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SHORT COMMUNICATION

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An ordinal day model of spruce beetle trap capture phenology in northern Colorado

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Abstract

Spruce beetle populations (*Dendroctonus rufipennis*) (Coleoptera: Scolytinae) in Engelmann spruce (*Picea engelmannii*) stands were monitored at twelve sites for 6 years in northern Colorado using pheromone-baited Lindgren funnel traps. During the trapping period, over 30,000 beetles were captured, and beetle abundance data were used to construct empirical models of trap capture phenology based on day of year, accumulation of thermal units and thermal day thresholds, with the goal of informing future regional trapping efforts and producing a simple model for use by forest managers. Ordinal day models outperformed thermal accumulation and thermal threshold models in both predictive power and parsimony. Mean date of earliest capture was Day 153 (June 2) and ranged from Day 126 to Day 161 (May 6–June 10), and mean date of final capture was Day 243 (August 31) and ranged from Day 220 to Day 286 (August 8–October 13). A two-parameter logistic function was the most parsimonious of several ordinal day models, accounting for 81% of the variance in cumulative trap capture across all sites and dates. The model predicts 50% of trap captures to occur by Day 181 (June 30). This model has application as a decision support tool for forest ecosystem managers concerned with the timing of trap deployment or *D. rufipennis* mitigation treatments.

KEYWORDS
bark beetle, flight period, integrated pest management, pheromones

1 | INTRODUCTION

Bark beetle (Coleoptera: Scolytinae) population activity is a constant management concern in the temperate, coniferous forests of North America—high-density beetle populations impact forest ecosystem functions including carbon fixation (Kurz et al., 2008), nutrient cycling (Edburg et al., 2012), hydrological yields (Mikkelson et al., 2013) and fire return intervals (Jenkins, Hebertson, Page, & Jorgensen, 2008). In the Rocky Mountain region of Colorado, both endemic and epidemic spruce beetle (*Dendroctonus rufipennis* Kirby) activity has affected an estimated 14 million spruce trees during the previous decade (Harris, 2016), and *D. rufipennis* has remained a primary biotic agent of tree mortality in high-elevation spruce (*Picea engelmannii* Parry ex Engelm.) forests for at least a century (Morris et al., 2015; Veblen, Hadley, Reid, & Rebertus, 1991). Despite repeated forest disturbance from *D. rufipennis* in Colorado (Eisenhart & Veblen, 2000; Kulakowski & Veblen, 2006) and ongoing research into the life history parameters of this insect (Hansen, Barbara, James, Gray, & Vandrygriff, 2011; Hansen & Bentz, 2003; Hansen, Bentz, & Turner, 2001), there are few reports in the literature from which to make regional projections about timing of pheromone trap deployment (but see Schaupp & Frank, 2000). Pheromone-baited traps are an important tool in the integrated management of *D. rufipennis*, and are an effective means of monitoring population abundances and potential biotic pressure from pest insects in general (Borden, 1989; Schlyter, Zhang, Liu, & Lan-Zhu, 2001; Witzgall, Kirsch, & Cork, 2010); however, the efficiency of trapping programs can be optimized by developing empirical models based on regional trap capture data.

Although models based on physiological requirements and thermal thresholds are accurate (e.g., Knutson & Muegge, 2010; Reding, Ranger, Oliver, & Schultz, 2013), these models can be more challenging to use than models based on easily interpreted and acquired metrics such as day of year (i.e., ordinal date). Thus, there is a need to develop models which are both accurate but also accessible and useful to managers, with little potential for user error. Here, this is addressed using beetle abundance data derived from a multiyear trapping study to develop a model of trap capture phenology. Models were constructed using both ordinal day (i.e., day of year) and thermal variables (degree-day accumulations and counts of days exceeding biologically relevant temperature thresholds). The models derived here can be used to inform the timing of trap placement for *D. rufipennis* captures in northern Colorado, and develop simple predictions about region-specific beetle populations.

2 | MATERIALS AND METHODS

2.1 | Spruce beetle trapping

Twelve trapping sites were established in Engelmann spruce-dominated stands in the Medicine Bow–Routt National Forest (Table S1), and traps were serviced at weekly or biweekly intervals between May 1 and November 1 from 2000 to 2005 (n = 6 years). The minimum distance between trapping locations was <2.0 km. Traps consisted of 16-unit Lindgren funnel traps (Lindgren, 1983) hung on conduit poles at a height of 1 m from the base of the collection cup to the ground surface and baited with standard *D. rufipennis* pheromone lures containing frontalin (release rate: 5 mg/day; Dyer, 1973) and the host kairomone α-pinene (release rate: 150 mg/day; PheroTech International, Inc., British Colombia). Lures were not changed during yearly collection periods and remained effective for capturing beetles well into fall, indicating that elution rates did not decline below a level suitable for attraction. Collection cups were supplied with pesticide strips (Vaportape™, Hercon Environmental, Emigsville, PA) to ensure that sample loss did not result due to predation or beetle escape. Two funnel traps were placed at each trapping site, and capture values were summed at each site to yield abundances of flying beetles orienting to baited traps per week. In total, there were 547 collection days over the period of study, with a total of four instances of trap loss (0.7% of collections).

2.2 | Statistical analysis

Beetle collections at each site were converted to cumulative capture (per cent of total), such that a trap capture accumulation curve was developed at each location for each year (i.e., for each site × year combination). Three different predictors were considered individually in separate models: (1) ordinal day (day of year), (2) accumulation of thermal units (degree days) and (3) tallies of days exceeding temperature thresholds. Surface meteorological data in the form of maximum daily temperature were acquired at a resolution of 1 km using the Daymet model (Thornton et al., 2016) and used to calculate accumulated degree days and tally number of days exceeding thermal thresholds, using base temperatures of 10°C, 13°C, 15°C and 16°C for each collection date (Holsten & Hard, 2001; Pruess, 1983; Safranyik & Linton, 1987). These base temperatures are consistent with previously reported thresholds for 1- or 2-year life cycles (i.e., 10–16°C; Werner & Holsten, 1985). It should be noted that our model uses air temperatures, but beetles likely experience more stable thermal conditions in the subcortical phloem environment.

Cumulative trap capture data are often modelled as sigmoid functions to account for the accumulation of sampled insects over time (e.g., Broatch, Dosdall, Clayton, Harker, & Yang, 2006; Jones et al., 2016; Jyoti, Shelton, & Barnard, 2003; Riedl, Croft, & Howitt, 1976); here, multiple candidate sigmoid models based on logistic and Gompertz functions were compared for each possible predictor. Cumulative trap capture data were modelled using two-, three- and four-parameter logistic and three- and four-parameter Gompertz functions. As an estimate of model accuracy, observed trap capture values were fitted against predicted values generated by model results. Trap capture data were fitted to candidate models in a regression framework using the statistical software JMP 12.0 (SAS Institute, Cary, NC), incorporating trapping site and year as random effects. The most parsimonious model was selected by minimizing Akaike's information criteria score (Akaike, 1974). Statistical significance for a regression of observed values on predicted values was established using a type I error rate of $\alpha = 0.05$.

3 | RESULTS AND DISCUSSION

During the period of record, a total of 32,695 *D. rufipennis* adults were captured in pheromone-baited Lindgren funnel traps. On average, 5,443 ± 516 SE *D. rufipennis* were caught each year, and ranged from 4,019 to 7,318 individuals. *Dendroctonus rufipennis* trap capture phenology varied from year to year; mean date of earliest capture was Day 153 ± 5 SE (June 2) and ranged from Day 126 to Day 161 (May 6–June 10), and mean date of final capture was Day 243 ± 10 SE (August 31) and ranged from Day 220 to Day 286 (August 8–October 13). The mean date of 50% trap catch was Day 174 ± 4 SE (June 20), and ranged from Day 150 to Day 202 (May 30–July 21). This range of trapping dates indicates that there may be considerable variation in the timing of *D. rufipennis* response to pheromone sources in northern Colorado. The extent to which this variability is mediated by microsite conditions, local weather patterns, beetle life cycle duration or site-specific beetle abundances remains unknown, but these potential sources of variation may be important for further understanding the biology of *D. rufipennis*.

All candidate models had similar coefficients of determination and root-mean-square errors (RMSE); however, the most predictive and parsimonious model overall was a two-parameter logistic model (1) based on ordinal day (Table 1A).

$$\text{Percentage of spruce beetle trap capture} = \frac{1}{(1 + \exp(-a * (\text{ordinal day} - b)))} \quad (1)$$

TABLE 1 (A) Parameter estimates for the most parsimonious model, based on ordinal day, of spruce beetle (*Dendroctonus rufipennis*) trap capture phenology (two-parameter logistic function). (B) Parameter estimates for the most parsimonious thermal model of spruce beetle trap capture phenology (three-parameter Gompertz function), based on a tally of the number of days exceeding 13°C

Predictor variable	Parameter	Estimate	Standard error	Lower 95% CL	Upper 95% CL
(A)					
Ordinal day	Growth rate, *a*	0.095	0.004	0.086	0.104
	Inflection point, *b*	182.472	0.548	181.397	183.547
(B)					
Number of days > 13°C	Asymptote, *a*	1.002	0.022	0.959	1.046
	Growth rate, *b*	0.062	0.005	0.051	0.073
	Inflection point, *c*	48.492	0.937	46.655	50.329

In this framework, the inflection point, *b*, denotes a shift in the expected numbers of beetles actively responding to pheromone sources in spruce stands; consistent with the day of year at which 50% total trap capture is predicted. The model accounts for 81% of the variance in cumulative *D. rufipennis* trap captures across site × years (RMSE = 0.16). Regressing expected values on observed values indicated that the model was effective at predicting trap capture accumulation ($F_{1,\,532}$ = 2,322.921; $p < .0001$, Figure 1a), and the model accounted for a large majority of variance in *D. rufipennis* cumulative trap captures in comparison with random (site and year) effects (Table S2). The best thermal model, although not as powerful as the ordinal day model, was a three-parameter Gompertz function (2) based on a tally of the days exceeding 13°C (Figure 1b, Table 1B).

$$\text{Percentage of spruce beetle trap capture} = a * \exp(-\exp(-b(\text{number days} > 13^\circ\text{C}))) \quad (2)$$

The ordinal day model predicts that earliest trap captures are likely to occur on Day 126 (May 6), with 5% trap capture occurring between Day 150 and Day 155 (May 30–June 4), 50% of the total trap capture by Day 182 (July 1), and cessation of captures (99% of total trap capture) is likely by Day 234 (August 22). Consequently, observational and model results generally agree that traps should be deployed by early May and serviced until late August if sampling across the duration of regional *D. rufipennis* flight periods is desired; however, trap deployment during June and early July is likely to provide conservative coverage for monitoring only newly emerged beetles.

The simplicity of this model will facilitate ease of use by managers concerned with the timing of trap placement, as the only input required is day of year (Box 1). Based on this single metric, users can determine the probable relative accumulation of flying beetles responding to pheromones. Although this model is a useful approximation of trap capture phenology, care should be taken in its use as the sampling period described here spans several beetle life stages; specifically, during the beginning of flight when overwintered re-emerged parents may be a portion of trap captures (Hansen & Bentz, 2003) or during late-summer and fall when re-emerged parents might comprise the entirety of flying beetles (Massey & Wygant, 1954). Thus, it cannot be assumed that all

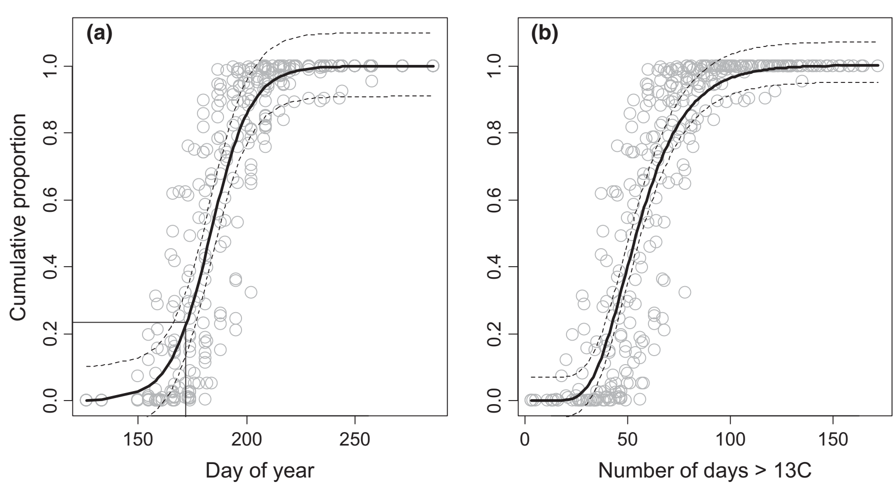

FIGURE 1 (a) Cumulative proportion of spruce beetle (*Dendroctonus rufipennis*) trap capture for each site × year combination (grey circles), and a two-parameter logistic function used to model *D. rufipennis* captures as a function of ordinal day (black line); the model coefficient of determination is R^2 = 0.81, with RMSE = 0.16. Thin solid lines represent a visual solution for the computation example provided in Box 1. (b) The best thermal model of cumulative trap capture was a three-parameter Gompertz function (heavy black line) based on a tally of the number of days exceeding 13°C; the model coefficient of determination is R^2 = 0.75, with RMSE = 0.18. In both panels, dotted lines show the 95% confidence interval of the model

BOX 1 The ordinal day model can be used to estimate the per cent of North American spruce beetle, Dendroctonus rufipennis Kirby, which have oriented to or will potentially orient to pheromone-baited Lindgren funnel traps in Engelmann spruce-dominated stands of the Rocky Mountain region. The application of this model is to determine whether deployment of pheromone traps for monitoring, research or management purposes is likely to be efficient, and to help practitioners time these activities based on their needs

Model *input* requires only day of year (ordinal date, 1 [Jan 1]–365 [Dec 31]), and model *output* will reflect the cumulative proportion (0%–100%) of beetles responding to pheromones; model parameter estimates (Table 1) and the model function are provided below:

$$\text{Percentage of spruce beetle} = \frac{1}{(1 + \exp(-a * (\text{ordinal day} - b)))}$$

where a = 0.095

and b = 182.472

As an example, if a user wished to deploy pheromone traps for monitoring on June 19, but first wanted to determine the potential efficiency of monitoring by estimating the proportion of the beetle flight that had already occurred, a user could first convert the date (June 19) to ordinal date, or day 170. Inserting this value into the equation yields the solution:

$$0.234 = \frac{1}{(1 + \exp(-0.095 * (170 - 182.472)))}$$

Thus, by June 19, a practitioner deploying pheromone traps could estimate that approximately 23.4% of the flight had likely already occurred, and that monitoring operations would potentially only capture up to 76.6% of ***D. rufipennis*** adults actively responding to pheromones. A similar, but less precise estimate can be generated by approximating the point of intersection for day of year and cumulative proportion along the curve (represented by solid lines in Figure 1a).

beetles responding to pheromone lures will have similar reproductive potential or represent the same "biotic challenge" to a host tree.

Future efforts aimed at elucidating patterns of emergence and flight phenology in *D. rufipennis* populations should focus on improving the accuracy and precision of models by incorporating physiologically important variables such as phloem temperatures and relative estimates of host availability or susceptibility. By further supplementing this easy-to-use model with more refined forecasting technologies and population models, trapping efficiency can be enhanced to improve efficacy of integrated pest management and beetle monitoring techniques. Developing multiple such models could reveal whether and to what extent pest insect flight patterns are affected by latitude, elevation or large-scale state factors such as precipitation and accumulation of thermal units; understanding these patterns will provide a quantitative basis for comparison across multiple biological systems.

The model presented here is derived from a comprehensive multiyear survey of *D. rufipennis* in high-elevation spruce stands in northern Colorado. This work will help to increase the efficiency of regional trapping efforts by allowing managers to easily estimate the window of *D. rufipennis* flight phenology, and provides a first quantitative decision support tool for practitioners concerned with the timing of trap placement and timing of forest treatment applications such as deployment of "trap trees" for attract-and-kill (Hansen, Munson, Blackford, Wakarchuk, & Baggett, 2016), anti-aggregation pheromones for protection of standing live spruce trees (Holsten, Shea, & Borys, 2003; Lindgren, McGregor, Oakes, & Meyer, 1989; Ross, Daterman, & Munson, 2004) or treatment of windthrow material to limit population build-up (Jenkins, Hebertson, & Munson, 2014; Schmid, 1981).

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AUTHOR CONTRIBUTION

TSD performed the statistical analyses and wrote the first draft of the manuscript. EMH designed the project and collected the data. Both authors contributed to revising the manuscript.

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SUPPORTING INFORMATION

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