WESTERN BALSAM BARK BEETLE, *DRYOCOETES CONFUSUS* SWAINE, FLIGHT PERIODICITY IN NORTHERN UTAH

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ABSTRACT.—The flight periodicity of western balsam bark beetle (*Dryocoetes confusus* Swaine) in Big Cottonwood Canyon, Utah, was studied during the summer months of 1992, 1993, and 1994. Contents of baited funnel traps were tallied by species up to 3 times weekly. Two main periods of flight activity were observed each year. The first and, generally, largest occurred in early summer soon after flight was initiated for the season. A 2nd period was observed in late summer, generally August. Timing of the 2 periods was influenced by unusually warm or cool weather in each study year. The 1st period had more males than females while the 2nd period had a majority of females. Except during periods of cool or wet weather, western balsam bark beetles were found to be active at least at minimal levels from June through September.

Key words: Dryocoetes confusus, flight periodicity, Scolytidae, insect control, insect phenology, Abies lasiocarpa, Utah forests.

The western balsam bark beetle, *Dryocoetes confusus* Swaine (Coleoptera: Scolytidae), is a serious insect pest of true firs. This insect's life cycle is not fully understood (Johnson 1985), however, possibly due to the traditionally low commercial value of its host. In British Columbia, for example, timber losses from western balsam bark beetles have only relatively recently been calculated (Doidge 1981). The need to understand the life cycle and behavior of this bark beetle has increased in relation to the increased commercial and aesthetic value of true firs.

Drought-subjected subalpine fir, Abies lasiocarpa (Hook.) Nutt., in northern Utah has been experiencing a western balsam bark beetle outbreak that began in 1989. Most of the affected trees are on the heavily visited Wasatch-Cache National Forest, including the canyons east of Salt Lake City where picnic areas, campgrounds, and ski resorts are common. This caused local forest managers to seek beetle abatement measures. Bark beetle control strategies, such as deployment of semiochemicals or cultural treatments, require knowledge of the time frame in which beetles emerge from infested host material to attack new hosts. This is a report of 3 yr of western balsam bark beetle flight periodicity data from Big Cottonwood Canyon, Utah. Sex

ratios, weather influences, and associated scolytids are also presented.

MATERIALS AND METHODS

Five plots were established on 5–6 June 1992 in Big Cottonwood Canyon, Utah, ranging from 2000 to 2840 m elevation. Plots were selected from areas of recent beetle activity indicated by fading or red subalpine fir crowns.

The plot at 2000 m has a white fir (Abies concolor [Gord and Glend.] Lindl. ex Hildebr.)/Douglas-fir (Pseudotsuga menziesii [Mirb.] Franco) mix and also had the least amount of fading host material of any plot. This is generally the lower elevational band for subalpine fir in Big Cottonwood Canyon. Small amounts of subalpine fir can be found immediately uphill from the plot. The higher plots are dominated by subalpine fir, sometimes in association with Douglas-fir, quaking aspen (Populus tremuloides Michx.), or Engelmann spruce (Picea engelmannii Parry ex Engelm.).

Each plot contained three 16-unit Lindgren funnel traps² spaced at about 50-m intervals in a triangular pattern. Traps were baited with a semiochemical mixture containing *exo*-brevicomin (racemic) released at 1 mg/24 h at $24 ^{\circ}\text{C}^3$ (Borden et al. 1987). Traps were hung as high

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as possible on branches, leaving the trap cup about 1.5 m aboveground. Trap cups were emptied up to 3 times weekly to reduce losses to predation. Cups were emptied less frequently late in each study year as captures diminished. Western balsam bark beetles were tallied along with associated scolytids and important predators, namely checkered beetles (*Enoclerus* spp.). Identification of associated scolytids was provided by Stephen L. Wood⁴. D. confusus captures for the entire season were then totaled for each plot. The percentage of the annual total caught at each observation was then plotted against date for each location.

The study was repeated starting in mid-May 1993 with 5 plots installed from 1750 to 2840 m elevation. Two sites from 1992 were reused, 2 were moved a short distance (about 100 m horizontal), and 1 was new. The lowest elevation plot was deliberately established in the white fir zone. Low-elevation plots were installed earlier in the year than in 1992 to ensure placement before beetle flight commenced. Plots at 1750 and 2350 m were installed 25 May 1993, and the plot at 2560 m was established 27 May 1993. The plot at 2660 m was installed on 8 June 1993 and the plot at 2840 m on 21 June 1993.

The 1994 flight periodicity study utilized the 4 highest sites from 1992, ranging in elevation from 2310 to 2840 m. These areas continued to contain fading host material throughout each study year. The low-elevation sites, lacking a substantial subalpine fir component, were dropped from the study due to the small populations of *D. confusus* in those areas. The plot at 2310 m was established on 10 May 1994, while the remaining plots were installed on 25 May 1994. This gives 3 consecutive years of flight period data for 4 locations.

The first 10 *D. confusus* from each trap cup observation, totaling 30 per plot, were tallied for sex in 1993 and 1994. Females were identified by a prominent setal brush on the frons (Borden et al. 1987). For 1993 and 1994 the sex ratio of each distinct flight surge was compared. The division between surges was determined from each significant flight activity lapse not associated with cool or wet weather.

Weather data from Brighton–Silver Lake⁵ was compared with flight activity for the plots

at 2600/2660 m and 2840 m (this station is geographically and elevationally between the 2 plots). Daily maximum/minimum temperatures and daily precipitation were plotted from 20 May through 31 October for each study year.

RESULTS

Flight Periodicity

1750 METERS.—This site was used only in 1993 with a total of 42 *D. confusus* captures. Consequently, I deleted it from consideration for the purpose of this study. Nearby white fir mortality that was examined contained evidence only of fir engraver beetle, *Scolytus ventralis* LeConte.

2000 METERS.—Because this site had relatively few captures, I used it only in 1992. Flight activity for that year sharply peaked in mid-to late June (Fig. 1). A substantially smaller surge occurred in early August. *D. confusus* captures totaled 1469. The 1st wave of activity accounted for 84% of total captures.

2310/2350 METERS.—The substantial number of captures at the first observation of 8 June 1992 indicates that flight was likely initiated before plot establishment (Fig. 2). Captures peaked in mid-June with activity continuing throughout the month. A 2nd surge began in mid-July and tapered off in mid-August. *D. confusus* captures totaled 19,071. Forty-one percent of the total occurred in the 1st surge.

In 1993 traps at this plot began to capture beetles in mid-June with a small peak occurring in late June. A 2nd wave of captures began in late July, peaking in mid- to late August. *D. confusus* captures were about 9% of those in 1992, totaling 1800. The 1st wave of captures accounted for 10% of the total.

Capture patterns of 1994 were very similar to those of 1992. The first positive observation was on 3 June 1994. An early summer peak occurred on 13 June 1994 with activity tapering off in late June through early July. A late-summer surge occurred in mid- to late July with captures gradually diminishing through early October. *D. confusus* captures totaled 2574, with 30% caught in the 1st surge.

2560 METERS.—The first 1992 observation was positive, indicating that flight was possibly initiated before plot establishment. Beetles

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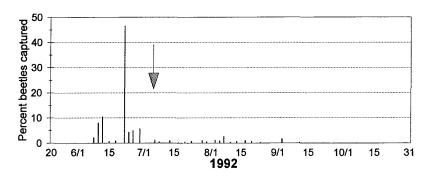


Fig. 1. Percentage of total (n = 1469) seasonal Dryocoetes confusus captures per observation at 2000 m, 20 May-31 October. Arrow indicates the trough between surges not associated with cool or wet weather.

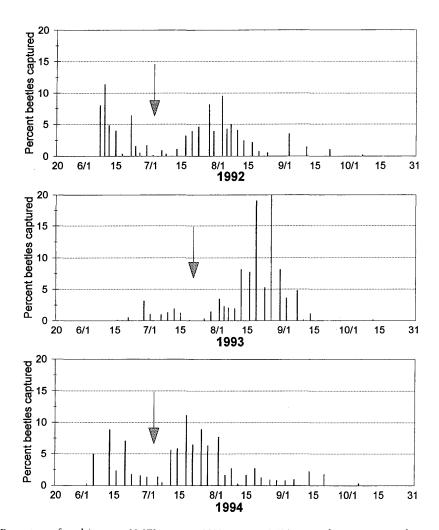


Fig. 2. Percentage of total ($n_{1992}=19{,}071$, $n_{1993}=1800$, $n_{1994}=2574$) seasonal *Dryocoetes confusus* captures per observation at 2310/2350 m, 20 May–31 October. Arrow indicates the trough between surges not associated with cool or wet weather.

were caught in large numbers throughout June with a 2nd surge of activity in early to mid-August (Fig. 3). *D. confusus* trap captures totaled 9164, with 66% captured in the 1st surge.

In 1993 captures began in late June, peaking in early to mid-July. A 2nd, substantially larger wave started in late July and peaked from mid-August through early September. Captures were about 41% of those in 1992, totaling 3763. Twelve percent of that total were caught in the 1st surge.

The pattern of 1994 captures was similar to that of 1992 with a sharp peak occurring in mid- to late June. A 2nd wave began in late July, peaking in early August. *D. confusus* captures totaled 4476, half of which were caught in the 1st surge.

2600/2660 METERS.—1992 captures began in mid-June with a sharp peak occurring in late June (Fig. 4). A 2nd wave began in late July with a mid-August peak. *D. confusus* captures totaled 7548, with 68% caught in the 1st surge.

In 1993 activity began in late June with an early summer peak in mid-July. A 2nd, substantially larger wave started in late July and peaked from late August through early September. *D. confusus* captures totaled 5882, 16% coming in the 1st surge.

In 1994 activity began in early June with a sharp peak in late June. A 2nd wave began in late July, peaking in early August. Captures were the fewest for any study year, totaling 1331.

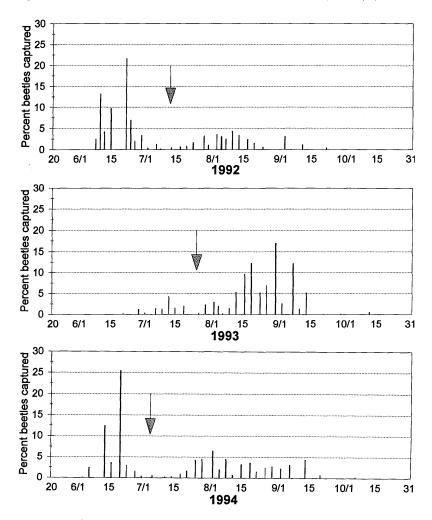


Fig. 3. Percentage of total ($n_{1992} = 9164$, $n_{1993} = 3763$, $n_{1994} = 4476$) seasonal *Dryocoetes confusus* captures per observation at 2560 m, 20 May–31 October. Arrow indicates the trough between surges not associated with cool or wet weather.

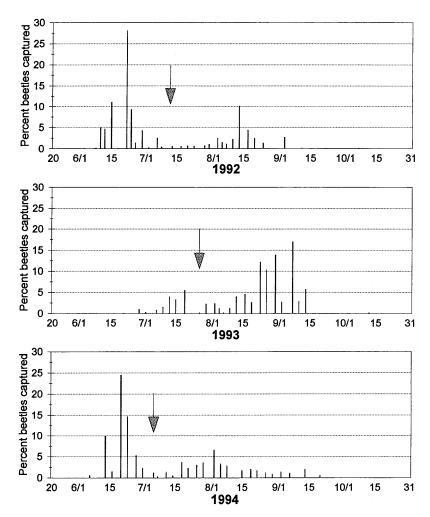


Fig. 4. Percentage of total ($n_{1992} = 7548$, $n_{1993} = 5882$, $n_{1994} = 1331$) seasonal *Dryocoetes confusus* captures per observation at 2600/2660 m, 20 May–31 October. Arrow indicates the trough between surges not associated with cool or wet weather.

Sixty percent of these were caught in the 1st surge.

2840 METERS.—In 1992 the 1st capture was observed on 22 June. Captures peaked in late June, and considerable activity continued through early July (Fig. 5). A 2nd surge occurred in mid- to late August. Captures totaled 17,542 with 72% caught in the 1st surge.

In 1993 activity began in early July with a very large peak occurring in mid- to late July. A 2nd surge occurred in mid- to late August. Captures were down from 1992 levels but were still substantial, totaling 10,344. Seventy-six percent of these were caught in the 1st surge.

In 1994 flight initiated in mid-June with a distinct spike in late June. A late-summer surge

began in late July and continued through mid-August. Captures were the greatest of any plot in any year, totaling 20,600. Sixty-seven percent were caught in the 1st surge.

Surge Activity

Considering only the 4 plots common to each study year, there is a trend for the 1st surge to be larger than the 2nd with increasing elevation (Table 1). The lowest elevation plot consistently captured more beetles in the 2nd wave. The highest plot, however, consistently captured more beetles in the 1st surge.

Weather Influences

Periods of cold and/or wet weather coincided with a reduction or pause in beetle

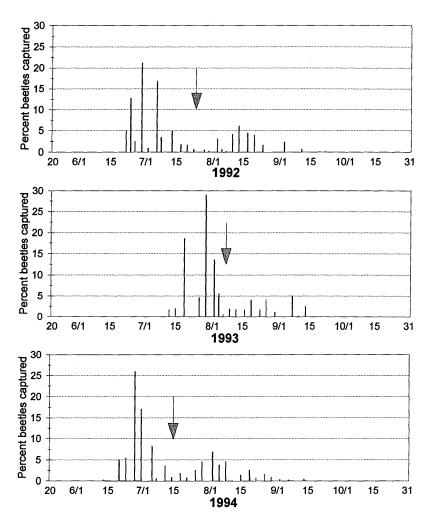


Fig. 5. Percentage of total $(n_{1992} = 17,542, n_{1993} = 10,344, n_{1994} = 20,600)$ seasonal *Dryocoetes confusus* captures per observation at 2840 m, 20 May–31 October. Arrow indicates the trough between surges not associated with cool or wet weather.

captures (Figs. 6–8). Very little flight occurred when daily maximum temperatures were less than 15°C, confirming Stock's (1991) findings. Lapses in flight activity between the main surges, however, are not necessarily associated with cool or wet weather. With 4–7 wk between peaks, warm, dry days were available during these spans of reduced flight.

One would expect delayed emergence and flight timing with increasing elevation. Initial captures at 2840 m were about 2–3 wk later than at 2310/2350 m each year. Timing of peak flight activity was similarly delayed with increasing elevation (Figs. 2–5).

February through May 1992 was the warmest on record for that period in northern Utah. June through August 1993 was the coolest on record while June through August 1994 was the warmest. The warm spring of 1992 coincided with an earlier than expected flight commencement. D. confusus were likely flying before trap placement, possibly as early as late May at lower elevations. In contrast, the snowy winter and spring of 1993 followed by a record cool summer resulted in a delayed beetle flight. In 1992 D. confusus were first captured at 2840 m on 10 June compared with 6 July in 1993. In each year, regardless of the overall weather regime, I observed that flight did not initiate until the local snowpack was mostly melted and that the early summer peak occurred after all snow patches were gone.

Sex Ratio

The early summer surge typically had a higher portion of male beetles (Table 2). Males were especially dominant during the first 5–10 d of emergence, comprising nearly all of those sampled. The sex ratio then became more evenly mixed for the remainder of the early summer, including during peak activity. The late-summer surge was dominated by females in each year, the ratio being more stable throughout the period.

Secondary Scolytids and Predators

Other scolytids captured include *Gnathotrichus sulcatus* LeConte (ambrosia beetle), *Pityokteines minutus* Swaine, *Xylechinus montanus* Blackman, *Hylastes subopacus* Blackman, *Scoly-*

TABLE 1. Percentage of total seasonal beetle captures per plot occurring in the 1st surge.

Year	Plot (elev. [m])	1st surge (%)
1992	2310/2350	41
	2560	66
	2600/2660	68
	2840	72
1993	2310/2350	10
	2560	12
	2600/2660	16
	2840	76
1994	2310/2350	30
	2560	50
	2600/2660	60
	2840	67

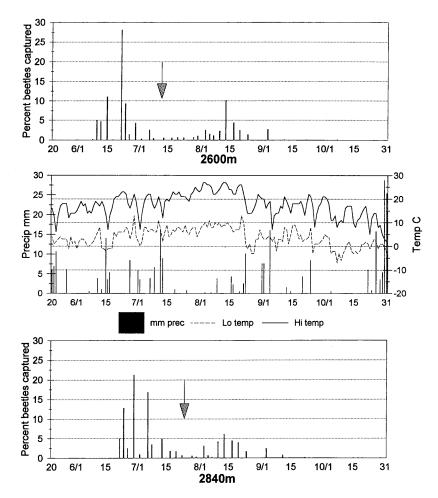


Fig. 6. 1992 daily weather conditions at Brighton–Silver Lake (2700 m) with *Dryocoetes confusus* flight activity at nearby plots. Arrow indicates the trough between surges not associated with cool or wet weather. Note the lag effect, resulting from 2- to 5-d observation intervals, which can give the illusion of flight activity during adverse weather.

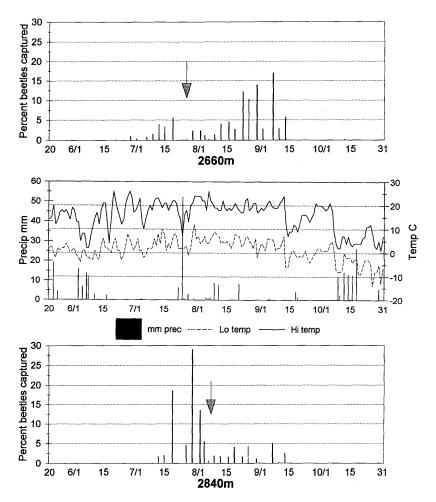


Fig. 7. 1993 daily weather conditions at Brighton–Silver Lake (2700 m) with *Dryocoetes confusus* flight activity at nearby plots. Arrow indicates the trough between surges not associated with cool or wet weather. Note the lag effect, resulting from 2- to 5-d observation intervals, which can give the illusion of flight activity during adverse weather.

tus ventralis LeConte (fir engraver beetle), Ips spp., Cryphalus ruficollis Hopkins, Hylurgops porosus (LeConte), Scolytus opacus Blackman, Dryocoetes affaber (Mannerheim), and Dryocoetes sechelti Swaine. Checkered beetles, Enoclerus spp., were the most common and important predaceous insect trapped. Other predators captured include snakeflies (Raphididae) and rhizophagids. Gnathotrichus sulcatus, Xylechinus montanus, Hylastes subopacus, Dryocoetes affaber, Enoclerus spp., and rhizophagids were caught in sufficient numbers to suggest that they possibly cue on exo-brevicomin.

Clerids, or checkered beetles (*Enoclerus* spp.), were captured before western balsam bark beetle flight commencement in each year.

Captures generally peaked in mid- to late June, then tapered off through August. Few clerids were captured later than the end of August in any year though *D. confusus* continued to be active. At the 4 plot locations common to each study year, a total of 242 clerids were caught in 1992, 357 in 1993, and 307 in 1994.

DISCUSSION

Flight Periodicity

Western balsam bark beetles were caught throughout the summer months for all study years. Beetle flight typically started in June and continued well into September with a few captures as late as early October. Once flight was initiated, only cool or wet weather could

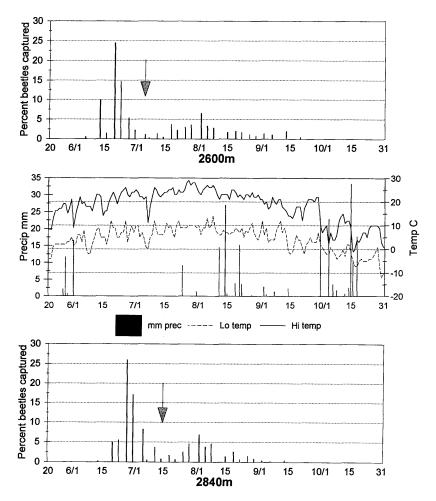


Fig. 8. 1994 daily weather conditions at Brighton–Silver Lake (2700 m) with *Dryocoetes confusus* flight activity at nearby plots. Arrow indicates the trough between surges not associated with cool or wet weather. Note the lag effect, resulting from 2- to 5-d observation intervals, which can give the illusion of flight activity during adverse weather.

completely curtail it. Some warm, dry periods, however, had dramatically reduced activity relative to the peaks. At each plot 2 distinct peaks of flight activity were seen every year. Some plots appeared to have a 3rd peak in September of 1992 and 1994, but this can be attributed to a reduction in trap checking frequency at those times. Generally, the 1st peak was sharp and occurred within 2–3 wk of initial emergence. A 2nd peak was observed 4–7 wk after the 1st.

This is similar to Stock's (1991) findings in British Columbia where there "were two major flight periods per year, the first commencing in mid- to late June, and the second in mid- to late August." Stock found this flight period to correspond well with the life cycle described by Mathers (1931).

Mathers (1931) studied the western balsam bark beetle life cycle at Stanley, B.C., using caged subalpine fir bolts. Young adults were found to emerge and attack fresh trees in June and Iuly. Eggs were laid through August before parents commenced feeding in tunnels before overwintering. Galleries were advanced the following June and July with continued egg laying. Parents then reemerged in July to attack a fresh host with a 3rd set of brood tunnels excavated, eggs being laid through August. Mathers concluded this to be the end of the life cycle. Eggs from the 1st brood overwintered as larvae before pupating the following summer. The 2nd winter was passed as young adults that emerged to attack fresh trees the following June and July. Eggs from the 2nd and 3rd broods overwintered as larvae that pupated the

TABLE 2. Percentage of females among sampled beetles in early and late-summer surges.

Plot (elev. [m])	1993		1994	
	1st surge (%)	2nd surge (%)	1st surge (%)	2nd surge (%)
2310/2350	47	74	38	51
2560	46	71	29	60
2600/2660	34	75	28	66
2840	52	64	44	60

following year and emerged as adults the next season. Given this life cycle, one would expect to find all life stages represented in any given year. Stock (1991) suggests that the August peak observed in his study corresponds to the July reemergence described by Mathers, the timing difference due to warmer conditions at Mathers' site. Using Mathers' life cycle, the 2 flight peaks must be of different generations, the June peak being of newly emerged young adults and the August peak being of reemerged 2nd-yr adults. This gives a 3-yr life cycle when the reemergence year is included. Beetles from eggs laid in 1991, for example, presumably might not complete their life cycle until 1994.

Bright (1963) suggests that parent beetles may die in their 1st or 2nd brood tunnels before reemerging to attack another host. This would account for the late-summer surge often having less activity than the early summer surge. Bright also believes *D. confusus* to have a 1-yr life cycle in the western United States, the life cycle proposed by Mathers (1931) being a phenomenon restricted to the insect's northern range. No data or references, however, are cited for this assertion.

The flight period data presented here produced noticeably different results each year. This is almost certainly associated with the record-setting weather regimes seen each study year. The double peak pattern was not as evident during the cool, wet summer of 1993. Only the highest elevation plot exhibited a large, early summer peak, July in this case. The lower elevation plots had a noticeably reduced early summer peak. The greatest activity at these plots occurred in late August. The record cool summer weather likely caused the delayed emergence seen in 1993, but this does not explain the diminishment of the early summer peak. Even with delayed development, I ex-

pected considerable activity once flight was initiated. Cold weather during emergence was explored as a possible cause for the reduction in the early summer peak. Night temperatures at 2700 m dropped to -4°C on 24 June 1993, which could have killed some new adults and further delayed the early summer flight (Barbara Bentz⁶ personal communication). Perhaps development of some new adults was delayed such that their emergence overlapped with that of reemerged adults in the late summer.

At the highest plot, Mathers' (1931) hypothesized life cycle corresponds well with the data. The 2nd and 3rd broods described by Mathers would assure an early summer surge each year even though 2 yr is required for sexual maturity. In other words, there is no "off year" such as with the 2-yr life cycle of the spruce beetle, Dendroctonus rufipennis (Kirby).

Some results from this study did not match Mathers' (1931) life cycle as well as did Stock's (1991). For example, assuming that the same local population was sampled each year, adults in the early summer flight of 1993 should be represented again in the late-summer flight of 1994. Allowing for some degree of mortality, I expected the late-summer surge to have fewer beetles than the early summer surge of the previous year for a given location. This study produced 2 examples where the late-summer surge contained several times more beetles than the early summer surge of the previous year. If, in fact, these plots did sample the same populations each year, then Mathers' (1931) life cycle may not be accurate for northern Utah.

Though funnel trap captures are not appropriate for adequately describing a life cycle, there are several possible explanations for the unexpected results at the 3 lower plots. The record-setting weather regimes in each year would have certainly affected beetle phenology. Perhaps some critical thresholds were not achieved in 1993, resulting in retarded development or mortality (Barbara Bentz personal communication). This may have affected young adults more so than reemerging adults. Conversely, record warm weather in 1992 and 1994 could have advanced development. Perhaps the 2nd and 3rd broods are not important in the overall life cycle. Amman and Bartos (1991) found reemerged mountain pine beetle, Dendroctorus ponderosae Hopkins, females to

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produce significantly fewer offspring than new females with males. Perhaps lower elevation beetles tend to have a 1-yr life cycle while 2 yr is required for beetles at higher elevations. Probably some combination of these factors plus some not explored, such as disease and predation, contributed to the results.

Sex Ratio

Stock (1991) found that the late-summer surge is comprised largely of females. Using August 1 to distinguish 1st and 2nd flight, Stock found females to comprise 48%, 29%, and 50% of the 1st flight during 3 consecutive years. The 2nd flight had 80%, 48%, and 66% females. I found similar trends in northern Utah. This predominance by females during 2nd flight is typical for other scolytids that exhibit reemergence (Anderbrandt et al. 1985, Flamm et al. 1987). This suggests that the late-summer surge, in fact, comprises reemerged adults. The dominance of males during the initial days of early summer emergence suggests that they are likely responsible for host selection and mate attraction.

Weather Influences

Stock (1991) found the majority of western balsam bark beetle flight to occur when the daily maximum temperature was greater than 15°C. The same trend is seen here. Periods of cool weather, especially when coupled with precipitation, essentially stopped beetle captures. Given warm, dry days, *D. confusus* was found to be active as late as early October, albeit in greatly reduced numbers. Any control strategy will need to consider this extended flight period.

Surprisingly, the cool, wet summer of 1993 failed to have any obvious effect on the 1994 beetle population other than to delay emergence. I hypothesized that this weather pattern would have increased beetle mortality, resulting in fewer trap captures in 1994. Elsewhere in the region, mountain pine beetle larvae were observed with retarded development, possibly leaving overwintering life stages more vulnerable to cold weather mortality. Assuming a 2-yr life cycle for western balsam bark beetle, perhaps the more cold-susceptible life stages would not have emerged until June 1995. It is also possible that winter temperatures in 1993–94 did not reach lethal levels.

While early emergence was associated with a record warm spring in 1992, the early summer peak was no earlier than after the more typical spring of 1994. Timing of the early summer peak for each plot occurred on essentially the same date in 1992 and 1994. Timing of the late-summer peak, however, was about 2 wk earlier during the record warm summer of 1994 than the more typical summer of 1992.

Conclusion

Once flight begins, activity typically builds to a sharp peak within 2 wk. This generally occurs from mid-June through early July. Activity then subsides before building to a 2nd peak 4–7 wk later, usually in August. Significant activity can continue into early September with some beetles flying as late as early October.

Cultural or semiochemical management of western balsam bark beetle will need to consider the double peak flight pattern of parent beetles and the fact that adult beetles can be found in some quantity throughout the warmer months. Removal of infested host material, for example, should be done in the fall when flight is complete. Anti-aggregation pheromones will need to be formulated to effuse up to 4 mon or, possibly, applied twice per season.

Further research is needed to confirm or revise the life cycles described by Mathers (1931) and suggested by Bright (1963) since control strategies for a 1-yr life cycle can be different from a 2- or 3-yr life cycle. Considering the 1st versus 2nd surge differences, this should be done for a range of elevations. The role of remerged adults in brood production must be determined for a more complete understanding of the overall life cycle. The conditions leading to an outbreak also need to be quantified such that cultural guidelines can be established.

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LITERATURE CITED

- AMMAN, G. D., AND D. L. BARTOS. 1991. Mountain pine beetle offspring characteristics associated with females producing first and second broods, male presence, and egg gallery length. Environmental Entomology 20: 1562–1567.
- ANDERBRANDT, O., F. SCHLYTER, AND G. BIRGERSSON. 1985. Intraspecific competition affecting parents and off-

- spring in the bark beetle *Ips typographus*. Oikos 45: 89–98.
- BORDEN, J. H., A. M. PIERCE, H. D. PIERCE, JR., L. J. CHONG, A. J. STOCK, AND A. C. OEHLSCHLAGER. 1987. Semiochemicals produced by western balsam bark beetle, *Dryocoetes confusus* Swaine (Coleoptera: Scolytidae). Journal of Chemical Ecology 13: 823–836.
- BRIGHT, D. R., JR. 1963. Bark beetles of the genus Dryocoetes (Coleoptera: Scolytidae) in North America. Annals of the Entomological Society of America 56: 103–115.
- DOIDGE, D. 1981. Western balsam bark beetle in British Columbia. Canadian Forest Service, Pacific Forest Research Centre. Victoria. B.C. Forest Pest Leaflet 64.
- FLAMM, R. O., S. P. COOK, T. L. WAGNER, P. E. PULLEY, AND R. N. COULSON. 1987. Reemergence and emergence of *Ips avulsus* and *Ips calligraphus* (Coleoptera: Scolytidae). Environmental Entomology 16: 869–876.
- JOHNSON, D. W. 1985. Forest pest management training manual. USDA Forest Service, Rocky Mountain Region. Lakewood, CO. 138 pp.
- MATHERS, W. G. 1931. The biology of Canadian bark beetles. The seasonal history of *Dryocoetes confusus* Sw. Canadian Entomologist 68: 247–248.
- STOCK, A. J. 1991. The western balsam bark beetle, *Dryocoetes confusus* Swaine: impact and semiochemical-based management. Unpublished doctoral dissertation, Simon Fraser University, Burnaby, B.C. 133 pp.

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