THE FLIGHT PERIODICITY, ATTACK PATTERNS, AND LIFE HISTORY OF *DRYOCOETES CONFUSUS* SWAINE (COLEOPTERA: CURCULIONIDAE: SCOLYTINAE), THE WESTERN BALSAM BARK BEETLE, IN NORTH CENTRAL COLORADO

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ABSTRACT.—*Dryocoetes confusus* Swaine, the western balsam bark beetle, is an important bark beetle associated with *Abies lasiocarpa* (Hook.) Nutt. (subalpine fir) in western North America. Little information is available on the life cycle and ecology of this insect in Colorado. In this study in north central Colorado, we examined its flight periodicity, attack patterns, and life cycle in downed trees. Flight season, as indicated by pheromone-trap catches, began in early June. Peak flight was observed during early to mid-July. A second peak in flight was observed in some years, but its occurrence was not consistent. Preferred attack sites on downed trees were the underside or side of the log and through branch stubs. The life cycle for this beetle was completed in 2 years, consistent with earlier observations from British Columbia. Sex ratio was 1:1, but a higher percentage of males fly earlier in the season.

Key words: Dryocoetes confusus, *western balsam bark beetle,* Abies lasiocarpa, *subalpine fir, flight periodicity.*

Bark beetles are among the most intriguing forest insects. North American species number over 500 and use conifers and broadleaves as hosts (Wood 1982). The plurality of species use the phloem, the live portion of the tree bark, as a source of nutrients and for habitat and reproduction. Bark beetles spend their entire life cycle in this subcortical environment, except for a few hours where efforts are focused on seeking new hosts. During host colonization, most species communicate through a sophisticated chemical process using pheromones (Wood et al. 1966, Borden 1974). A few bark beetle species are known to cause extensive tree mortality in coniferous forests and are often considered a nuisance. Yet they contribute to essential ecological processes such as nutrient cycling, forest regeneration, and habitat creation for many wildlife species.

The genus *Dryocoetes* Eichhoff includes 7 species in North America (Bright 1963). Perhaps the most notorious is the western balsam bark beetle (*Dryocoetes confusus* Swaine). The original description of *D. confusus* was presented by Swaine (1912) and the genus was revised by Bright (1963). The insect is about 3–4 mm in length and dark reddish brown in color. Its geographical range extends from British Columbia and Alberta, south to Arizona and New Mexico (Wood 1982). An important host for *D. confusus* is subalpine fir (*Abies lasiocarpa* [Hook] Nutt.). Other reported hosts include *Abies amabilis* (Douglas ex Louden) Douglas ex Forbes, *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr., and *Picea engelmannii* Parry ex Engelm. (Bright 1963).

High mortality levels of subalpine fir have been observed in recent years across the western United States and in Colorado (Harris et al. 2001). Although various factors, such as root disease and abiotic factors, appear to be at play, the western balsam bark beetle is frequently present. This situation may be related in part to the short-lived nature of subalpine fir. Although many trees live to be older than 250 years, most succumb at an early age (Alexander et al. 1984). A general tree decline before 200 years may make trees more susceptible to insect and disease attack. Additionally, *Dryocoetes confusus* is known to carry the fungus *Ceratocystis dryocoetidis* Kendrick & Molnar, a blue-stain fungus with pathogenic properties (Kendrick and Molnar 1965, Molnar 1965). The insect transmits the fungus upon attack.

Subalpine fir has not been a species of commercial importance in the United States, and this is most likely why few studies have

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been conducted with *D. confusus* in the United States. More studies have been conducted in Canada, where subalpine fir is used for forest products (Greenwood and Borden 2000, Maclauchlan et al. 2003, Jeans-Williams and Borden 2006).

Dryocoetes confusus is known to preferentially attack trees exhibiting reduced tree vigor. Characteristics of susceptible trees include lower percentage of bole covered by crown, lower crown volume, slow growth in the 5 years prior to attack, older age, and larger diameter (Bleiker et al. 2003). The authors suggest that larger diameter and older age are correlated and may indicate tree senescence, which may also be related to reduced vigor. Stock (1991) indicated that *D. confusus* will attack fresh downed trees suggesting that blowdowns may provide resources for population increase. McMillin et al. (2003) confirmed this to be the case in 3 blowdown areas in the Bighorn National Forest, Wyoming. Stock (1991) and Hansen (1996) examined *D. confusus* flight patterns in British Columbia and northern Utah, respectively. Both studies reported 2 major flights, 1 in early summer and 1 in late summer.

Mathers (1931), working in British Columbia, conducted the only study to date on the life cycle of this insect and indicated completion of the life cycle in 2 years. Bright (1963) suggested that in the western and southwestern United States, the life cycle may be completed in 1 year or less. A bark beetle species may often exhibit variability in its life cycle across geographic regions. For example, *Dendroctonus rufipennis* Kirby, the spruce beetle, most commonly exhibits a 2-year life cycle, but life cycles from 1 year up to perhaps 4 years are possible (Massey and Wygant 1954, Knight 1961, McCambridge and Knight 1972). Therefore, it is of interest and relevance to study the biology and ecology of *D. confusus* in Colorado. In this paper, we present results from studies on the flight periodicity, patterns of downed-tree attack, and life cycle of *D. confusus* in north central Colorado.

METHODS

Study Site

The study was conducted at the Fraser Experimental Forest located in the Sulphur Ranger District of the Arapaho and Roosevelt National Forests in north central Colorado (UTM: Zone 13, East 0424500, North 4417400). Elevation at the experimental forest ranges from 2680 to 3900 m. Long, cold winters and short, cool summers characterize the forest. At forest headquarters, (elevation 2745 m), mean average yearly temperature is 0.5 °C and mean monthly temperature is –10 °C for January and 12.7 °C for July. About two-thirds of the precipitation is in the form of snow from October to May, with an average of 584 mm at forest headquarters and 737 mm over the entire experimental forest. The majority of the forest developed after a stand-replacing fire in 1685. The subalpine forests in the experimental forest site include predominantly subalpine fir and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) at higher elevations, north slopes, and along streams; these subalpine forests also include predominantly lodgepole pine (*Pinus contorta* Dougl. Ex. Loud.) at lower elevations and on drier slopes. Aspen (*Populus tremuloides* Michx.) is also distributed throughout the forest.

Flight Periodicity

Borden et al. (1987) indicated that *exo*-brevicomin is the most important aggregation pheromone of *D. confusus.* This pheromone has been used to attract *D. confusus* to Lindgren funnel traps (Stock 1991, Hansen 1996). For this study, we used 16-funnel Lindgren funnel traps baited with *exo*-brevicomin to monitor flight periodicity of *D. confusus.* We used a commercial tree bait as a release device which elutes (±)-*exo*-brevicomin at 1.2 mg per 24 hours (Pherotech International, Delta, British Columbia, www.pherotech.com).

In 1996, we used 4 traps at each of 3 elevations: 2769 m, 2923 m, and 3077 m. Traps at each elevation were separated by 325 m. Every year from 1997 to 2000, 7 traps were set the same distance apart at each of the 3 elevations. A small piece of insecticide strip was placed in the collection cup of every trap to kill the insects and reduce cannibalism. Traps were deployed on the following dates: 25 June 1996; 13 June 1997 for the 2769-m and 2923-m traps and 9 July 1997 for the 3077-m traps; 8 June 1998; 5 June 1999; and 5 June 2000. Each year, specimens were collected from the traps once a week and frozen until they were processed in the laboratory. Traps were serviced each year until the last week in September of

that year. In the laboratory, *D. confusus* beetles were counted and sorted by sex, the presence of hair tufts on the head distinguishing the females. Air-temperature data were obtained from weather-station records at the experimental forest headquarters (elevation 2745 m). We plotted maximum temperatures at forest headquarters against flight periodicity to visually examine the relationship between air temperature and insect flight at the lowest elevation. We also graphed the cumulative emergence of beetles and the percentage of males caught throughout the season for each year and across all elevations. We calculated the mean number of beetles caught per week per trap across years and elevations and tested for differences using mixed procedures in SAS (Littell et al. 1996). Using generalized additive models, we tested the hypothesis that more male beetles would be caught early in the season (Hastie 1992). A loess curve was fit to all percentages of males caught across all Julian dates and years. The effect of years was then removed and the effect of Julian dates tested against a null model. To test the influence of years in the relationship, a model with only years was tested against a model with both years and Julian dates.

Attack Patterns in Downed Trees

In July 2000, we felled a group of 5 trees at one location and a group of 6 trees at another location within Fraser Experimental Forest at an elevation of about 2300 m. Because we were working with endemic population levels of *D. confusus*, we baited the area by placing an *exo*-brevicomin attractant in each group. In the fall 2000, we divided the bole of each downed tree into thirds and sampled 15 × 30-cm areas in the top, bottom, and sides of each third of the tree. In each sample we counted the number of *D. confusus* attacks, which can be identified by the presence of boring dust and frass at the entrance of the holes. We also recorded whether the point of entry into the bole was at the base of branch stubs. These data were analyzed with multiresponse permutation procedures (Mielke and Berry 2001). When multiple comparisons were relevant, the Peritz closure method was used (Petrondas and Gabriel 1983).

Life Cycle

We used the same groups of felled trees described above to examine the life cycle of *D. confusus* at these sites. We collected two 15 ×

15-cm bark samples from each tree at both sites. We intended to take one sample from the top of the downed tree and one from the bottom; however, accessibility to the bottom of the downed tree was difficult; therefore, most of the samples were collected from the top and one of the sides of the tree. Samples were collected 4 times: September 2000, June 2001, July 2001, and September 2001. For each sample, we recorded the number and length of galleries for each attack, number of eggs, number of live larvae, and number of brood adults. No pupae were observed in the samples. In spring 2002, we cut 2 sections 46 cm in length from the lower bole of each of the downed trees and placed them in emergence cages at the site. Collections from the emergence cages were made periodically through 2002 and the number of emerging beetles from each cage recorded. The PROC MIXED routine in SAS (Littell et al. 1996) was used for repeated-measures analysis, and multiple comparisons were conducted using Tukey's studentized range test.

RESULTS

Flight Periodicity

In 1996, *D. confusus* had started flight at all elevations by the time we checked our traps for the first time on 3 July 1996 (Fig. 1). At the low elevation, we observed somewhat higher catches on 9 July. The observed increase on 28 August was due to logistical difficulties that prevented servicing the traps on 21 August; therefore, the catches on 28 August actually represent 2 weeks. Trap catches at the mid-elevation site peaked before we serviced our traps for the first time. At the high site, we also saw slightly elevated catches on 9 July and on 31 July.

In 1997, we caught one beetle in the mid-elevation traps and no beetles in the low-elevation traps on 18 June (Fig. 1). Peak flight at these 2 lower elevations was observed on 9 July. Snow cover prevented us from deploying high-elevation traps until 7 July. These traps were first serviced on 16 July, which was the highest catch observed for that elevation. This suggests that peak flight may have already occurred at that elevation. A second flight peak was observed at the low elevation on 28 August. Logistical problems resulted in the loss of data for the mid-elevation traps on 21
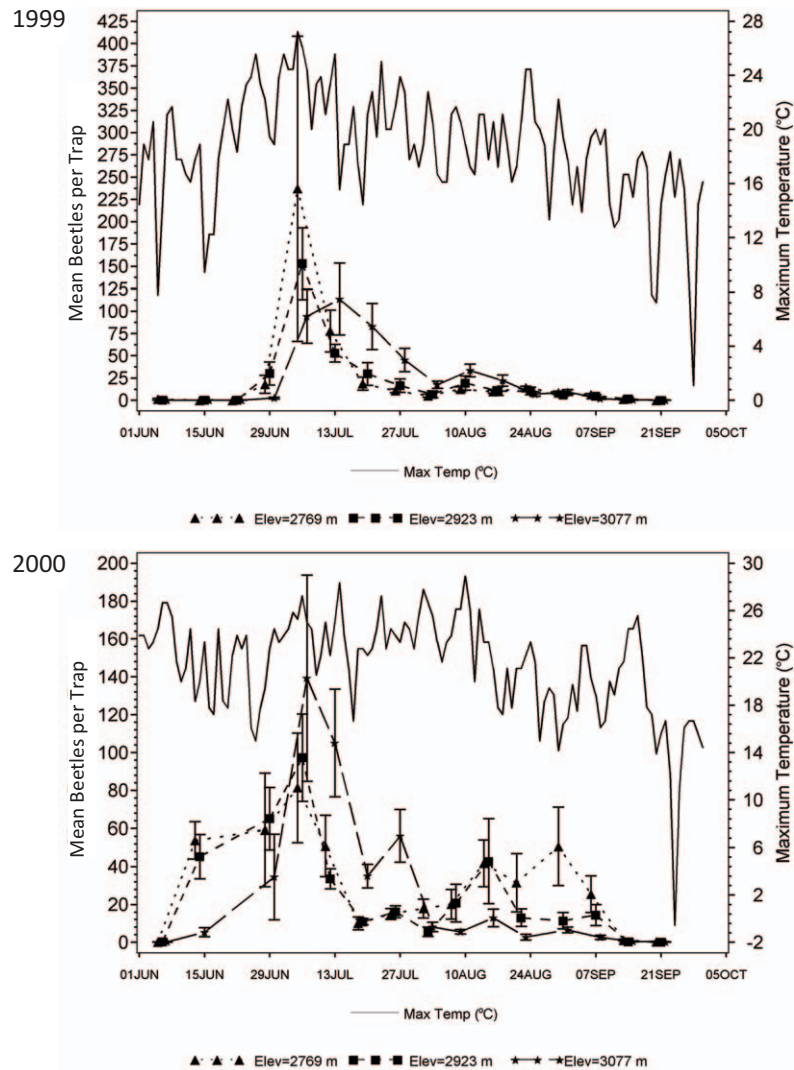
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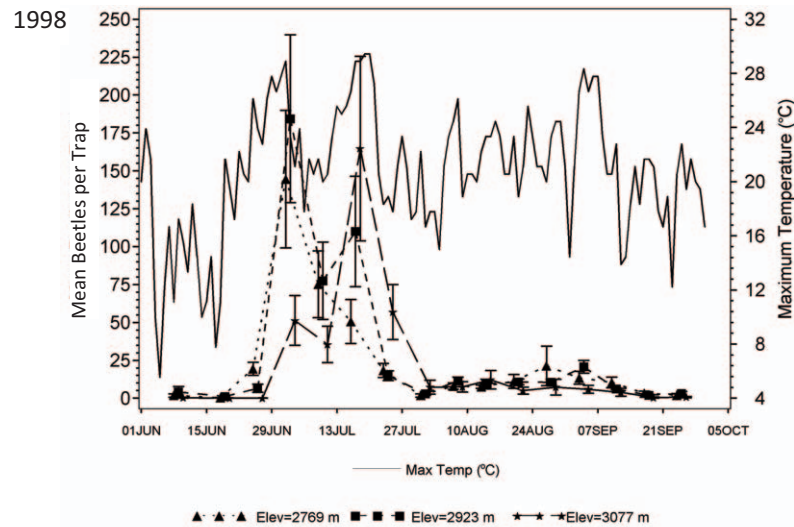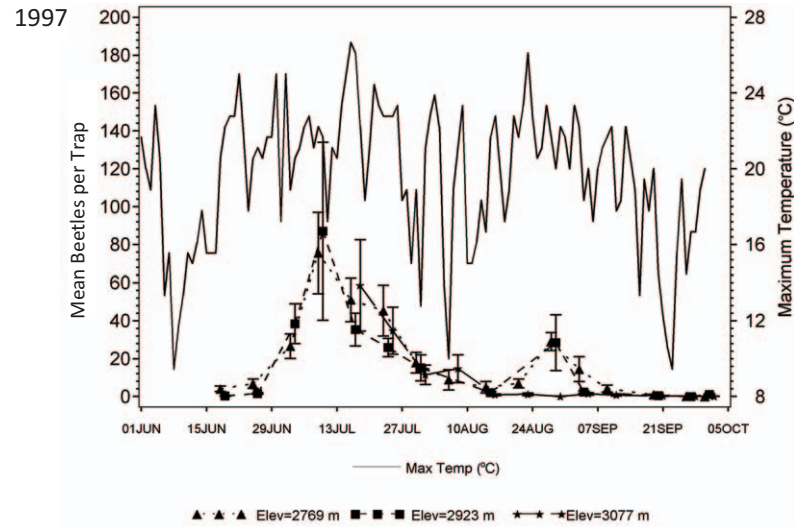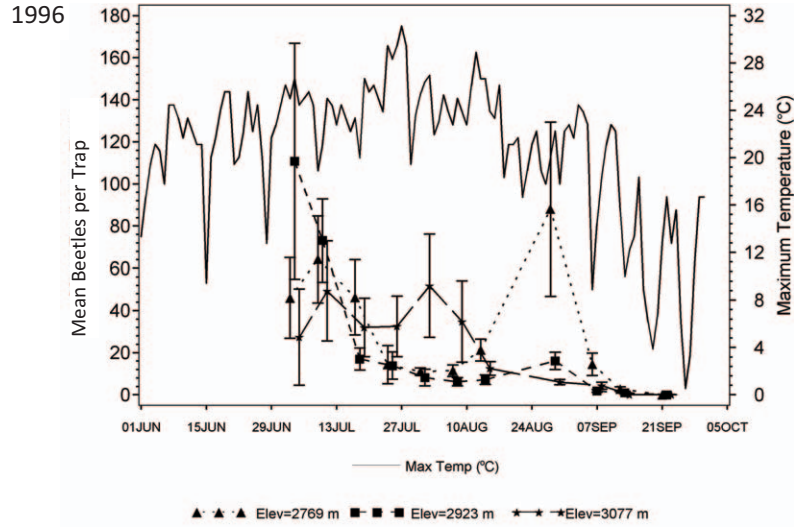
Fig. 1. Mean number of *Dryocoetes confusus* per trap by elevation during the 1996–2000 flight periods and maximum daily temperature at 2745 m elevation. Error bars indicate standard error of the mean. For easier inspection of the graph, collection dates have been shifted by one day. Fraser Experimental Forest, Fraser, Colorado, 1996–2000.

August and for the high-elevation traps on 28 August. Nevertheless, it appears that a second, smaller peak was also observed on 28 August for the mid-elevation. No second peak was observed for the highest elevation.

In 1998, few insects were caught on 18 June, and numbers increased the following week on 25 June at the low- and the mid-elevation sites (Fig. 1). The first date insects were collected from traps at all elevations was 25 June. Peak flight at the 2 lower elevations was observed on 2 July and at the highest

elevation on 16 July. No late-season increases were observed at any of the sites.

In 1999, the first insects at the middle elevation were caught on 14 June, which was the first trap-servicing date (Fig. 1). At the low and high elevations, the first insects were caught on 28 June. Peak flight was on 5 July at the 2 lowest elevations and on 12 July at the highest elevation. Small increases in trap catches were observed again for all elevations on 9 August.

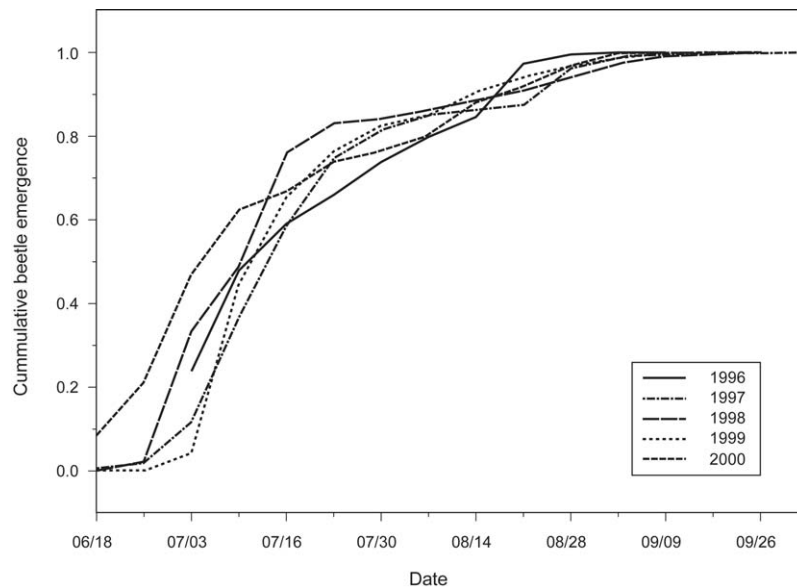In 2000, the first insects were caught on 13 June at all elevations (Fig. 1). Peak flight

Fig. 2. Cumulative per-year trap catches of *Dryocoetes confusus* in pheromone traps across all elevations. Fraser Experimental Forest, Fraser, Colorado, 1996–2000.

TABLE 1. Mean number ($s_{\bar{x}}$) of *Dryocoetes confusus* attacks per m² on downed trees by attack surface and position in bole, and mean number of attacks with bole surface or branch stubs as the point of entry, Fraser Experimental Forest, Fraser, Colorado, 2001.

Location	Mean ($s_{\bar{x}}$) number of attacks per m²
Attack surface	
Top	12.4 (3.4) b*
Side	24.7 (2.9) a
Bottom	21.5 (3.6) ab
Position in bole	
Upper	15.1 (3.0) a
Middle	21.7 (3.2) a
Lower	26.2 (3.9) a
Point of entry	
Bole surface	14.7 (2.3) b
Branch stub	27.1 (3.0) a

*Means followed by the same letter are not significantly different at the 0.05 level, multiresponse permutation procedures (Mielke and Berry 2001) and Peritz closure method (Petrondas and Gabrriel (1983).

was observed at all elevations on 5 July. Small increases were observed on 14 and 30 August at the mid- and low-elevation sites, respectively.

Cumulative flight-trap catches of beetles for all years indicate that about 50% of the insects were caught by the middle of July and 80% by the end of July or beginning of August (Fig. 2). Flight was complete by the beginning of September in all years, as no beetles were caught thereafter.

Trap Catches and Air Temperatures

In 1996, when flight was already in progress during our first sampling date, maximum temperatures had already exceeded 21 °C (Fig. 1). In 1997, flight was just beginning by the time of our first sampling, and again maximum temperatures had just reached 21 °C. Peak flight occurred when maximum temperatures were consistently above the high 15s and low 20s (°C) (Fig. 1). Again in 1998, maximum temperatures had increased to around 21 °C when flight began and had surpassed 27 °C prior to peak flight (Fig. 1). In 1999, temperatures again surpassed 21 °C when flight began and had reached the mid-20s (°C) at peak flight (Fig. 1). In 2000, similar patterns were observed, with maximum temperatures exceeding 21 °C at the beginning of flight and reaching the mid-20s (°C) during peak flight (Fig. 1).

Attack Patterns in Downed Trees

The number of attacks of *D. confusus* per square meter ranged from 12.4 to 27.1, depending on the attack location (Table 1). More attacks were observed in the sides and undersides of trees, although there were no significant differences between the mean number of attacks on the undersides and the tops. We observed no significant differences in the mean number

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TABLE 2. Mean ($s_{\bar{x}}$) number of galleries per attack, gallery length, eggs per attack, and live larvae per attack of *Dryocoetes confusus* at 4 sampling dates and by attack surface on bole across all 4 dates. Fraser Experimental Forest, Fraser, Colorado, 2000–2001.

	Mean number of galleries per attack	Mean gallery length (cm)	Mean total eggs per attack	Mean total live larvae per attack
Date				
13 September 2000	3.6 (0.6) a*	3.3 (0.1) a	15.6 (5.8) a	15.8 (2.3) a
1 June 2001	3.4 (0.7) a	3.5 (0.2) a	22.0 (6.3) a	3.1 (2.5) b
28 June 2001	4.7 (0.6) a	5.4 (0.2) b	77.4 (7.9) b	1.8 (3.2) b
1 September 2001	3.1 (0.9) a	5.6 (0.5) b	n/a	3.6 (4.9) b
Attack surface				
Side	3.8 (0.4) a	4.5 (0.1) a	38.2 (3.9) a	1.4 (0.2) a
Top	3.6 (0.6) a	4.4 (0.2) a	22.7 (7.4) a	0.5 (0.4) b

*Means followed by the same letter are not significantly different at the 0.05 level, Tukey's studentized range test.
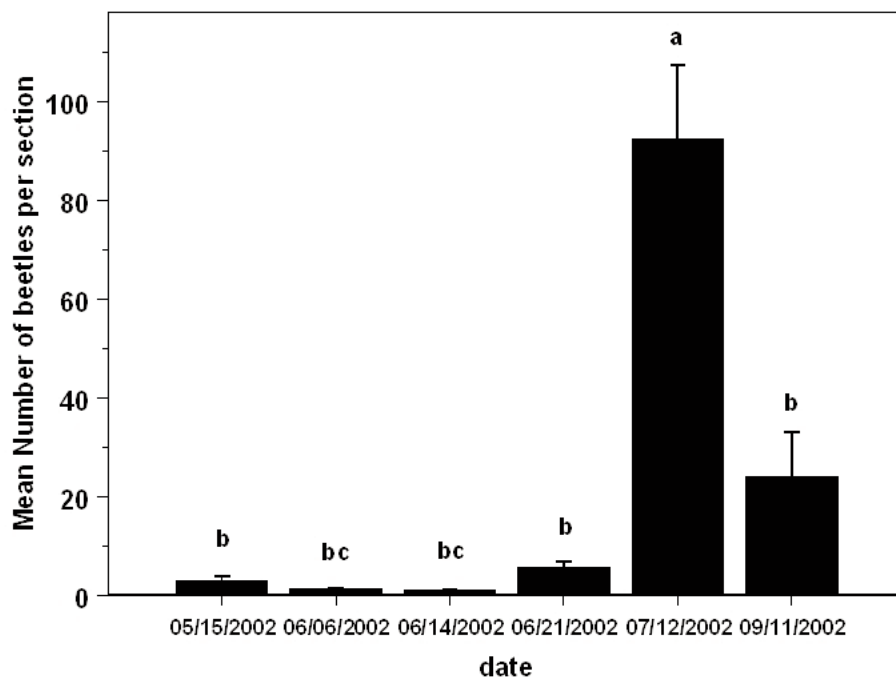

Fig. 3. Adult emergence of *Dryocoetes confusus* from tree sections placed in emergence cages. Fraser Experimental Forest, Fraser, Colorado, 2002.

of attacks among the 3 parts of the bole. Higher numbers of attacks, however, were observed in the branch stubs of the trees compared to bole surfaces (Table 1).

Egg Galleries and Life Stages

The number of galleries per attack was not different among any of the sampling dates, but gallery length was significantly longer on 28 June and 1 September 2001 compared to the first and second sampling dates (Table 2). Eggs were observed on all sampling dates except the last, with the highest number on 28 June 2001.

Live larvae were observed on all sampling dates and were significantly higher on 13 September 2000. Across all dates, no significant differences were observed between the sides and the tops of the boles in mean number of galleries per attack, mean gallery length, or mean number of eggs per attack. We did observe significantly more live larvae per attack in the sides of the boles compared to the tops. Brood adults were observed only on the last sampling date, with 3.4 ($s_{\bar{x}}$ = 2.0) beetles per sample. Emerging adult beetles were collected from bolts in emergence cages on all sampling dates (Fig. 3).

TABLE 3. Mean ($s_{\bar{x}}$) percentage of male *Dryocoetes confusus* caught in pheromone traps per year and mean weekly catch of beetles by year and elevation. Fraser Experimental Forest, Fraser, Colorado, 1996–2000.

	Mean ($s_{\bar{x}}$)
Percent males caught by year*	
1996	44.0% (4.4)
1997	31.3% (5.0)
1998	52.7% (5.0)
1999	42.7% (6.9)
2000	50.0% (3.7)
Mean weekly catch per trap by year	
1996 ($n = 125$)	29.8 (5.8) a[†]
1997 ($n = 193$)	23.6 (4.9) a
1998 ($n = 265$)	32.6 (4.0) a
1999 ($n = 239$)	35.1 (4.2) a
2000 ($n = 251$)	34.6 (4.1) a
Mean weekly catch per trap by elevation	
2769 m ($n = 393$)	31.2 (3.4) a
2923 m ($n = 383$)	29.6 (3.4) a
3077 m ($n = 297$)	32.6 (4.0) a

[*]$\chi^2 = 1.0$, df = 4, $P = 0.06$.
[†]Means followed by the same letter are not significantly different at the 0.05 level, Tukey's studentized range test.
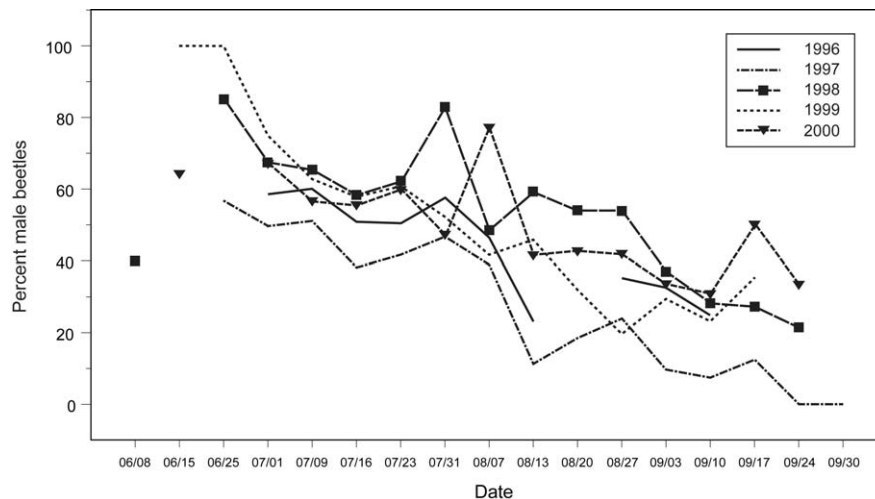

Fig. 4. Percentage of *Dryocoetes confusus* males emerging weekly for each year. Fraser Experimental Forest, Fraser, Colorado, 1996–2000.

Significantly more beetles were collected on 12 July 2002 than on the other sampling dates.

Sex Ratio, Percent Males, and Percent Male Emergence

Male-to-female ratio across all sampling dates, elevations, and years was 1.3:1 with no significant bias toward either sex ($\chi^2 = 0.6$, df = 2, $P = 0.90$). Percentage of male beetles caught per year across all sampling dates and elevations ranged from 31% in 1997 to 53% in 1998 (Table 3; $\chi^2 = 1.0$, df = 4, $P = 0.06$).

Mean weekly catch per trap across years and mean weekly catch per trap across elevations showed no significant differences. Yearly catch of male beetles across all elevations exhibited a significant declining trend with a higher percentage of males emerging earlier in the season (Fig. 4). This is indicated by the significant fit of the loess regression model to the percentage of males caught by Julian day across all years ($P < 0.001$) and for each year ($P < 0.001$; Fig. 5). The fit of the relationship, however, was influenced by year ($P < 0.001$).
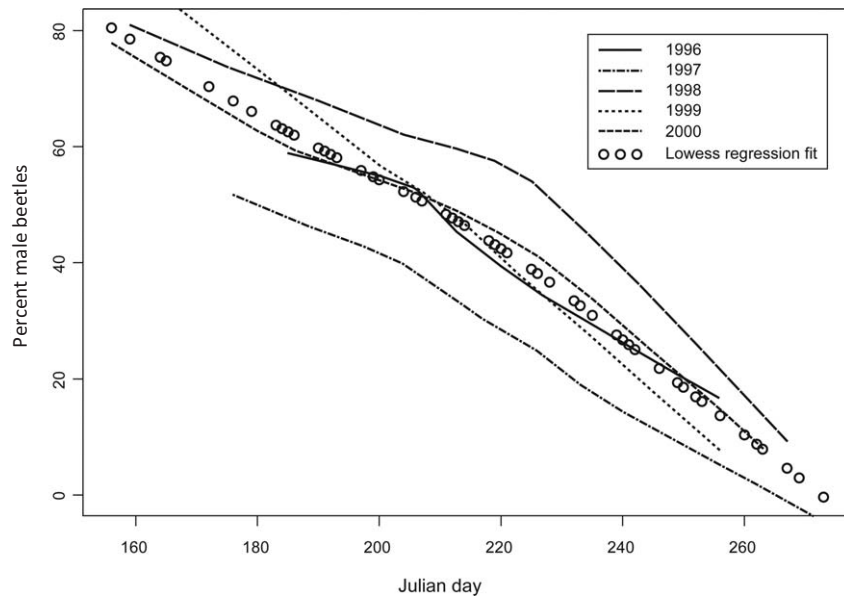
Fig. 5. Loess regression fit to percentage of male *Dryocoetes confusus* catches in pheromone traps across all elevations and years. Circles represent fit across all years and lines represent fit for the indicated year. Fraser Experimental Forest, Fraser, Colorado, 1996–2000.

DISCUSSION

Results from this study indicate that in north central Colorado, *D. confusus* most commonly begins flight in early June, as described by pheromone trap catches, although emergence from trees may begin as early as late May. Peak flight occurs around the first or second week in July. A second peak in flight catches was not consistently observed but was distinct in 1997 and 2000, occurring at all elevations in late August or early September. In 1996, the second peak was in early August at the mid-elevation site and in late August at the low-elevation site.

The flight pattern in 1997 and 2000 is similar to previous studies, although our first observed peak in trap catches occurred later than that observed by Stock (1991) and Hansen (1996). Stock (1991) reported 2 periods of increased flight in British Columbia: mid–late June and mid-August. Hansen (1996) examined flight periodicity in Utah and reported 2 periods of increased activity, the first peak occurring sometime between mid-June and early July and a smaller peak in late summer, mainly in August. Both Stock (1991) and Hansen (1996) suggested that the second peak in flight is the result of reemerging parent adults. This question was not examined in our study, but

the inconsistency of a second peak observed in Colorado warrants further examination of this question. Hansen (1996) indicated that flight began from early to late June, and our data confirm this finding.

Initiation and peak flight appear to be strongly influenced by air temperatures and are complete by the beginning of September. Insect catches in pheromone traps began slowly in early June and were undoubtedly influenced by temperatures associated with each elevation. Stock (1991) reported little flight when temperatures were below 16 °C and peak flights when temperatures were between 16 and 26 °C. Our data are consistent with these observations, as flight in our study sites generally began when temperatures were around 21 °C. Primary dispersal flight occurred consistently from early to mid-July. Attacks were initiated on new hosts at this time.

Attacks on downed trees were observed mostly on the sides and to a lesser extent the undersides of the log and along any part of the bole, with points of entry into the bole primarily at the base of branches. The number of attacks observed in our study ranged from 12.4 to 27.1 attacks · m^2, which was much lower than the number found by Stock (1991). That study presented a mean of 124 attacks · m^2 from the

upper surface of felled trees. It should be noted, however, that our study was conducted with endemic populations, whereas Stock's (1991) was conducted with epidemic populations. Stock (1991) also did not indicate preference of any surface for attack. It may be that surface preference for attack of a downed tree is only evident in low-level populations.

Our study indicates that *D. confusus* exhibits a 2-year life cycle, spending the first winter as a larva and the second winter as a brood adult. This observation is consistent with the study conducted by Mathers (1931) in British Columbia. Mathers (1931) indicated that parent adults were in the overwintering stage during the first winter, and his study reported the presence of larvae by June the following year; however, Mathers' last observation for the year was on 16 August. Our first life-stage sampling in downed trees was in September 2000, just prior to winter. Oviposition began soon after attack, as indicated by the presence of eggs and first instar larvae by 13 September 2000. This appeared to be the primary overwintering stage because by this time, weather at the study site had become unfavorable for continued larval development.

Although we did not separate observed larvae by head-capsule sizes, by 1 June 2001, most of the larvae observed appeared to be second or third instars based on their relative size. Parent adults that had attacked in the previous year continued extending their egg galleries, and gallery-length data demonstrate that gallery length was significantly longer for the 28 June and 1 September 2002 samples. These parent adults also continued laying eggs, as new eggs were observed in the samples taken on 28 June 2001. Mathers (1931) indicated that the initial parent adults would lay a second cohort of eggs in their first tree and emerge for a second time before attacking a second tree. We did not examine that part of the life cycle, but first instar larvae, as evident by their approximate size, were also observed on 28 June 2001. These were undoubtedly larvae hatching from the second cohort of eggs deposited by the adults that attacked the logs in summer 2000.

Brood adults were first observed on 1 September 2001. These adults were in the overwintering stage for the second winter. Emergence from the logs in cages began by the middle of May 2002. This was earlier than when flight

catches generally started in the beginning of June. The early emergence may be due to the disturbance associated with cutting the logs and perhaps to higher temperatures inside the cages. Peak emergence from the logs occurred by mid-July 2002, which is consistent with our flight data.

During the second summer, the number of galleries per attack remained around 3–4, all from the initial attack in 2000, suggesting, as expected, no further attraction of females after the initial attack. Gallery length was further extended by the parent adults in the second summer, but we did not observe very many new eggs. This is the time when brood adults begin emerging, but no new attacks were observed in our samples. Most of the live larvae were observed on the first sampling date in September 2000, which is the time of year when egg hatching occurs. The live larvae we did observe in the second summer were significantly higher in the sides of the boles compared to the tops. We were unable to adequately sample the bottoms of the logs, but since the number of attacks were not significantly different between the sides and the bottoms of the trees, we would expect a similar number of surviving larvae in the bottoms of the boles.

The sex ratio observed from trap catches across all elevations and years was essentially 1:1, which agrees with data presented by Hansen (1996). When sex ratio was examined by years, it was also essentially 1:1, although we observed bias toward females (3:1) in 1997. The lack of significant differences in the numbers of beetles caught per trap across years suggests a stable population during our sampling years, and this population level may serve as a basis to characterize endemic population levels. Although no significant differences were detected in the number of beetles per week per trap across elevations, it should be noted that, in general, beetle flight started about the same time in the spring but ended about 2 weeks earlier in the highest elevation, suggesting a more compact flight season.

We confirmed that males comprised a higher percentage of beetles in the early part of the flight and decreased through the season. Graves (2008) also indicated a higher percentage of male *Ips perturbatus* Eichhoff caught in pheromone traps earlier in the year in Alaska. The percentage of male beetles in our study was influenced by years, likely due to the

female-biased sex ratio in 1997. The influence of year in the pattern of male emergence may also be due to the influence of temperature variations on the timing for emergence and peak flights. Earlier emergence by males, the sex responsible for locating new hosts, may facilitate dispersal into new areas. These males may provide new, unexploited resources for the population and, in addition, enhance genetic diversity by breeding with new populations (Stock 1991).

Bright (1963) had suggested the possibility of a one-year life cycle for *D. confusus* in some sites but this was not the case in our study. This insect may be a good model to examine the influence of increased temperatures on insect development under a climate-change scenario. Warmer temperatures could trigger faster development of the insects. Extended warmer temperatures starting in the spring and continuing into the fall could trigger emergence of brood adults prior to temperatures becoming cold enough to arrest insect flight. However, the emergence of brood adults in the fall may actually be disadvantageous for the insect, as brood adults would only have a short time for mating and oviposition. Moreover, if males begin their flight and cold weather sets in before females follow suit, then availability of males in the following spring could be substantially reduced.

The spruce beetle has demonstrated the ability to complete its development in one year with no adverse effect on reproduction. Actually, populations may build up faster under such conditions (Hansen and Bentz 2003). A one-year life cycle is also a possibility for *D. confusus*, if accelerated development occurs the year following oviposition. Our results provide baseline information for comparing development under warming temperature scenarios

Our study provides a better understanding of the life cycle and biology of *D. confusus* in Colorado. Studies are still needed on the relationship of *D. confusus* with its blue-stain fungus, and with the host tree, as this system has not been rigorously explored. Interactions with root disease and other biotic agents also need attention since these interactions may be of relevant in shaping the structure of subalpine-fir forests in Colorado.

ACKNOWLEDGMENTS

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