ [40-90] | Hours above 12°C, 40 to 90 days after peak flight | 0.6388 |
| H ₁₂ [30-90] | Hours above 12°C, 30 to 90 days after peak flight | 0.6323 |
| H ₁₄ [40-90] | Hours above 14°C, 40 to 90 days after peak flight | 0.4720 |

NOTE: Partial correlation coefficients are adjusted for sample height, aspect, height-by-aspect interaction, and physiographic class. Variables listed in boldface type were selected for use in random-effects mixed models (see Table 3).

sections were each considered to represent one-half of tree circumference. The ground level sample location was considered to represent the vertical distance from the ground to 0.9 m; the 1.8 m sample location from 0.9 to 3.5 m; and the 4.6 m sample location from 3.5 to 12.2 m, the typical upper bole limit of spruce beetle infestation (Schmid and Frye 1977). Diameters at the top and bottom of each vertical section were estimated using the taper function for white spruce, *Picea glauca* (Moench) Voss, given by Newnham (1992) and calculations were made assuming a tree of 51-cm diameter at breast height and 27.4-m total height (a typical-sized Engelmann spruce in infested areas). Estimated habitat surface areas were calculated using the equation for a frustum of a cone lateral surface area (Husch *et al.* 1982). The resulting estimates of habitat area within a tree, north or south, are 0.96 m² at ground level, 2.12 m² at 1.8 m, and 6.67 m² at

4.6 m. The density of surviving brood is assumed equal at all six aspect-by-height combinations. Although attack density is higher on the lower bole (Schmid and Frye 1977), our field observations indicate that intraspecific competition results in roughly equivalent brood density throughout at least the lower 5 m of bole.

Results

Voltinism model

The best model, as judged by AIC, uses cumulative hours above a threshold of 17°C from 40 to 90 days subsequent to peak flight (Table 3). This model also includes the fixed effects of height, aspect, and physiographic class. The equation for predicted logit of univoltine proportion is

$$\text{Logit}_{ij} = -3.9540 + (0.01944 \times \text{HR}_{17[40-90]}) - 1.0350 \times N + 0.5120 \times H \\ - 1.8821 \times L - 1.2941 \times D \quad [2]$$

where $\text{HR}_{17[40-90]}$ is cumulative hours above 17°C from 40 to 90 days subsequent to peak flight; $N = 1$ if aspect is north, 0 otherwise; $H = 1$ if height is 4.6 m, 0 otherwise; $L = 1$ if height is ground level, 0 otherwise; and $D = 1$ if physiographic class is draw/bottom, 0 otherwise (Table 4). Basal area was a significant variable but was eliminated from the model using the minimum AIC rule. The predicted logits can be back-transformed into the original scale with the equation:

$$\pi_{ij} = 1 / (1 + e^{-\text{logit}}) \quad [3]$$

where π_{ij} is the predicted proportion of univoltine beetles for each aspect (i) by height (j) combination.

Calculating a loglikelihood-based generalized R^2 , such as proposed by Nagelkerke (1991), for our model is confounded because the output from GLIMMIX is not interpretable for this purpose. Omitting the random effects of area and tree within area, however, we estimated $R^2_{\text{adj}} = 0.5999$, using a linear regression model where the dependent variable is in logit scale. Perhaps the best indicator of model fit is graphically summarized by comparing the 95% prediction intervals with the observations (Figs. 2, 3). The covariance parameter estimate for the random effect of area indicates little variability among areas not explained by the model ($Z = 0.95$; $P|Z| = 0.171$); however, there was variability among trees within areas ($Z = 2.85$; $P|Z| = 0.002$).

From the bootstrap-derived confidence limits, most parameter estimates are acceptably stable. The temperature variable, $\text{HR}_{17[40-90]}$, was particularly stable during the 5500 bootstrap samples (Table 4). The coefficient that displayed the greatest instability was that associated with the 4.6-m sample height. Although samples at 4.6 m generally had higher proportions of univoltine beetles than those at 1.8 m, there is a considerable degree of uncertainty regarding the magnitude (*i.e.*, there is substantial variability in the additional univoltine proportions at 4.6 m).

Voltinism estimates for a population

From the estimated habitat surface areas, the sample locations, north or south, were calculated to represent the following proportions of habitat per tree: Low 5%; Medium 11%; and High 34%. Hence, voltinism for an entire tree is derived by weighting the predicted proportions by the habitat surface proportions:

TABLE 3. Significant ($\alpha = 0.05$) variables in mixed-effects logistic models predicting the proportion of univoltine *Dendroctonus rufipennis* from air temperature.

| Temperature variable* | Significant fixed effects and interactions | AIC difference [†] |
|-------------------------|--|-----------------------------|
| H _{17[40-90]} | Aspect, height, physiographic class | — |
| H _{16[40-90]} | Aspect, height, physiographic class | 3.1 |
| H _{17[40-80]} | Aspect, height, physiographic class | 4.3 |
| H _{15[30-90]} | Aspect, height, physiographic class | 7.1 |
| DH _{11[40-80]} | Aspect, height | 12.0 |
| H _{15[30-90]} | Aspect, height | 12.2 |
| DH _{11[40-80]} | Aspect, height, physiographic class | 16.7 |
| DH _{10[40-80]} | Aspect, height | 20.9 |
| DH _{6[30-90]} | Aspect, height, physiographic class, DH _{6[30-90]} × height | 63.4 |
| Avg _{4[40-80]} | Aspect, height, physiographic class, aspect × height | 71.1 |

* Definitions of variables are given in Table 2.

[†] AIC is the loglikelihood value with a penalty for the numbers of model parameters (AIC = $-2 \log \text{likelihood} + 2K$) (Burnham and Anderson 1998). Models are ranked by AIC differences, where $\Delta_i = \text{AIC}_i - \text{minimum AIC}$.

$$\pi_{\text{Tree}} = 0.34(\pi_{\text{NH}}) + 0.34(\pi_{\text{SH}}) + 0.11(\pi_{\text{NM}}) + 0.11(\pi_{\text{SM}}) \\ + 0.05(\pi_{\text{NL}}) + 0.05(\pi_{\text{SL}}) \quad [4]$$

where π_{ij} is the aspect (i) by height (j) predicted proportion of univoltine beetles. Because a single tree represents a sample from a stand, the same proportions apply to voltinism predictions for the stand-level population. The breadth of inference should be based on the input air-temperature values, which, for this model, are assumed to be at the stand level.

Discussion

Our model can be used to forecast stand-level proportions of univoltine spruce beetle brood based on air temperature. The model was built from four geographically distinct areas, and bootstrap methods demonstrated acceptable stability of the parameter coefficients despite the diversity of sampling areas. Although validation is needed, we suspect that the model will perform satisfactorily throughout western North America. Despite the possibility of brood in some individual trees being not well predicted by the model, height by aspect-specific predictions for a stand should be accurate within a 10–20% margin of error (Figs. 2, 3).

Effect of temperature

Temperature has been linked to spruce beetle voltinism, yet we found no specific threshold that was distinctly superior in predicting the probability of univoltine samples, including previously reported values (see Dyer *et al.* 1968; Dyer and Hall 1977; Werner and Holsten 1985). Indeed, most temperature variables tested were roughly equivalent in terms of the partial correlation coefficient of the logit-scale univoltine proportions (Table 2). This may be an artifact of the high degree of correlation among the variables, all of which were derived from the same temperature records. Conversely, timing of the thermal input appears critical, because most of the best-fitting variables are based on the temperature record ranging from 30 to 90 days after peak flight. Temperature summaries based on the entire interval (10–90 days after peak flight) or only on some early

TABLE 4. Parameter estimates for the mixed logistic regression model predicting the logit of univoltine *Dendroctonus rufipennis* based on cumulative hours above 17°C from 40 to 90 days subsequent to peak flight ($H_{17[40-90]}$).

| Effect | Bole aspect | Bole height | Physiographic class | Estimate | SE | P _{adj} | 5th percentile | 95th percentile |
|---------------------|-------------|-------------|---------------------|----------|--------|------------------|----------------|-----------------|
| Intercept | | | | -3.7856 | 0.3686 | <0.0001 | -4.5433 | -3.6241 |
| $H_{17[40-90]}$ | | | | 0.0192 | 0.0017 | <0.0001 | 0.0186 | 0.0228 |
| Bole aspect | North | | | -1.0387 | 0.1502 | <0.0001 | -1.5553 | -0.7302 |
| | South | | | 0.0000 | — | — | — | — |
| Bole height | | 4.6 m | | 0.5095 | 0.1616 | 0.0018 | 0.1114 | 0.9114 |
| | | Ground | | -1.8776 | 0.2021 | <0.0001 | -2.7107 | -1.3971 |
| | | 1.8 m | | 0.0000 | — | — | — | — |
| Physiographic class | | | Draw | -1.1923 | 0.3323 | 0.0008 | -1.6541 | -0.9416 |
| | | | Ridge | 0.0000 | — | — | — | — |

NOTE: The coefficient confidence limits, which reflect data variability and coefficient stability, are calculated from the distribution of 5518 bootstrap samples. The bootstrap confidence limits do not necessarily equal the parameter estimates ± 2 SE, which are derived from the mixed logistic regression model (full data set).

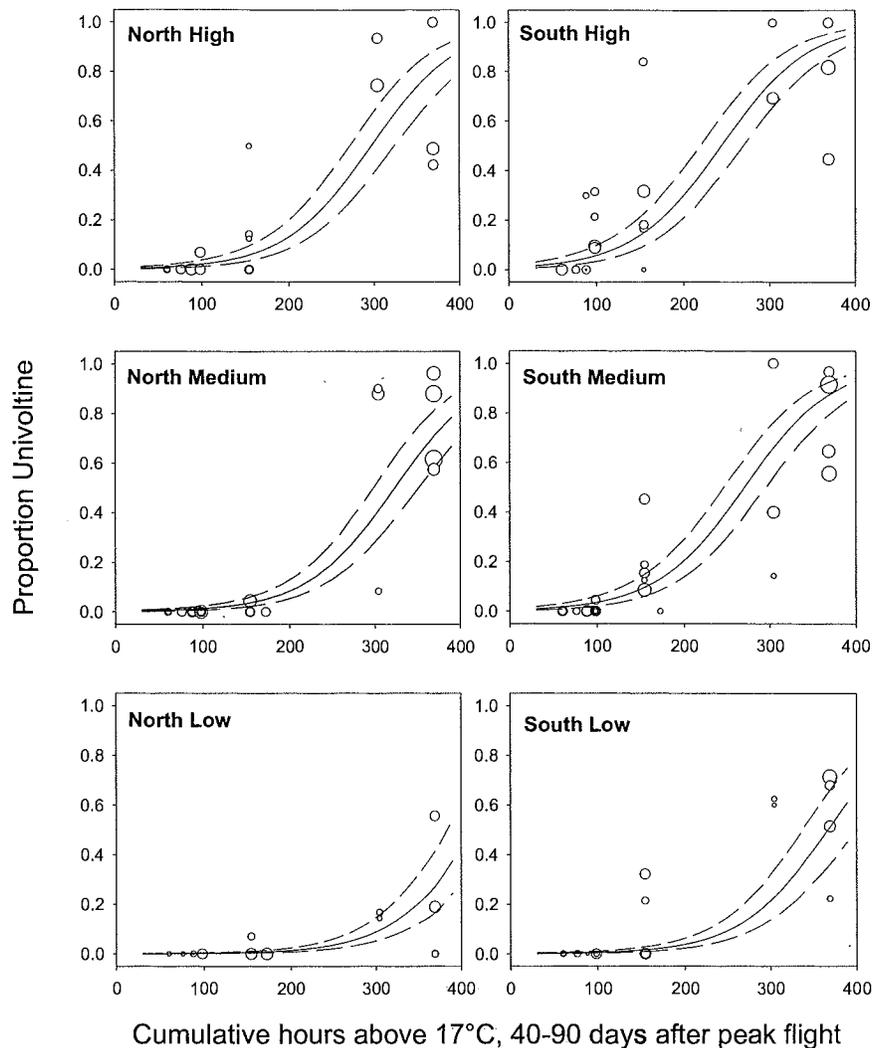


FIGURE 2. Comparison of observed univoltine proportions (open circles) and model prediction interval (with 95% confidence band) for bottom/draws. Circle area is proportional to the number of beetles in each sample.

portion of the interval (*e.g.*, 10–50 days after peak flight) were noticeably less strongly correlated with the response variable.

Microhabitat-temperature surrogate

Although air temperature is a gross indicator of the microhabitat conditions of bark beetles, ancillary factors can be combined with air temperature to serve as a surrogate for the subcortical environment. Bole aspect was consistently significant in model runs and substantially improved the accuracy of our predictions, regardless of the temperature variable used. Clearly, south-bole aspects respond differently from north-bole aspects because of solar radiation variances. Likewise, sample height was consistently

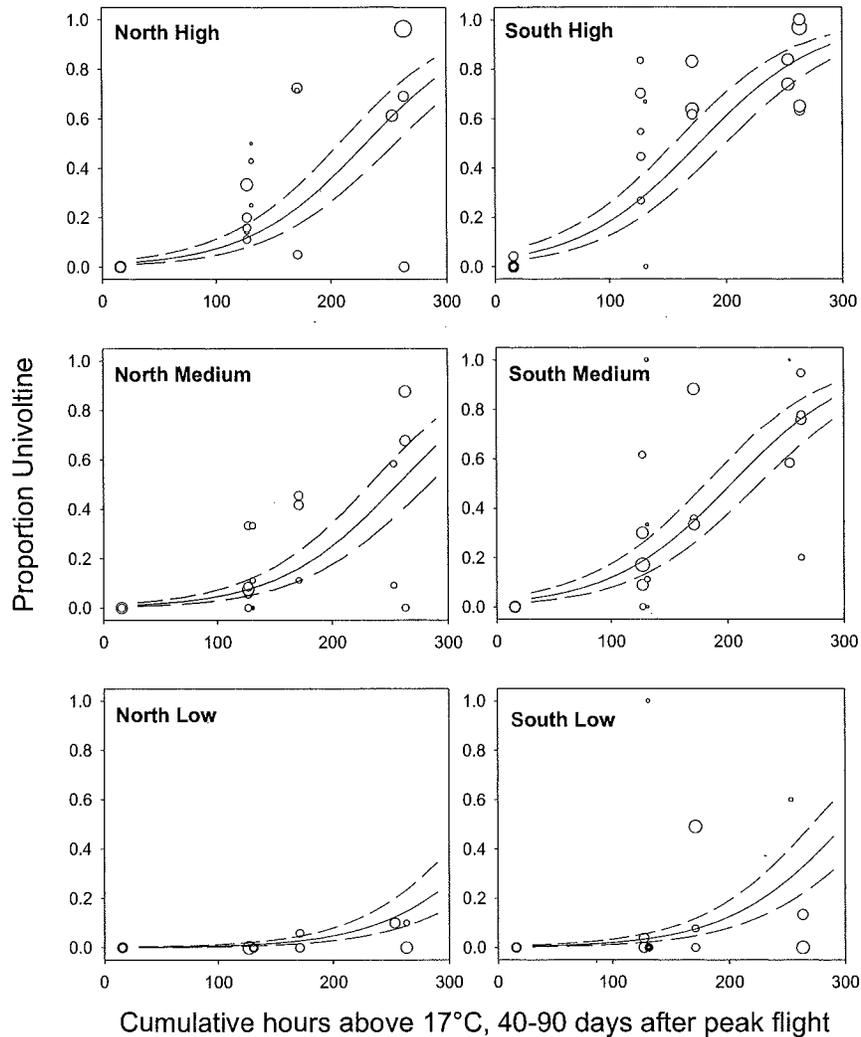


FIGURE 3. Comparison of observed univoltine proportions (open circles) and model prediction interval (with 95% confidence band) for ridges/slopes. Circle area is proportional to the number of beetles in each sample.

important, apparently owing to nighttime inversions that cool the lower bole much more than the upper bole.

Because cool air sinks, physiography can influence local temperature regimes. Draws and bottoms generally experience cooler overnight lows even as daytime highs may equal or exceed those on nearby slopes and ridges. Dyer (1969) found substantially fewer univoltine beetles at valley bottom sites compared with a nearby slope. Our model results indicate that sampling areas in draws and bottoms had fewer univoltine beetles, despite similar elapsed time above threshold values. Conceivably, the cooler nighttime conditions in bottoms and draws cool the thermal mass of boles more than on slopes and ridges. Consequently, equivalent daytime heating of the air in both physiographic categories probably does not result in equivalent microhabitat temperatures.

TABLE 5. Cumulative air-temperature hours above 17°C, elapsed from 40 to 90 days after peak flight, associated with estimated proportions of univoltine *Dendroctonus rufipennis* at the tree (or stand) population level.

| Physiographic class | % univoltine beetles | | | |
|---------------------|----------------------|-----|-----|-----|
| | 1 | 25 | 50 | 75 |
| Draw/bottom | 40 | 225 | 285 | 350 |
| Slope/ridge | 0 | 155 | 220 | 285 |

NOTE: Cumulative-hour values are derived from iterations of Equations [2] – [4].

Error sources

Plots of the residuals revealed two explainable categories of outliers (as well as unexplainable outliers). The first type of outlier consists of observations on south-bole aspects where shading on an individual tree was reduced relative to other trees in the sampling area. Predictably, because of increased solar radiation, the observed proportions of univoltine beetles for these samples were higher than the corresponding predictions. South-aspect samples tended to be more variable than north-aspect samples. Even if a reasonable measure of this tree-level effect could be made, it would not be of value, because the objective of this model is to predict voltinism on a stand level. The second type of outlier consists of observations where few or no univoltine brood were sampled, despite nearby analogous samples on trees that contained predominantly univoltine brood. At two sampling areas, all six samples on a tree had lower proportions of adults than analogous samples on the other trees within the same area. We suspect that these two trees were infested many days, or even weeks, after the other nearby trees. Although adult flight typically has a discernible peak, the attack period for a specific site can last 5–6 weeks (Schmid and Frye 1977). Moreover, re-emerged females may construct a second brood gallery on the same or another host (Schmid and Frye 1977). Thus, a significant source of fluctuation is represented by the fact that timing of peak flight, as measured by pheromone traps, is only loosely linked to infestation timing of an *individual* host. To the extent that our samples represent the variability of infestation timing found at the stand level, however, we believe that this variation does not diminish the utility of our model.

Using the model

Pheromone-baited traps are effective for catching spruce beetles (Werner and Holsten 1995) and are routinely used to monitor flight periodicity. Deployment of air-temperature data loggers in areas with baited traps will allow use of the model to forecast univoltine brood proportions. Cumulative hours above 17°C, elapsed from 40 to 90 days following peak flight, and physiographic class are input into Equation [2] and the resulting six aspect by height specific-logits are back-transformed using Equation [3]. Stand (or other area represented by the air thermometer) voltinism is derived using Equation [4]. Alternatively, a lower level of resolution is adequate for most applications and has the added benefit of reducing the effect of potential errors associated with the model. For example, entomologists and managers may only need to know if brood in an infested stand is primarily semivoltine (*e.g.*, <1% univoltine), mostly semivoltine (1–25% univoltine), majority semivoltine (25–50% univoltine), majority univoltine (50–75%), or mostly univoltine (>75%) (Table 5). A stand in a draw/bottom, for example, with 120 h above 17°C should have mostly semivoltine beetles. Such information could be interpreted to indicate only a small risk of accelerated spruce mortality due to univoltine broods. Our samples do not permit an estimate of the heat input required to

result in primarily univoltine beetles at the tree level and, in fact, we suspect that this level may be unattainable. Spruce forests rarely, if ever, experience temperatures warm enough to result in a preponderance of univoltine brood at the ground level portion of the bole, especially on north-bole aspects (Figs. 2, 3).

Knowledge of spruce beetle life cycles are critical for timely management action, and our model can potentially be used to produce landscape-scale forecasts from remotely sensed weather data. Forest entomologists generally assume the semivoltine life cycle in the Rocky Mountains (Schmid and Frye 1977), but this is not appropriate under certain localized conditions. The time frame for management action is clearly much shorter if any significant proportion of the brood complete development in 1 year. Furthermore, year-to-year climatic variability can potentially result in occasional univoltine broods in areas that typically have semivoltine broods.

Because the trend in local spruce beetle population, which is partially a function of univoltine brood proportions, has been identified as a significant factor in determining the risk of a spruce beetle outbreak (Reynolds and Holsten 1994), our model can be used to help assess outbreak risk. Furthermore, because spruce beetle population size and infested-tree density appear to be related to the proportion of univoltine brood (Safranyik *et al.* 1990), our model can be used to evaluate the rate of spruce forest disturbance. The model also represents a tool for assessing the effects of global climate change on spruce beetle dynamics and, consequently, disturbance of spruce ecosystems.

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