# Influence of Temperature on Spring Flight Initiation for Southwestern Ponderosa Pine Bark Beetles (Coleoptera: Curculionidae, Scolytinae)

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**ABSTRACT** Determination of temperature requirements for many economically important insects is a cornerstone of pest management. For bark beetles (Coleoptera: Curculionidae, Scolytinae), this information can facilitate timing of management strategies. Our goals were to determine temperature predictors for flight initiation of three species of *Ips* bark beetles, five species of *Dendroctonus* bark beetles, and two genera of bark beetle predators, *Enoclerus spp.* (Coleoptera: Cleridae) and *Temnochila chlorodia* (Mannerheim) (Coleoptera: Ostomidae), in ponderosa pine forests of northcentral Arizona. We quantified beetle flight activity using data loggers and pheromone-baited funnel traps at 18 sites over 4 yr. Ambient air temperature was monitored using temperature data loggers located in close proximity to funnel traps. We analyzed degree-day accumulation and differences between minimum, average, and maximum ambient temperature for the week before and week of first beetle capture to calculate flight temperature thresholds. Degree-day accumulation was not a good predictor for initiation of beetle flight. For all species analyzed other than *D. adjunctus* Blandford, beetles were captured in traps only when springtime temperatures exceeded 15.0°C. *D. adjunctus* was collected when maximum temperatures reached only 14.5°C. Once initial flights had begun, beetles were often captured when maximum ambient air temperatures were below initial threshold temperatures. Maximum and average air temperatures were a better predictor for beetle flight initiation than minimum temperature. We establish a temperature range for effective monitoring of bark beetles and their predators, and we discuss the implications of our results under climate change scenarios.

**KEY WORDS** degree day, *Dendroctonus*, *Ips*, temperature, *Pinus ponderosa*

Temperature is generally acknowledged as a key factor in regulating seasonality of insects (Zaslavski 1988, Powell et al. 2000) by directly impacting development rates (Miller and Keen 1960, Hansen et al. 2001b, Netherer and Pennerstorfer 2001). This information can be used to develop degree-day models to predict the onset of bark beetle (Coleoptera: Curculionidae, Scolytinae) activity (Pruess 1983, Higley et al. 1986, Ayres et al. 2001, Hansen et al. 2001a, Kennedy and McCullough 2002) and temperature thresholds required for flight (Miller and Keen 1960, McCambridge 1971, Livingston 1979, Holsten and Hard 2002). Predicting emergence and first flight of bark beetle species can facilitate timing of monitoring activities and management strategies, such as single tree protection treatments, thinning, and slash removal.

The ponderosa pine forests (*Pinus ponderosa* Douglas ex. Lawson) of northern Arizona are home to multiple species of bark beetles including *Dendroctonus brevicomis* LeConte, *D. frontalis* Zimmermann, *D. adjunctus* Blandford, *D. approximatus* Dietz, *D. valens* LeConte, *Ips pini* (Say), *I. latidens* (LeConte), *I. lecontei* Swaine, *I. knausi* Swaine, and *I. calligraphus* (Germar) (Wood 1982, Villa-Castillo and Wagner 1996, Sanchez-Martinez and Wagner 2002, McHugh et al. 2003, Gaylord et al. 2006). *D. ponderosae* Hopkins also has been reported in trapping studies; however, its distribution and impacts are limited south of the Grand Canyon (Sanchez-Martinez and Wagner 2002, McHugh et al. 2003, Williams et al. 2008, USDA Forest Service 1976–2000, 2001–2003).

Minimum flight thresholds and optimum temperatures for flight have been reported in other geographic locations for some of the beetle species present in northern Arizona. In the northwestern United States, ambient air temperatures for initial flights of *I. pini* are reported as being between 15.6 and 21.1°C (Livingston 1979). For *D. brevicomis* in California, this threshold has been reported as 15.6°C (Miller and Keen 1960). Under field conditions in Louisiana, flight thresholds as low as 6.7°C have been reported for *D. frontalis* (Moser and Thompson 1986). However, there is a paucity of information on flight temperatures required for these species and others in the southwest. Few studies report degree-day requirements for beetle de-

**Table 1. Trap locations, trapping dates, and no. of traps/site used to collect bark beetles in ponderosa pine forests in north central Arizona**

| Year | Elevation | Collection dates | No. of traps/site | Sites |
|------|-----------|------------------|-------------------|-------|
| 2002 | 2,080 m | 1 Jan. to 31 Dec. | 10 | Centennial Forest |
| 2003 | 2,080 m | 1 Jan. to 31 Dec. | 10 | Centennial Forest |
| 2005 | 1,600–1,736 m | 8 Mar. to 6 Dec. | 3 | Christopher Creek, Haigler Creek, Moore Creek, Tonto 2, Marsh Creek |
|      | 2,058–2,230 m | 23 Mar. to 8 Dec. | 3 | Walnut Canyon, Marshall Lake, Mormon Lake, Schultz Pass, Cinder Hills, Rim |
|      | 2,505–2,651 m | 25 April to 28 Nov. | 3 | Newman Hill, Viet Springs, Saddle Mtn. Mt. Elden, Friedlein Prairie, Mormon Mtn. South |
| 2006 | 1,600–1,736 m | 7 Mar. to 12 Dec. | 3 | Christopher Creek, Haigler Creek, Moore Creek, Tonto 2, Marsh Creek |
|      | 2,058–2,230 m | 9 Mar. to 7 Dec. | 3 | Walnut Canyon, Marshall Lake, Mormon Lake, Schultz Pass, Cinder Hills, Rim |
|      | 2,505–2,651 m | 27 Mar. to 6 Dec. | 3 | Newman Hill, Viet Springs, Saddle Mtn. Mt. Elden, Friedlein Prairie, Mormon Mtn. South |

velopment (Ayers et al. 2001, Kennedy and Mc-Cullough 2002), and none of these are geographically specific to northcentral Arizona. Similarly, to the best of our knowledge, there are no data available on temperature requirements for flight or development for *Enoclerus sphegus* Fabricus (Coleoptera: Cleridae), *E. lecontei* (Wolcott), and *Temnochila chlorodia* (Mannerheim) (Coleoptera: Ostomidae), three prominent bark beetle predators in northern Arizona (Blackman 1931, Ostmark 1966, Gaylord et al. 2006).

Our goal was to determine predictive tools for bark beetle flight for species occurring in ponderosa pine forests of northcentral Arizona. We examined both degree-day data and temperature thresholds reached before initial bark beetle flight. In addition, we examined whether beetle flight is most closely associated with maximum, minimum, or average temperatures. This information will provide managers with an easily accessible tool to predict flight initiation and periods of beetle flight activity. In addition, this information may help predict what impact increasing global temperatures could have on bark beetle populations including their interactions with predators and interspecies competition (Ayers et al. 2001, Williams and Liebhold 2002, Aukema et al. 2005, Logan et al. 2006).

## Materials and Methods

### Site Description

Our study sites were located across the ponderosa pine forest type in northcentral Arizona. Our study used trap catch data from five to seven different sites in each of three different elevation bands: low (1,600–1,736 m), mid (2,058–2,230 m), and high (2,505–2,651 m; Table 1). At the low elevation sites, ponderosa pine stands were interspersed with alligator juniper (*Juniperus deppeana* Steud.), Arizona white oak (*Q. arizonica* Sarg.), and open grassland. At middle elevations, forest overstory was comprised of ponderosa pine, which occurred in near monocultures, and Gambel oak (*Quercus gambelii* Nutt.). At the high elevation sites, forest composition included ponderosa pine, Douglas fir (*Pseudotsuga menziesii* Mirbel), limber pine (*P. flexilis* James), and quaking aspen (*Populus tremuloides* Michx.).

### Study Design

To assess bark beetle flight activity with regard to air temperatures, we monitored bark beetle flight activity in 2002 and 2003 at one mid-elevation site using two clusters of five, 8-unit Lindgren funnel traps (Phero Tech, Delta, British Columbia, Canada) (Lindgren 1983) in a pentagon-shaped arrangement with a different lure type for each trap in a cluster (Table 2). Traps were monitored from 1 January 2002 through 31 December 2003. In 2005 and 2006, our study was conducted at five low-elevation, six mid-elevation, and six high-elevation sites. Each site consisted of a triangular arrangement of three 12-unit funnel traps (Synergy; Phero Tech), each baited with a different lure type (Table 2). Traps in 2005 and 2006 were monitored from March or April (depending on elevation and site accessibility) through November. Lures at all sites were changed regularly: approximately every 6 wk for *I. pini* and every 7–8 wk for *I. lecontei, D. brevicomis, D. frontalis, D. valens,* and *D. ponderosae.* Traps were hung on 3-m conduit poles with the bottom of traps ≈1 m from the ground and placed ≈15 m apart. Traps were rotated on a regular basis to minimize location impacts. A small piece of Spectracide Bug Stop pest strip (18.6% Dichlorvos; United Industries, St. Louis, MO) was placed in each collection cup to kill trapped insects and minimize predation.

Beetles and their associated predators were collected from traps every 1–2 wk and were sorted to species according to Furniss and Carolin (1977), Chansler (1964), and Wood (1982). Voucher speci-

**Table 2. Lures and lure components used to attract bark beetles in ponderosa pine forests in north central Arizona**

| Year | Lure type | Components |
|------|-----------|------------|
| 2002–2003 | *D. brevicomis* | *exo*-Brevicomin, frontalin, myrcene |
|           | *D. ponderosae* | Myrcene, *exo*-brevicomin, *trans*-verbenol |
|           | *D. frontalis* | Frontalin |
|           | *D. valens* | *a*-Pinene, *beta* pinene and 3-carene |
|           | *I. pini* | Lanierone, 50/50 ipsdienol |
| 2005–2006 | *D. brevicomis* | *exo*-Brevicomin, frontalin, myrcene |
|           | *I. pini* | Lanierone, +03/−97 ipsdienol |
|           | *I. lecontei* | *cis*-Verbenol +17/−83, ipsdienol +50/−50, ipsenol +50/−50 |

Table 3.   Degree-day accumulation between peak bark beetle catches in successive years (base 11) for all sites and years in ponderosa pine forests in north central Arizona

| Location | Species | | | | | | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | Ips pini | Dendroctonus brevicomis | Dendroctonus frontalis | Dendroctonus valens | Dendroctonus adjunctus | Dendroctonus approximatus. | Enoclerus spp. | Temnochila chlorodia |
| 2002–2003 | | | | | | | | |
| Centennial Forest | 125 | 276 | 240 | 835 | 2,505 | —[a] | 869 | 1,224 |
| 2005–2006 | | | | | | | | |
| Freidlein Prairie | — | — | — | 640 | — | — | — | — |
| Mormon Mountain | — | — | — | — | — | 665 | 416 | 845 |
| Cinder Hills | — | 605 | 605 | — | — | 405 | — | 789 |
| Chris Creek[b] | — | — | 596 | — | — | 560 | — | 661 |
| Haigler[b] | — | — | 345 | — | — | 599 | — | 755 |
| Moore Creek | — | 563 | 733 | — | — | 761 | — | 836 |
| Marsh Creek | — | 447 | 447 | — | — | — | — | 801 |
| Mormon Lake | 114 | — | — | — | 2,461 | — | — | 1,193 |
| Rim | — | — | 612 | — | — | — | — | 1,343 |
| Newman | — | — | — | — | — | — | 284 | 701 |
| Viet Spring | — | — | — | — | — | 450 | — | — |
| P value[c] | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 |

We used only those sites where at least 50 bark beetle or bark beetle predators were collected for the season.
[a] — indicates inadequate data for a site or analysis.
[b] One week of temperature data missing. Temperature data for this week were substituted from similar site.
[c] $\chi^2$ analysis H0: all sites = avg sum of all degree days.

mens are maintained in the Forest Entomology Laboratory at Northern Arizona University and the Rocky Mountain Research Station, USDA Forest Service, Flagstaff, AZ.

Temperature data were recorded using a Campbell Data logger (Campbell Scientific, Logan UT) and shaded thermocouple, located ≈1.4 m above the ground, which measured air temperature every 30 min (2002 and 2003). In addition, HOBO data loggers (Onset Computer, Bourne, MA), which were installed on the north side of a tree nearest to the center of the plot to record temperature once every 1 or 3 h throughout the trapping season (2005 and 2006). Not all temperature data sets were complete because of occasional battery failure or malfunction of the data loggers.

## Statistical Analysis

We used day-degree accumulation (Pruess 1983), i.e., the sum of the degrees by day exceeding the minimum developmental threshold (11.0°C based on Miller and Keen 1960 and Ungerer et al. 1999) from the last fall peak flight to first peak spring flight, or, in the case of strongly univoltine species, i.e., *D. adjunctus*, peak flight to successive year peak flight. We defined "peaks" as those periods during which more than two beetles were collected for at least 2 successive wk. For each species, we analyzed degree-days for those locations and years where we captured at least 50 beetles through the season and where temperature loggers were installed before last fall flight of the respective year. In some cases, temperature data were missing, and we substituted temperature data from the closest site with similar elevation. Temperature data were only missing for three sites for 9 d per site. To test for significant differences in degree-day accumulation for each species by site and year, we used a $\chi^2$ analysis.

The null hypothesis was no difference in degree-day accumulation between the sites, i.e., the expected value at each site was the average of the degree-day sum of all sites. Significance was established at $\alpha = 0.05$.

For those species for which we had at least four sites where >50 individuals of the respective species were captured over the season, and where traps were deployed for at least 2 wk before first beetle capture (indicating we captured the first beetles flying for the season), we used a paired by location t-test to analyze the difference between the minimum, average, and maximum temperatures for the weeks before first flight and the week of first flight. Based on results from the prior analysis, we determined that maximum daily temperature was the best indicator for predicating flight. Therefore, to assess temperature thresholds, we analyzed only the maximum daily temperature by the average number of beetles captured by species for each trapping period.

## Results

### Degree Days

*Ips pini.* For *I. pini*, we only had two locations where temperature data and beetle trap catches could be analyzed for degree-day accumulation (Table 3). Degree day values were 114 and 125 ($P < 0.0001$).

*Dendroctonus brevicomis.* We analyzed four sites for degree-day (base 11) accumulation for *D. brevicomis* (Table 3). Degree day accumulation ranged from 276 to 605 ($P < 0.0001$).

*Dendroctonus frontalis.* Seven sites were analyzed for degree-day (base 11) accumulation for *D. frontalis* (Table 3). Values ranged from 240 to 733 ($P < 0.0001$).

***Dendroctonus valens.*** Two sites were analyzed for degree-day (base 11) accumulation for *D. valens (Table* 3). Degree day values were 640 and 835 (*P* < 0.0001).

***Dendroctonus adjunctus.*** Two sites were analyzed for degree-day (base 11) accumulation for *D. adjunctus* (Table 3). For *D. adjunctus*, we calculated values from peak fall flight to peak fall flight (because *D. adjunctus* is univoltine and seems to have strong seasonal synchrony; Gaylord et al. 2006 and Williams et al. 2008). Degree-day accumulations for fall flight to fall flight were 2,461 and 2,505 (*P* < 0.0001).

***Dendroctonus approximatus.*** Six sites were analyzed for degree-day (base 11) accumulation for *D. approximatus* (Table 3). Values ranged from 405 to 761 (*P* < 0.0001).

***Enoclerus* spp.** Three sites were analyzed for degree-day (base 11) accumulation for *Enoclerus spp.* (Table 3). Values ranged from 284 to 869 (*P* < 0.0001).

***Temnochila chlorodia.*** Ten sites were analyzed for degree-day (base 11) accumulation for *T. chlorodia* (Table 3). Values ranged from 661 to 1,343 (*P* < 0.0001).

**Threshold Temperature**

***Ips pini.*** The majority of *I. pini* (98% or 14,110 of 14,398) were collected when temperatures exceeded 17.0°C (Fig. 1a). The minimum temperature did not differ between the week before first beetle capture and the week of first beetle capture (Table 4; Fig. 2). The average and maximum temperatures were higher for the first week of the year in which beetles were collected than the week prior. The lowest maximum temperature at any site for initial beetle flight was 16.1°C (Fig. 1a). The lowest maximum temperature at which *I. pini* was captured during our study was 11.7°C in March.

***Ips lecontei.*** The majority (98.7% or 1,917 of 1,942) of *I. lecontei* were captured when maximum daily temperatures exceeded 19.0°C (Fig. 1b). The lowest maximum temperature at any site for initial beetle flight was 19.0°C. Because of low beetle numbers at some sites, only two sites were available for this analysis. Therefore, we were unable to statistically analyze these data. The lowest maximum temperature for any trapping period during which *I. lecontei* was captured was 15.2°C in March.

***Ips calligraphus.*** The majority (98.3%, or 2,634 of 2,680) of *I. calligraphus* were captured when maximum daily temperatures were between 20.0 and 38.9°C (Fig. 1c). The lowest maximum temperature at any site for initial beetle flight was 21.0°C. Because of low beetle numbers at some sites, only three sites were available for this analysis. Therefore, we were unable to statistically analyze these data. The lowest maximum temperature for any trapping period during which *I. calligraphus* was captured was 15.5°C in October.

***Dendroctonus brevicomis.*** The majority (98.3% or 6,742 of 6,859) of *D. brevicomis* were captured when maximum daily temperatures were between 19.0 and 38.9°C (Fig. 3a). The minimum temperature did not differ between the week before first beetle capture and the week of first beetle capture (Table 4; Fig. 4a). The average and maximum temperatures were higher for the first week of the year in which beetles were collected than the week prior. The lowest maximum temperature at any site for initial beetle flight was 18.6°C; however, later in the season (October), *D. brevicomis* was captured when maximum temperatures for the trap period did not exceed 13.1°C (Fig. 3a).

***Dendroctonus frontalis.*** The majority (98.6% or 12,908 of 13,091) of *D. frontalis* were captured when maximum temperatures were between 19.0 and 37.9°C (Fig. 3b). The minimum temperature did not differ between the week before first beetle capture and the week of first beetle capture (Table 4; Fig. 4b). The average and maximum temperatures were higher for the first week of the year in which beetles were collected than the week prior. The lowest maximum temperature at any site for initial beetle flight was 17.8°C; however, *D. frontalis* was captured later in the season (November) when maximum temperatures for the trap period did not exceed 10.4°C (Fig. 3b).

***Dendroctonus valens.*** The majority (98.2% or 1,864 of 1,898) of *D. valens* were captured when maximum temperatures were between 19.0 and 37.9°C (Fig. 3c). There was no difference between the minimum temperatures for the week before first beetle capture and the week of first beetle capture (Table 4; Fig. 4c). There was a significant difference between average and maximum temperatures for the week before and the week of first beetle capture. The lowest maximum temperature at any site for initial beetle flight was 16.1°C (March), which was also the lowest maximum temperature for a capture period for *D. valens* (Fig. 3c).

***Dendroctonus adjunctus.*** The majority (97.3% or 6,854 of 7,044) of *D. adjunctus* were captured when maximum temperatures were between 14.0 and 27.9°C (Fig. 3d). There was no difference between the minimum temperatures for the week before and the week of first beetle collection (Table 4; Fig. 4d). There was a significant difference between average and maximum temperatures for the week before and the week of first beetle capture. The lowest maximum temperature at any site for initial beetle flight was 14.5°C; however, *D. adjunctus* was captured later in the season (November) when maximum temperatures for the trap period did not exceed 11.4°C (Fig. 3d).

***Dendroctonus approximatus.*** The majority (99.9% or 2,905 of 2,908) of *D. approximatus* were captured when temperatures exceeded 17.0°C (Fig. 3e). There was no difference between minimum temperature for the week before and the week of first beetle capture (Table 4; Fig. 4e). Average and maximum temperatures were higher for the first beetle capture period compared with the trap collection before first beetle capture. The lowest maximum temperature at any site for initial beetle flight was
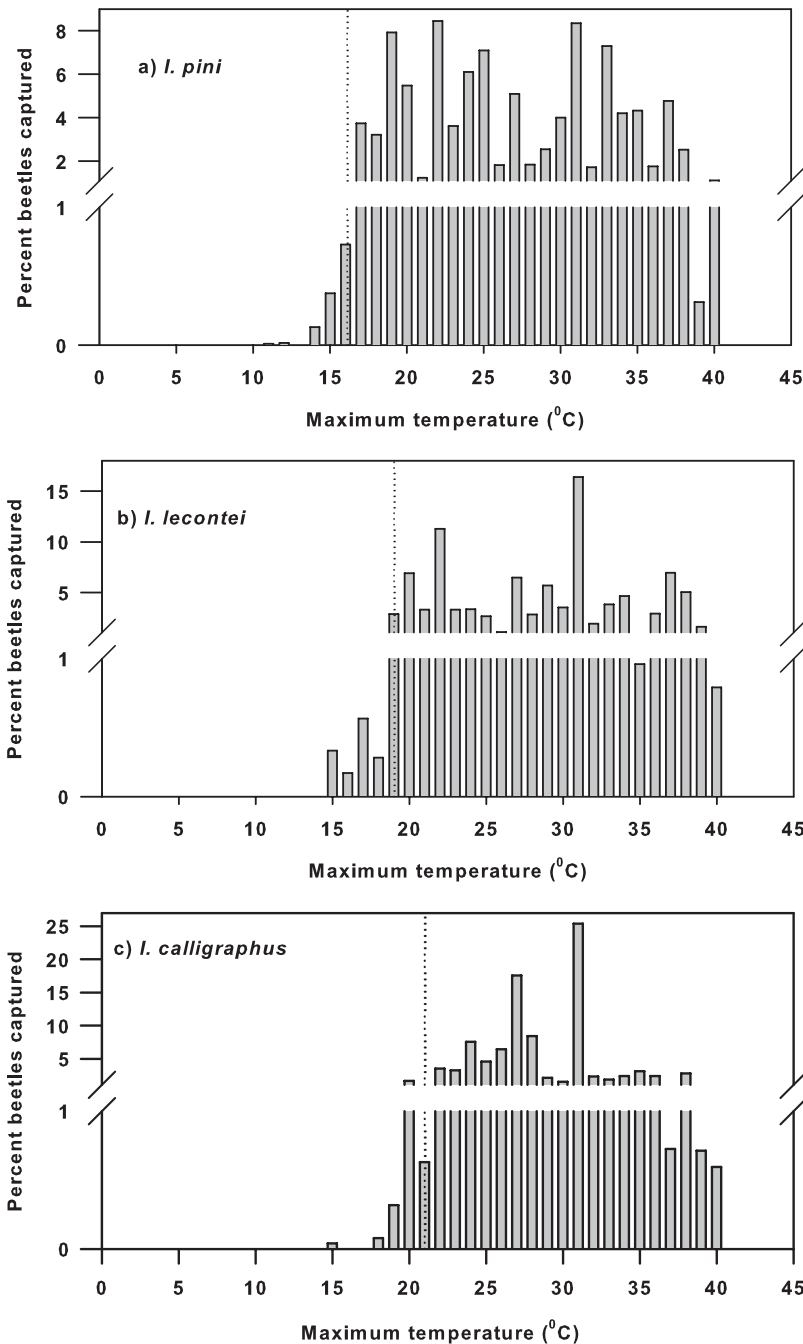
**Fig. 1.** Percent of total (a) *I. pini*, (b) *I. lecontei*, and (c) *I. calligraphus* beetles captured in 2002, 2003, 2005, and 2006 by maximum temperature for the capture period in ponderosa pine forests in north central Arizona. Y axis scale varies among graphs. Dotted line indicates lowest recorded temperature for first seasonal flight.

17.5°C; 16.3°C was the lowest maximum temperature recorded for any trapping period when *D. approximatus* was captured (April; Fig. 3e).

**Enoclerus spp.** The majority (99.5% or 3,740 of 3,759) of *Enoclerus* were captured when temperatures were between 17.0 and 38.9°C (Fig. 5a). Minimum, average, and maximum temperatures were

higher for the first beetle capture period compared with the trap collection before first beetle (Table 4; Fig. 6a). The lowest maximum temperature at any site for initial beetle flight was 17.4°C; however, beetles were captured when maximum temperatures for a trap period did not exceed 10.2°C (May; Fig. 5a).

**Table 4. Results of paired by site *t*-test for minimum (min), average (avg.), and maximum (max) temperatures for the week before flight and week of first flight by bark beetle species in ponderosa pine forests of northcentral Arizona**

| | Species | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | *Ips pini* | *Dendroctonus brevicomis* | *Dendroctonus frontalis* | *Dendroctonus valens* | *Dendroctonus adjunctus* | *Dendroctonus approximatus* | *Enoclerus* spp. | *Temnochila chlorodia* |
| Min | | | | | | | | |
| df | 8 | 12 | 14 | 7 | 7 | 11 | 12 | 20 |
| *t* value | −2.11 | 0.94 | 1.44 | 0.30 | 0.85 | 0.82 | 2.52 | 2.36 |
| *P* value | 0.0680 | 0.3639 | 0.1709 | 0.7714 | 0.4259 | 0.4281 | 0.0269 | 0.0286 |
| Avg | | | | | | | | |
| df | 8 | 12 | 14 | 7 | 7 | 11 | 12 | 20 |
| *t* value | 5.41 | 2.65 | 4.59 | −5.55 | −2.78 | 3.95 | 6.53 | 6.60 |
| *P* value | 0.0006 | 0.0213 | 0.0004 | 0.0009 | 0.0274 | 0.0023 | <0.0001 | <0.0001 |
| Max | | | | | | | | |
| df | 8 | 12 | 14 | 7 | 7 | 11 | 12 | 20 |
| *t* value | 10.20 | 4.21 | −5.30 | −5.44 | −4.66 | 3.81 | 7.21 | −4.24 |
| *P* value | <0.0001 | 0.0012 | 0.0001 | 0.0010 | 0.0023 | 0.0029 | <0.0001 | <0.0001 |

***Temnochila chlorodia.*** The majority (98.3% or 7,390 of 7,518) of *T. chlorodia* were captured when the maximum ambient temperature for a capture period exceeded 24.0°C (Fig. 5b). Minimum, average, and maximum temperatures were higher for the first beetle capture period compared with the trap collection period before first beetle capture (Table 4; Fig. 6b). The lowest maximum temperature at any site for initial beetle flight was 19.0°C; however, *T. chlorodia* was captured when maximum temperatures for a trap period did not exceed 16.0°C (March; Fig. 5b).

## Discussion

Our data suggest that degree-day models using pheromone trap catch data to determine dates for fall oviposition and spring emergence may not be a reliable method for predicting the onset of bark beetle flight for most species in the southwestern United States. There are several reasons that may explain the variability observed in our data. For instance, recent studies have shown that pheromone catches may not be an exact temporal measure of bark beetle emergence (Kennedy and McCullough 2002, Bentz 2006)
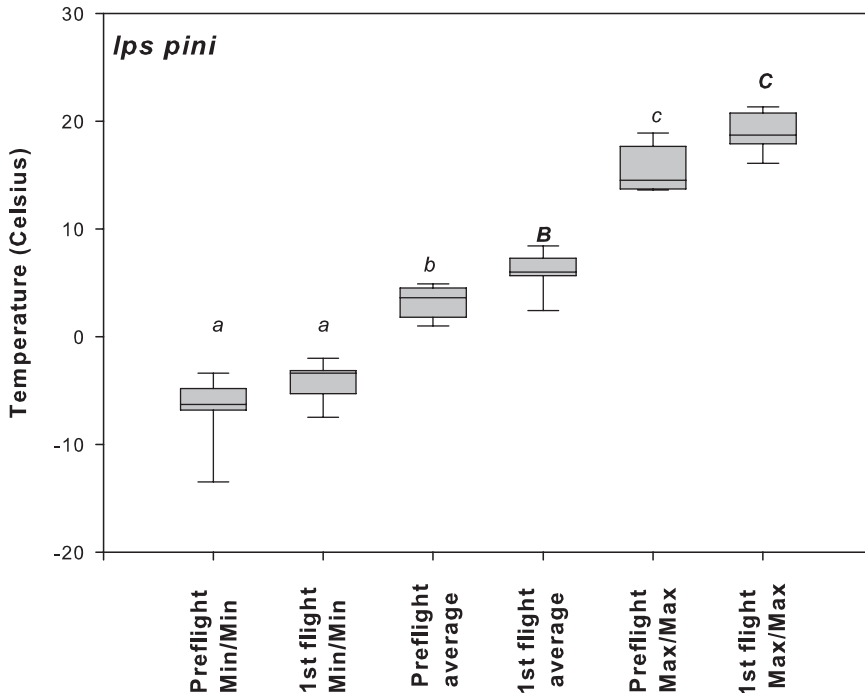


**Fig. 2.** Temperature range for the minimum, average, and maximum recorded temperatures at nine sites in ponderosa pine forests in northcentral Arizona for the capture period before first *I. pini* capture (preflight) and during first beetle capture (first flight) for the year. The center line in each box represents the median, upper and lower box boundary represents the 75th and 25th percentile, respectively, and error bars indicate 90th and 10th percentile. Columns with similar letters were compared using paired-by-site *t*-tests. Lowercase letters indicate no significant differences between columns ($\alpha = 0.05$).
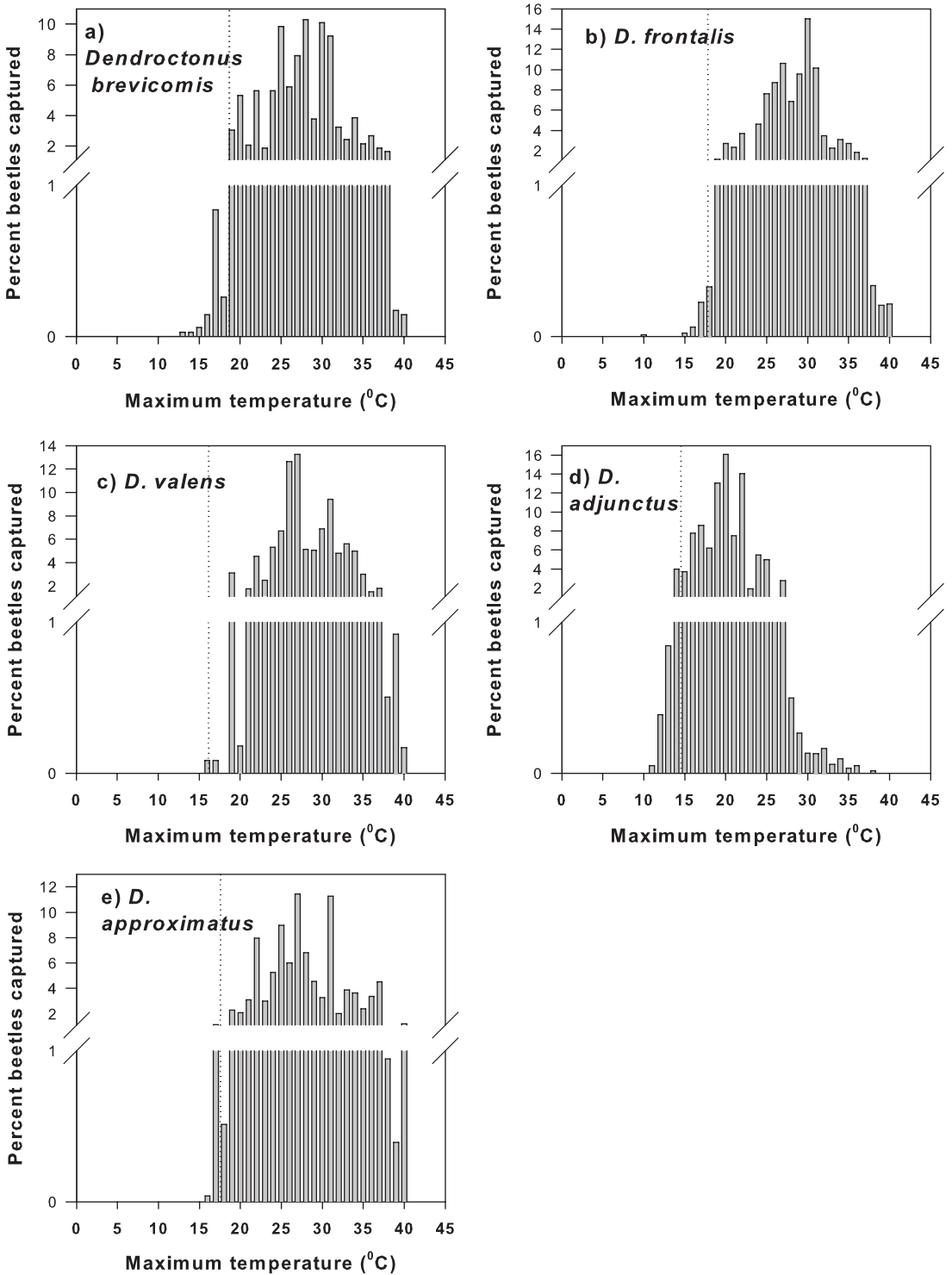
**Fig. 3.** Percent of total (a) *D. brevicomis*, (b) *D. frontalis*, (c) *D. valens*, (d) *D. adjunctus*, and (e) *D. approximatus* beetles captured in 2002, 2003, 2005, and 2006 by maximum temperature for the capture period in ponderosa pine forests in north central Arizona. Y axis scale varies among graphs. Dotted line indicates lowest recorded temperature for first seasonal flight.
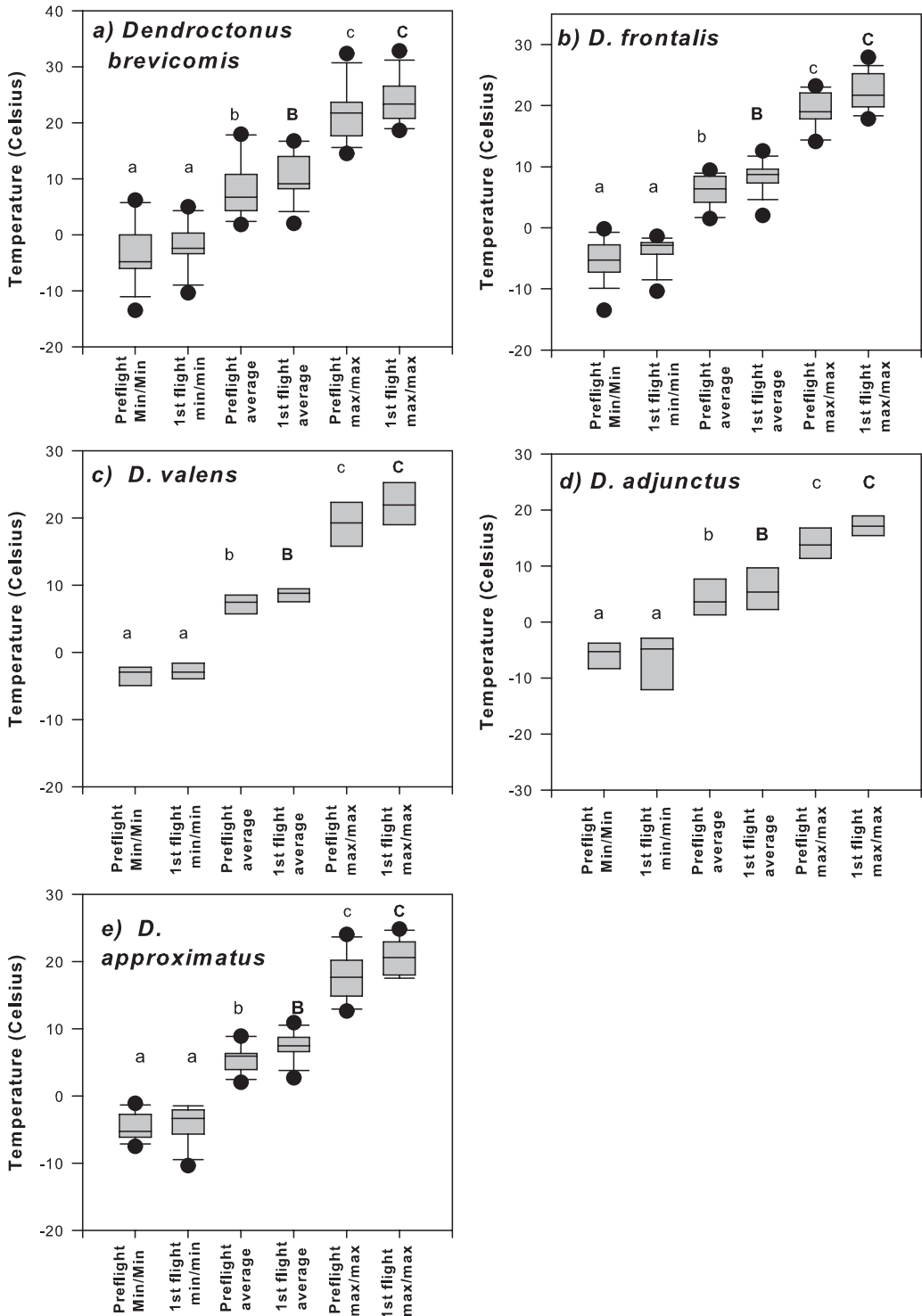
**Fig. 4.** Temperature range for the minimum, average, and maximum recorded temperatures in ponderosa pine forests in northcentral Arizona at (a) 13, (b) 15, (c) 8, (d) 8, and (e) 12 sites for the capture period before first beetle capture (preflight) and during first beetle capture (first flight) of *Dendroctonus* species. Columns with similar letters were compared using paired-by-site *t*-tests. Lowercase letters indicate no significant differences between columns ($\alpha = 0.05$). The center line in each box represents the median, upper and lower box boundary represents the 75th and 25th percentile, respectively, and error bars indicate 90th and 10th percentile. Dots represent outliers.
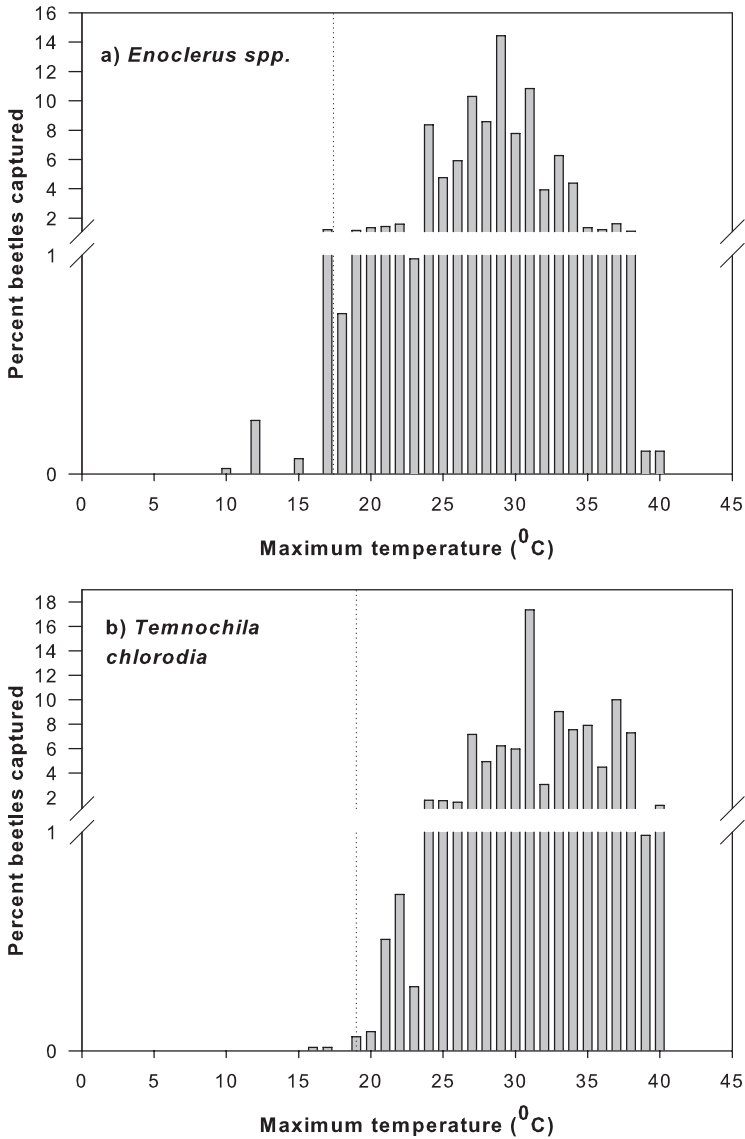
**Fig. 5.**   Percent of total (a) *Enoclerus* sp. and (b) *T. chlorodia* beetles captured in 2002, 2003, 2005, and 2006 by maximum temperature for the capture period in ponderosa pine forests in northcentral Arizona. Y axis scale varies among graphs. Dotted line indicates lowest temperature observed for first seasonal flight.

and that beetles initially captured may be parent adults rather than brood adults (Bentz 2006). In addition, phloem temperatures, rather than ambient air temperatures, are more reflective of the actual conditions experienced by developing larvae (Werner and Holsten 1985) and potentially overwintering adults. Previous studies suggest that the phloem temperature in attacked trees may differ substantially from ambient air temperatures (Beal 1934, Schmid et al. 1993); however, more recent research suggests that phloem temperatures differ from ambient temperature by 1–2°C (Bolstad et al. 1997, Ungerer et al. 1999). We would therefore recommend a more comprehensive experimental design that includes the date of last

fall oviposition observed in the tree, collection of temperature data from oviposition to first beetle emergence, and a more rigorous experiment and/or model to determine temperature requirements and development rates of different beetle species and their respective instars.

Our data generally correspond with previous studies from other geographic regions for flight temperature requirements of bark beetles. *I. pini* began flying in our study when temperatures exceeded 16.0°C, corresponding with the reported range of 15.6–21.1°C for onset of flight activity in the northwest (Livingston 1979). For *D. brevicomis*, the range of temperature for flight activity has been reported as 7.2–35.0°C (Miller
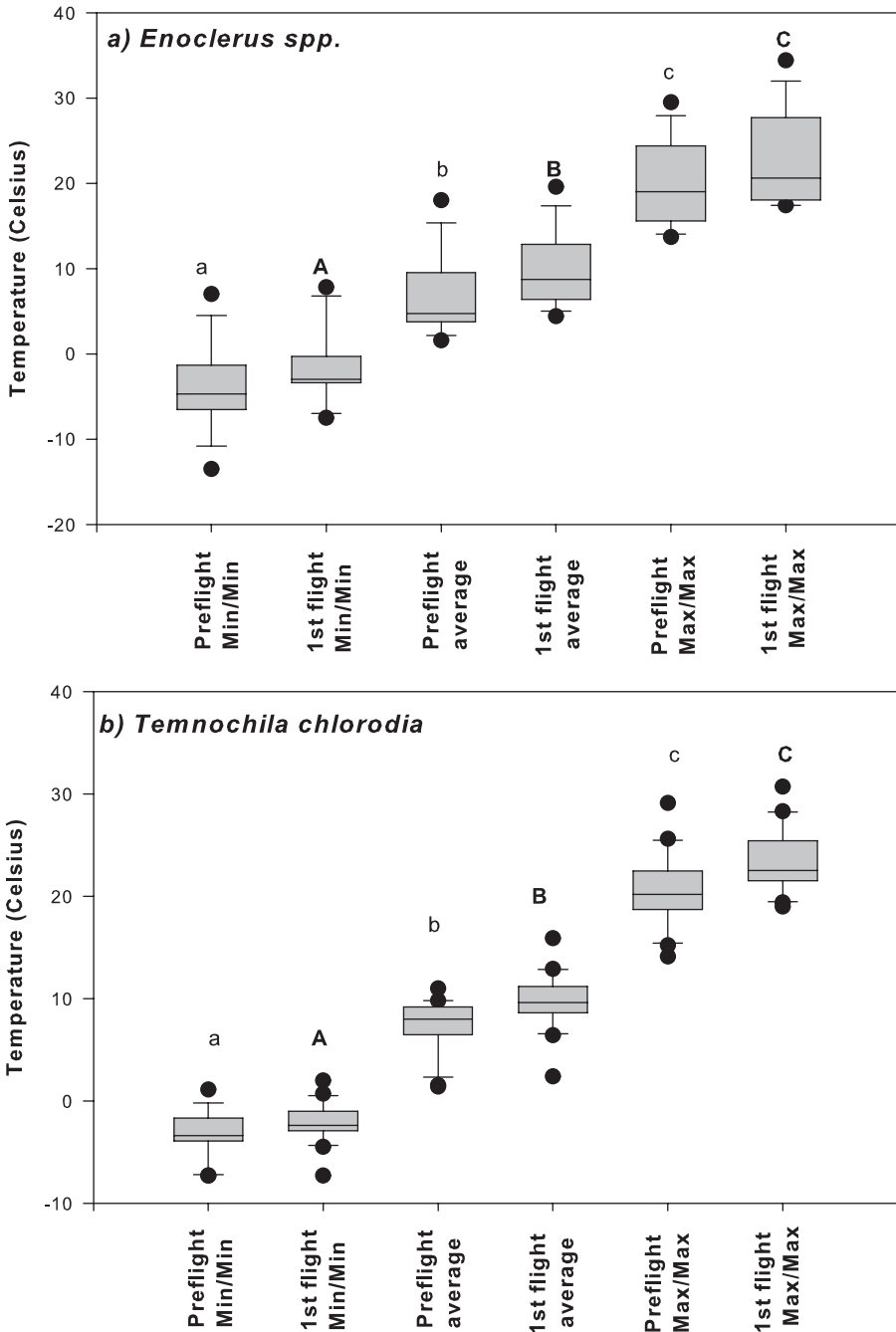
**Fig. 6.** Temperature range for the minimum, average, and maximum recorded temperatures at (a) 13, and (b) 21 sites in ponderosa pine forests in northcentral Arizona for the capture period before first apture (preflight) and during first capture (first flight) of bark beetle predators. Columns with similar letters were compared using paired-by-site *t*-tests. Lowercase letters indicate no significant differences between columns ($\alpha = 0.05$). The center line in each box represents the median, upper and lower box boundary represents the 75th and 25th percentile, respectively, and error bars indicate 90th and 10th percentile. Dots represent outliers.

1931, Miller and Keen 1960). Our study showed spring beetle flight activity beginning when temperatures exceeded 18.6°C and continuing in the fall until temperatures dipped below 13.0°C. Captures of *D. brevi-*

*comis* declined when temperatures exceeded 38.9°C. For *D. frontalis,* flight usually occurs between 22.0 and 36.7°C (White and Franklin 1976, Greer et al. 1981, Moser and Thompson 1986) but has been reported as

low as 6.7°C (Moser and Thompson 1986). Our study found spring flight initiating at 16.1°C, but later season flights continued when temperatures were as low as 10.4°C (Fig. 4b). Our data do not necessarily contradict earlier findings that *D. frontalis* flies at lower temperatures, because we cannot be sure exactly what day *D. frontalis* was flying and there were numerous capture periods where minimum temperatures were below 6.7°C. Captures for *D. frontalis* declined when temperatures exceeded 37.9°C. Emergence for *D. adjunctus* has been reported at temperatures as low as 4.4°C (Lucht et al. 1974); however, temperature requirements for emergence may be lower than those for flight initiation. Our study found *D. adjunctus* flying in the spring when temperatures reached 14.5°C, but later in the fall, flights continued when maximum daily temperatures did not exceed 11.4°C.

Our data indicate that flight activity for *I. pini* seems to be strongly associated with a temperature threshold. For instance, in 2003, *I. pini* was captured in all months other than February and December (Gaylord et al. 2006). In addition, *I. pini* beetles were captured during the first week of trap collection in 2006 (2–7 March), when maximum recorded temperatures at the low-elevation sites ranged from 19.0 to 20.2°C (Williams et al. 2008). Temperatures then declined (maximum recorded temperatures ranged from 14.1 to 16.0°C) for the next 2 wk (8–21 March), and no beetles were captured. However, beetle captures resumed when temperatures once again warmed above threshold levels, 19.0–22.1°C for 22–28 March. This same pattern was observed for *I. lecontei*, but not for *I. calligraphus.* In addition, only three *D. brevicomis* were captured across all sites during the first week of March 2006 and no other *Dendroctonus* were collected until the 28 March 2006 collection, when temperatures warmed again. Therefore, we suggest that the majority of the *Dendroctonus* beetles, while sensitive to temperature, also require some other cue before flight occurs in the spring, and this may be true for *I. calligraphus* as well. Some of the differences we observed in terms of flight initiation in response to increasing temperature could be caused by differences in overwintering biology of different beetle species and/or ability to supercool (Lombardero et al. 2000). Research from other regions has shown that *D. frontalis* and *D. brevicomis* (Wood 1982) may overwinter in all stages, including the adult, and therefore might be able to initiate flight as soon as temperatures warm; however, this has not been verified in our region. Anecdotal reports (J.D.M., unpublished data) indicate that most *D .brevicomis* in northern Arizona overwinter in the larval stage, and Tran et al. (2007) observed that the majority of successfully overwintering *D. frontalis* in New Jersey, in the northernmost range of this species, overwinter as prepupae.

For the two genera of predators we monitored, *Enoclerus* spp. seems to have a threshold temperature for flight similar to bark beetle species (17.0°C). *T. chlorodia* has a warmer threshold (≈24°C) for flight. This is consistent with previous reports that *T. chlorodia* flight tends to start later in the season than that of most bark beetle species (Gaylord et al. 2006). Because we did not identify individuals to the species level, results for *Enoclerus* should be interpreted with caution.

Our data indicate that once the crucial flight temperature threshold has been reached in the spring, beetles may subsequently remain active at lower temperatures until late fall. For instance, the lowest maximum temperature at any site for initial flight of *I. pini* was 16.1°C; however, at six different sites, beetles were captured when maximum temperatures were below this threshold (ranging from 11.7 to 15.9°C). Similar observations were made for all other species monitored in this study, with the exception of *D. valens.*

The relationship between *D. adjunctus* trap captures and temperature was unique among the beetle species studied, with more flights occurring when temperatures were cooler. This is the only species where an argument could be made for an upper temperature threshold, with most (98.6%) beetles captured when maximum temperatures were below 27.0°C (Fig. 3d). *D. adjunctus* is a univoltine species that shows strong flight synchrony with a small spring flight peak, and the majority of beetles captured in funnel traps over a 2- or 3-wk period in the fall (Chansler 1967, Massey et al. 1977, Wood 1982, Gaylord et al. 2006, Williams et al. 2008). Further research is necessary to determine whether these beetles respond to declining temperatures in the fall or if there are other environmental cues that trigger emergence and host searching. Previous research has suggested *D. adjunctus* may have developed a later seasonal flight period to exploit host trees already weakened but not yet colonized by other beetle species (Wood 1982).

For all species analyzed, other than *D. adjunctus*, it is unclear if the maximum temperature at which flight can occur was exceeded. For several species, i.e., *I. calligraphus, D. brevicomis, D. frontalis, D. valens,* and *Enoclerus* spp., lower percentages of beetles were captured when temperatures increased above 37–38°C. We also had fewer capture periods (<4%) when temperatures exceeded 36.0°C, so the low percentage may simply reflect number of days with warm temperatures as opposed to beetle response. In addition, because our trap catch data were collected over a 7-d period, it is impossible to verify on what day beetles were flying. Therefore, an upper temperature threshold may have been exceeded on certain days. Similarly, beetles may have been flying at lower temperatures than our figures suggest because we presented the maximum recorded daily temperature for the capture period. Although no beetles were ever collected when maximum temperatures for the collection period were <10.0°C, it is important to note that we actually only had four collection periods in all 4 yr where a maximum temperature of at least 10.0°C was not reached at some point during the collection period.

## Implications

Differences in average and maximum temperature between the week before beetle capture and the week of first beetle capture were significant for all bark beetle species and predators examined, whereas differences in minimum temperatures were significant only for the predator species. Therefore, we conclude that initiation of beetle and predator flight can be predicted by monitoring maximum daily temperatures. Because daily maximum temperature is generally easy to obtain, this should provide a simple tool for land managers. Our data suggest that monitoring for the majority of beetle species should initiate as soon as daily temperatures begin to exceed 15.0°C. If *D. adjunctus* is of particular interest, we would recommend trap installation when maximum daily temperatures exceed 14.0°C. In addition, fall monitoring of bark beetle species should continue until temperatures regularly drop below 15.0°C for *I. lecontei, I. calligraphus, D. valens, D. approximatus*, and *T. chlorodia*, 13.0°C for *D. brevicomis*, and 10.0°C for *I. pini, D. frontalis, D. adjunctus*, and *Enoclerus* spp.

Our results indicate that several *Ips* and *Dendroctonus* species are responsive to temperature for flight initiation and, presumably, host seeking and attack. Previous research indicates that temperature also influences developmental rates, voltinism, emergence synchrony, and geographic distribution of bark beetles (Miller and Keen 1960, Wagner et al. 1984, Bentz et al. 1991, Logan and Bentz 1999, Ungerer et al. 1999, Hansen et al. 2001a, Williams and Liebhold 2002, Friedenberg et al. 2007, Williams et al. 2008). Warming temperatures may lengthen the period of bark beetle flight activity, increase voltinism, and expand the geographic range of many species, potentially causing more bark beetle–related tree mortality (Williams and Liebhold 2002). Conversely, increasing temperatures may reduce the range of other bark beetle species and/or their hosts. Changes in temperature regimens may also alter emergence patterns of offspring cohorts that influence beetle aggregation patterns and host colonization success (Tran et al. 2007, Friedenberg et al. 2007). In short, increasing temperatures could benefit some bark beetle species and hinder others. Furthermore, interactions with changes in predator populations, predator and host phenology, and host range shift could confound the direct impacts of temperature on bark beetle development rates and seasonal flight initiation and cessation (Williams and Liebhold 2002, Aukema et al. 2005, Lange et al. 2006, Logan et al. 2006).

## Acknowledgments

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