

# Comparison of reproductive capacity among univoltine, semivoltine, and re-emerged parent spruce beetles (Coleoptera: Scolytidae)

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**Abstract**—New spruce beetle, *Dendroctonus rufipennis* (Kirby), adults of univoltine and semivoltine life cycles, as well as re-emerged parent beetles, were laboratory-tested for differences in reproductive capacity and brood characteristics. Parameters measured from the three groups include dry weight, lipid content, and egg production. Brood characteristics measured include egg length, development rates, and survival densities. Although there were some differences in dry weight and lipid content, females from the univoltine, semivoltine, and re-emerged parent groups did not greatly differ in egg production. Egg length was slightly smaller for eggs from univoltine parents, but other measured brood characteristics did not differ among the three parent groups, including the density of the surviving brood. In a field study, re-emerged parent beetles were determined to be flight capable. These findings imply that populations with univoltine broods will have higher growth rates than semivoltine populations. Consequently, the presence of univoltine broods, which is weather dependent, increases the risk of a beetle outbreak or can accelerate the rate of spruce mortality in an established outbreak. These results also indicate that re-emerged parent beetles can contribute substantially to brood production. Suppression strategies can be more effective if managers consider the ecological consequences of brood production from the three parent groups.

Hansen EM, Bentz BJ. 2003. Comparaison du potentiel reproductif chez des scolytes de l'épinette (Coleoptera : Scolytidae) univoltins et semivoltins, ainsi que chez des parents émergés pour une seconde fois. *The Canadian Entomologist* **135** : 697–712.

**Résumé**—Des nouveaux adultes du scolyte de l'épinette, *Dendroctonus rufipennis* (Kirby), à cycles univoltin et semivoltin, de même que des parents qui émergent une seconde fois, ont été testés en laboratoire afin d'y identifier les différences entre leurs potentiels reproductifs et entre les caractéristiques de leurs progénitures. Les variables mesurées chez les trois groupes sont la masse sèche, le contenu en lipides et la production d'oeufs. Nous avons examiné les caractéristiques de la progéniture, soit la longueur des oeufs, le taux de développement et les densités de survie. Il y a des différences de masse sèche et de contenu en lipides entre les femelles univoltines, les femelles semivoltines et les femelles émergées à nouveau, mais la production d'oeufs est semblable chez les trois groupes. Les oeufs issus des parents univoltins sont légèrement plus courts, mais les autres caractéristiques sont comparables chez les trois groupes de parents, y compris la densité des progénitures survivantes. Au cours de tests en nature, les parents émergés pour une seconde fois se sont révélés capables de voler. Ces résultats semblent vouloir dire que les populations aux progénitures univoltines auront des taux de croissance plus rapides que les populations semivoltines. En conséquence, la présence de progénitures univoltines, qui dépend de la température, augmente les risques d'une épidémie de scolytes ou peut accélérer la mortalité des épinettes au cours d'une épidémie établie. Ces

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résultats laissent croire aussi que les parents émergés pour une seconde fois peuvent contribuer substantiellement à la production de la progéniture. Les stratégies de suppression seront plus efficaces si les gestionnaires tiennent compte des conséquences écologiques de la reproduction des trois groupes de parents.

[Traduit par la Rédaction]

## Introduction

The spruce beetle, *Dendroctonus rufipennis* (Kirby) (Coleoptera: Scolytidae), is the most significant mortality agent of spruces, *Picea* spp. (Pinaceae), throughout western North America (Holsten *et al.* 1999). Efforts to understand spruce beetle life-history strategies and to predict population dynamics have been confounded by the plasticity with which this species' life cycle responds to variations in environmental conditions (Knight 1961; Dyer 1969). Described life cycles range from 1 to 3 years (McCambridge and Knight 1972), and the duration of each life-history pathway will greatly influence the rate of population growth for this organism. Additionally, iteroparity, or breeding multiple times, also influences the rate of population increase (Cole 1954). Although parent beetles (*i.e.*, beetles that have already produced at least one egg gallery) are known to often re-emerge and construct a second egg gallery (Massey and Wygant 1954; Schmid and Frye 1977), the significance of this phenomenon on population dynamics has not been quantified. These beetles are hereinafter referred to as re-emerged parent beetles, and their life cycle could be any of those expressed by the species.

In the Rocky Mountains, coastal Alaska, and interior British Columbia, a 2-year (semivoltine) life cycle is considered predominant (Schmid and Frye 1977; Werner and Holsten 1985). Adults typically fly in June or July and infest new host trees, with eggs being deposited soon thereafter. By October, the majority of the brood has developed to the prepupal life stage (Schmid and Frye 1977; Hansen *et al.* 2001*b*). Development is resumed the following summer and marked by pupation and eclosion into adults. The new adults overwinter and emerge the following June or July to infest fresh hosts, thus renewing the cycle. A 1-year (univoltine) life cycle is considered typical along the Pacific Northwest coast (Schmid and Beckwith 1975) but has also been found under relatively warm conditions in the Rocky Mountains (Massey and Wygant 1954; Hansen *et al.* 2001*a*), British Columbia (Dyer 1969), and Alaska (Werner and Holsten 1985). Relative to the semivoltine life cycle, egg and larval development is accelerated, resulting in adult brood before the first winter. A 3-year life cycle has also been described from cool sites (*i.e.*, high elevation, northerly aspect), wherein the first winter is passed as an early-instar larva, the second as a prepupa, and the third as an adult (Massey and Wygant 1954; McCambridge and Knight 1972). Regardless of the life-cycle duration, reproductive diapause requires new adults to overwinter before oviposition can commence (Safranyik *et al.* 1990).

Evidence indicates that life-cycle duration is environmentally regulated rather than genetically regulated; *i.e.*, genetics provide the potential for divergent life history, but the outcome is dependent on weather (Massey and Wygant 1954; Dyer 1970; Werner and Holsten 1985; Hansen *et al.* 2001*a*). Microhabitat temperature differences can result in univoltine and semivoltine broods within the same tree. Furthermore, because of the extended ovipositional phase for a single female beetle, intra-brood cohorts will experience significantly different environmental conditions that can result in both univoltine and semivoltine cycles among siblings (EM Hansen and BJ Bentz, unpublished data).

The impact of univoltine broods on spruce beetle population dynamics has not been quantified. Hypothetically, increases in spruce beetle populations from univoltine broods should result in accelerated spruce mortality. For example, the extent of

infestation can be magnified when beetles maturing in 1 year combine with beetles maturing in 2 years to infest new hosts (Dyer 1969). Anecdotal evidence suggests that an unprecedented series of warm summers during the 1990s, which resulted in univoltine broods, contributed to recent outbreaks in Utah and Alaska (Logan *et al.* 2003). For example, univoltine broods predominated during some years in south-central Alaska where over 1 million hectares of spruce have been killed since 1990 (E Holsten, personal communication).

From the equation for instantaneous rate of population increase,  $r = \log_e(R_0/T)$  (Price 1997), where  $R_0$  is the net replacement rate for females and  $T$  is the generation time, semivoltine generations will have a much smaller  $r$  value than univoltine generations if  $R_0$  is held constant. In other words, univoltine populations will have an accelerated growth rate relative to semivoltine populations, other factors being equal; however, any brood population size differences (affecting  $R_0$ ) inherent to each life cycle will also significantly affect the  $r$  value. For example, Mousseau and Roff (1989) found adult size trade-offs associated with shifts in voltinism for a cricket along a latitudinal/climate gradient, and Reid (1962) and Amman (1972) found a positive correlation between body size and fecundity for the mountain pine beetle, *Dendroctonus ponderosae* Hopkins. Conceivably, univoltine beetles may be smaller and less fecund than semivoltine beetles because of reduced feeding time. Additionally, there may be differences in brood survival between the two life cycles that further influence  $R_0$ .

Knowledge of fecundity differences or similarities for new univoltine adults, new semivoltine adults, and re-emerged parent beetles will increase our understanding of spruce beetle population ecology and improve forecasts of disturbance to spruce ecosystems. Furthermore, suppression techniques, including their timing, may need to be modified to address differences among the three groups. The objective of this laboratory study was to compare the reproductive potential of univoltine, semivoltine, and re-emerged parent spruce beetles by measuring (i) parent weight and lipid content; (ii) gallery establishment, egg-free and total gallery lengths, egg production, and egg length; (iii) brood development rates; and (iv) brood survival. An additional objective, evaluated in a field study, was to determine if overwintered, re-emerged parent beetles are capable of flight.

## Methods

### Collection of beetle groups

Adult beetles were identified and collected from infested Engelmann spruce (*Picea engelmannii* Parry *ex* Engelm.) within a single stand on the Dixie National Forest, Utah (37.57°N, 112.85°W). Univoltine and semivoltine adults can be distinguished easily in the field, even in strip-attacked trees that are infested during consecutive years (Table 1). Re-emerged parent beetles, however, can be confused with univoltine hibernators. The spruce beetle is unique among *Dendroctonus* species in that recently eclosed adult beetles often emerge from their pupal chambers and re-enter the same host near the groundline (Schmid and Frye 1977). Re-emerged parent beetles have also been observed hibernating at the root collar (Massey and Wygant 1954; Dyer 1973). To assess classification success of re-emerged parent beetles, we checked for differences in results between univoltine and re-emerged parent groups. Beetles were collected from under the bark of 2–3 trees (40–100 cm DBH) per adult group. Two collections were made: the first being just before flight in early June 2001 and the second being in November 2001 when the beetles' reproductive diapause should have been near completion (Hansen *et al.* 2001b; EM Hansen, unpublished data). To assure that these

TABLE 1. Guidelines used to distinguish univoltine, semivoltine, and re-emerged parent *Dendroctonus rufipennis* from under the bark of infested *Picea engelmannii*.

	Univoltine	Semivoltine	Re-emerged
Host-tree characters	Infested during most recent summer; retaining lightly fading needles; phloem relatively moist	Infested two summers prior; substantial or complete needle loss; phloem relatively dry	Infested during most recent summer (see univoltine)
Life stages in samples	Mixture of teneral adults and larvae/prepupae*	Adults only	Adults only or mixed with immature current broods
Sample position	1–2 m above ground level; collected only from pupal chambers (parent galleries avoided)	1–2 m above ground level; collected only from pupal chambers (parent galleries avoided)	Root collar; collected from mass aggregations in feeding tunnels <sup>†</sup>
Other characters	—	—	Lightly sclerotized individuals avoided <sup>‡</sup>

\* A currently infested tree with univoltine teneral adults also contains some proportion of semivoltine larval broods (Hansen *et al.* 2001a).

<sup>†</sup> New adults and re-emerged parent beetles have been observed hibernating at the root collar (Massey and Wygant 1954; Dyer 1973; Schmid and Frye 1977). Although this habit has been less commonly observed in the Rocky Mountains among univoltine broods (Hansen *et al.* 2001a), its occurrence can confound successful classification of re-emerged parents.

<sup>‡</sup> Recently eclosed adults are light brown and darken increasingly through sclerotization (Linton *et al.* 1984), the rate of which is time and temperature dependent (Hansen *et al.* 2001b). Therefore, univoltine adults are generally lighter than re-emerged parents. Exclusive reliance on this character, however, will result in increasingly frequent classification errors as univoltine broods age. Bias against lightly sclerotized individuals resulted in the disproportionate selection of black morphs over red morphs (Linton *et al.* 1984).

beetles completed their diapause development before use in the experiments, they were held at 0°C for 1 week, 7°C for 2 weeks, and room temperature for 3 days.

### **Parent weight and lipid content**

A random subsample of adult females and males in each parent group, 30 each, was taken from the June and November 2001 collections. Individual specimens were oven-dried for 24 h at 70°C and weighed. Fats were extracted with petroleum ether for 8 h in a soxhlet apparatus (Hagen and Atkins 1975). Beetles were then redried for 8 h and reweighed. Lipid content was calculated as the percent dry body weight.

### **Gallery establishment, egg-free and total gallery lengths, egg production, and egg length**

A live Engelmann spruce, 35 cm DBH, was felled on the Cache National Forest, Utah (41.87°N, 111.48°W), and cut into 30 cm length bolts in November 2000. Bolt ends were sealed with paraffin wax to reduce desiccation and each bolt was numbered sequentially starting from the basal bolt. A treatment (parent group) was randomly assigned to bolt 1, 2, or 3 and every third bolt thereafter. From the June 2001 collections, beetle sex was determined (Lyon 1958) and randomly selected female–male pairs were introduced into predrilled holes in the phloem of green bolts. Introductions were spaced 10 cm on the circumference, two bolts per parent group, resulting in 18–20 possible galleries per group. Bolts were held at room temperature (about 21°C) throughout the experiment. Because of the increased difficulty in counting eggs after eclosion (Knight 1969; Safranyik and Linton 1999), bolts were sampled every 10 days beginning 10 days after infestation. On the first sample, the lowest 8 cm of phloem was removed from each gallery and all eggs and larvae were counted, and the distance to the first egg was measured (egg-free gallery length). On the second sample, another 5 cm of phloem was removed. The final sample, wherein all remaining phloem was removed, was taken 30 days after infestation when near maximal gallery development should have occurred (Sahota and Thomson 1979). Total gallery length was also measured at this time. Although this combination of timing and sampling length was designed to allow gallery advancement beyond the sampling area while ensuring sampling before eclosion, the parents in many galleries had not advanced beyond the sampling area and were killed or disturbed. Data from disturbed samples were used up to and including the date of disturbance, but sample sizes were small by the final sample date. Additionally, some introductions were unsuccessful in producing a gallery, and the proportion of successfully established galleries was noted for each parent group.

Because disturbed galleries in the above experiment resulted in small sample sizes, the experiment was repeated using beetles collected in November 2001. In this experiment, a green tree was cut as described above in November 2001. Four bolts each were infested using beetles from the three parent groups, resulting in 30–31 introductions per group. In an attempt to prevent gallery disturbance, sample intervals were extended and sample length was reduced relative to the first experiment. Because of the small number of successful galleries among the semivoltine beetles in the experiment using November-collected beetles, another four and two bolts were infested with semivoltine and univoltine beetles, respectively. This brought the total number of introductions up to 42 for univoltine beetles and 54 for semivoltine beetles. Egg-free gallery length was not measured in this experiment.

Egg length was measured from eggs taken during the second sampling dates for both collection dates. Eggs from each gallery were placed together into a petri dish by parent source and a subsample from each group was measured with a micrometer on a

dissecting microscope. Eggs were not measured for re-emerged parents from the November collection.

### **Brood development rates**

Phloem sandwiches (Hansen *et al.* 2001b) were constructed using eggs collected from the egg production samples, 8 sandwiches per parent group, 10 eggs per sandwich. Sandwiches were held at room temperature, about 21°C, in a constant-humidity desiccator, about 95% RH, and each specimen was monitored daily for eclosion and molting. The response variable is total time, in days, per surviving individual from egg eclosion to teneral adult eclosion.

### **Brood survival**

Another set of four bolts per parent group was infested using beetles from the November 2001 collection. In each bolt, four to five adult pairs were introduced into green phloem sections measuring 15 cm wide × 25 cm high. A 2 cm wide vertical phloem strip was removed between phloem sections to prevent larvae from mining into adjacent sections. After 90 days from time of infestation, all bark was removed to measure the response variable "total surviving brood".

### **Flight capability of re-emerged parent beetles**

A mark-recapture study was used to determine if re-emerged parent beetles were capable of flight. Overwintered parent beetles were identified at the bases of 14 recently attacked Engelmann spruce on the Fishlake National Forest, Utah (38.20°N, 112.43°W). Sampling at three bole heights of these trees revealed <0.1% univoltine brood, indicating little chance of the study being confounded by current univoltine brood hibernators that overwinter with re-emerged parents. A multiple-unit funnel trap baited with  $\alpha$ -pinene and frontalin (Pherotech, Inc, Delta, British Columbia) was deployed before flight commencement in the immediate vicinity of infested trees. Eight of the infested trees were within 50 m of the trap and another six ranged 50–100 m from the trap. Fluorescent powder (Day-Glo® Color Corp, Cudahy, California) was applied to the basal 0.5 m of each selected tree using a ketchup dispenser (Dodds and Ross 2002), with blue on trees within 50 m and pink on trees 50–100 m from the trap. Trap contents were checked weekly and spruce beetles were examined for presence of powder under a UV light. No attempt was made to estimate the number of beetles that may have been marked in the study. The study was established in May 2002 and was completed by August 2002.

### **Analyses**

ANOVAs (PROC GLM; SAS Institute Inc 1989) were conducted to test for differences among the three parent groups for each measurement described above. When necessary, response variables were transformed to meet the normality assumptions. When data could not be successfully transformed, as tested by the Shapiro-Wilk statistic, analyses were conducted using the nonparametric Kruskal-Wallis test of ranks (Zar 1996). The model statements included the effect of collection date, as well as the interaction between collection date and parent group. Identifications of group differences were conducted using the Ryan-Einot-Gabriel-Welsch multiple range test.

**TABLE 2. Dry weights of *Dendroctonus rufipennis* female and male adults identified as univoltine, semivoltine, or re-emerged parents.**

	Female dry weight (mg)		Male dry weight (mg)	
	Mean ± SE	<i>n</i>	Mean ± SE	<i>n</i>
Univoltine	7.34±0.21 <i>a</i>	59	7.02±0.21 <i>a</i>	60
Re-emerged	8.21±0.21 <i>b</i>	60	8.37±0.21 <i>b</i>	58
Semivoltine	8.37±0.21 <i>b</i>	60	8.07±0.21 <i>b</i>	58

NOTE: Means followed by the same letter within the same column are not different (Ryan–Einoṡ–Gabriel–Welsch multiple range test,  $P > 0.05$ ).

**TABLE 3. Lipid content of *Dendroctonus rufipennis* female and male adults identified as univoltine, semivoltine, or re-emerged parents from two collection dates.**

	Female lipid content (% dry weight) in June 2001		Female lipid content (% dry weight) in November 2001		Male lipid content (% dry weight) in June 2001		Male lipid content (% dry weight) in November 2001	
	Mean ± SE	<i>n</i>	Mean ± SE	<i>n</i>	Mean ± SE	<i>n</i>	Mean ± SE	<i>n</i>
Univoltine	28.35±1.22 <i>a</i>	29	22.73±0.90 <i>a</i>	30	23.70±1.07 <i>a</i>	29	18.90±0.89 <i>a</i>	30
Semivoltine	29.09±1.22 <i>a</i>	30	18.71±0.90 <i>b</i>	30	26.88±1.06 <i>b</i>	30	18.21±0.92 <i>a</i>	28
Re-emerged	15.19±1.22 <i>b</i>	30	20.58±0.90 <i>ab</i>	30	14.99±1.09 <i>c</i>	28	18.21±0.89 <i>a</i>	30

NOTE: Means followed by the same letter within the same column are not different (Ryan–Einoṡ–Gabriel–Welsch multiple range test,  $P > 0.05$ ).

## Results

### Parent weight and lipid content

For female dry weight, there was no collection date by parent group interaction ( $F_{2,173} = 1.13$ ,  $P = 0.3261$ ) or effect of collection date ( $F_{1,173} = 0.32$ ,  $P = 0.5723$ ). Univoltine females, however, were lighter than either semivoltine or re-emerged females ( $F_{2,173} = 7.22$ ,  $P = 0.0010$ ) (Table 2). For male dry weight, there was no collection date by parent group interaction ( $F_{2,170} = 1.46$ ,  $P = 0.2359$ ), but there were effects of parent group and collection date. Univoltine males were lighter than either semivoltine or re-emerged males ( $F_{2,170} = 11.59$ ,  $P < 0.0001$ ). Also, November-collected males were lighter than June-collected males ( $F_{1,170} = 10.98$ ,  $P = 0.0011$ ; November: least squares mean = 7.42 mg, SE = 0.17,  $n = 178$ ; June: least squares mean = 8.22 mg, SE = 0.17,  $n = 177$ ).

For female lipid content, the collection dates were analyzed separately because there was an interaction between collection date and parent group ( $F_{2,173} = 34.02$ ,  $P < 0.0001$ ). For the June collection, data did not meet the normality assumptions and could not be successfully transformed. Therefore, the nonparametric Kruskal–Wallis test of ranks was performed. Re-emerged females had less lipid content than either univoltine or semivoltine females ( $F_{2,86} = 40.64$ ,  $P < 0.0001$ ) (Table 3). For the November collection, a square-root transformation was used to normalize the data. Results differed from the June collection, as semivoltine females had less lipids than univoltine females, and re-emerged females were not different from either univoltine or semivoltine females ( $F_{2,87} = 4.76$ ,  $P = 0.0109$ ). For male lipid content, the collection dates were analyzed separately because there was an interaction between collection date and parent group ( $F_{2,169} = 18.59$ ,  $P < 0.0001$ ). For the June collection, semivoltine males had higher lipid content than univoltine males, and univoltine males had higher lipid content than

**TABLE 4. Comparison of gallery establishment success, under laboratory conditions, for *Dendroctonus rufipennis* adults identified as univoltine, semivoltine, or re-emerged parents from two collection dates.**

	Percentage of successful galleries in June 2001		Percentage of successful galleries in November 2001	
	Mean $\pm$ SE	<i>n</i>	Mean $\pm$ SE	<i>n</i>
Univoltine	85.0 $\pm$ 9.7 <i>a</i>	20	85.7 $\pm$ 6.8 <i>a</i>	42
Semivoltine	83.3 $\pm$ 9.7 <i>a</i>	18	33.3 $\pm$ 6.0 <i>b</i>	54
Re-emerged parents	66.7 $\pm$ 9.2 <i>a</i>	18	66.7 $\pm$ 8.0 <i>a</i>	30

NOTE: Means followed by the same letter within the same column are not different (Ryan–Einot–Gabriel–Welsch multiple range test,  $P > 0.05$ ).

**TABLE 5. Egg-free gallery lengths (distance to first egg) for *Dendroctonus rufipennis* adults identified as univoltine, semivoltine, or re-emerged parents in the June 2001 collection.**

	Egg-free length (cm)	
	Mean $\pm$ SE	<i>n</i>
Univoltine	4.74 $\pm$ 0.2072 <i>a</i>	17
Semivoltine	3.42 $\pm$ 0.3540 <i>b</i>	14
Re-emerged parents	2.99 $\pm$ 0.3824 <i>b</i>	12

NOTE: Means followed by the same letter within the same column are not different (Ryan–Einot–Gabriel–Welsch multiple range test,  $P > 0.05$ ).

re-emerged parent males ( $F_{2,84} = 32.53$ ,  $P < 0.0001$ ) (Table 3). Data from the November collection required a square-root transformation to meet the normality assumptions. Results were unlike those for the June collection, as no differences were detected among the parent groups ( $F_{2,85} = 0.18$ ,  $P = 0.8326$ ). For females and males in the univoltine and semivoltine groups, lipid content was higher in the June collection than in the November collection, whereas the reverse was true for the re-emerged parents.

### Gallery establishment, egg-free and total gallery lengths, egg production, and egg length

Because an interaction was detected between collection date and parent group ( $F_{2,176} = 5.95$ ,  $P = 0.0032$ ), the proportions of successful galleries were analyzed separately for the two collections. For the June collection, no differences were found among parent groups in success of gallery establishment ( $F_{2,53} = 1.11$ ,  $P = 0.3376$ ) (Table 4). For the November collection, however, semivoltine beetles were less successful with establishing galleries than either the univoltine or re-emerged parent groups ( $F_{2,123} = 17.38$ ,  $P < 0.0001$ ).

A square-root transformation was used to normalize the response data for egg-free gallery length. Egg-free gallery length was longer for univoltine parents than for either semivoltine parents or re-emerged parents for beetles in the June collection ( $F_{2,40} = 7.12$ ,  $P = 0.0023$ ) (Table 5). This parameter was not measured for beetles in the November collection. Because an interaction was detected between collection date and parent group ( $F_{2,53} = 3.21$ ,  $P = 0.0485$ ), total gallery length was analyzed separately for the two collections using the Kruskal–Wallis test of ranks, as the transformed data did not meet the normality assumptions. Total gallery length for parent groups in the June collection did not differ ( $F_{2,7} = 0.78$ ,  $P = 0.4940$ ) (Table 6). Semivoltine parents in the



**TABLE 6. Total gallery lengths for *Dendroctonus rufipennis* adults identified as univoltine, semivoltine, or re-emerged parents from two collection dates.**

	Total gallery lengths (cm) for June 2001		Total gallery lengths (cm) for November 2001	
	Mean $\pm$ SE	<i>n</i>	Mean $\pm$ SE	<i>n</i>
Univoltine	14.20 $\pm$ 1.57 <i>a</i>	3	14.05 $\pm$ 0.44 <i>a</i>	29
Semivoltine	16.76 $\pm$ 1.36 <i>a</i>	4	11.97 $\pm$ 0.71 <i>b</i>	11
Re-emerged parents	16.13 $\pm$ 1.57 <i>a</i>	3	15.63 $\pm$ 0.78 <i>a</i>	9

NOTE: Means followed by the same letter within the same column are not different (Ryan–Einot–Gabriel–Welsch multiple range test,  $P > 0.05$ ).

November collection, however, produced shorter galleries than either univoltine parents or re-emerged parents ( $F_{2,46} = 6.21$ ,  $P = 0.0041$ ).

Because of differences in sampling protocols for measuring egg production, the two collection dates were analyzed separately. For the June collection, a square-root transformation was performed on the number of eggs produced 10 days after infestation. Re-emerged parents produced more eggs than semivoltine parents, and semivoltine parents produced more eggs than univoltine parents ( $F_{2,40} = 10.90$ ,  $P = 0.0002$ ) (Table 7). At 20 and 30 days after infestation, however, no differences were detected among the parent groups ( $F_{2,31} = 0.57$ ,  $P = 0.5720$  and  $F_{2,7} = 0.52$ ,  $P = 0.6137$ , respectively).

For the November collection, a log transformation was needed to normalize the data for the number of eggs produced 14 days after infestation. Re-emerged parents produced more eggs than univoltine parents ( $F_{2,27} = 4.01$ ,  $P = 0.0298$ ), but semivoltine parents were not different than either re-emerged parents or univoltine parents (Table 7). At 21 days after infestation, re-emerged parents produced more eggs than semivoltine parents ( $F_{2,61} = 3.26$ ,  $P = 0.0454$ ), but univoltine parents were not different than either re-emerged parents or semivoltine parents. At 27 and 30 days after infestation, univoltine parents produced more eggs than semivoltine parents ( $F_{2,52} = 3.89$ ,  $P = 0.0266$  and  $F_{2,46} = 5.42$ ,  $P = 0.0077$ , respectively), but re-emerged parents were not different than either univoltine parents or semivoltine parents.

Because egg length was found to have an interaction between collection date and parent group ( $F_{1,219} = 5.40$ ,  $P = 0.0210$ ), the June and November collections were analyzed separately. For both collections, the data did not meet the normality assumptions and could not be successfully transformed, which resulted in the use of the Kruskal–Wallis test of ranks. Eggs from univoltine beetles in the June collection were shorter than eggs from semivoltine or re-emerged parent beetles ( $F_{2,136} = 10.55$ ,  $P < 0.0001$ ) (Table 8). Egg lengths from beetles in the November collection, however, did not differ ( $F_{1,83} = 0.09$ ,  $P = 0.7616$ ).

### Brood development rates

The Kruskal–Wallis test of ranks was performed because the data did not meet the normality assumptions and could not be successfully transformed. No differences in brood development rates were detected among the three parent beetle groups ( $F_{2,106} = 1.17$ ,  $P = 0.3156$ ; univoltine: least squares mean = 39.8 days, SE = 0.8,  $n = 26$ ; semivoltine: least squares mean = 38.3 days, SE = 0.6,  $n = 47$ ; re-emerged: least squares mean = 39.2 days, SE = 0.7,  $n = 36$ ).

**TABLE 7. Number of eggs produced, at various intervals, by *Dendroctonus rufipennis* females identified as univoltine, semivoltine, or re-emerged parents from two collection dates.**

	Cumulative eggs produced (days after infestation) in June 2001						Cumulative eggs produced (days after infestation) in November 2001							
	Day 10		Day 20		Day 30		Day 14		Day 21		Day 27		Day 30	
	Mean ± SE	<i>n</i>	Mean ± SE	<i>n</i>	Mean ± SE	<i>n</i>	Mean ± SE	<i>n</i>	Mean ± SE	<i>n</i>	Mean ± SE	<i>n</i>	Mean ± SE	<i>n</i>
Univoltine	13.6±4.3a	17	90.6±10.9a	14	130.0±25.0a	3	2.3±1.7a	33	45.6±4.2ab	32	89.3±4.7a	29	114.6±6.2a	29
Semivoltine	28.1±4.8b	14	110.0±14.5a	8	163.8±21.6a	4	9.3±2.5ab	16	38.7±6.2a	15	65.5±7.1b	13	75.5±10.1b	11
Re-emerged parents	45.1±5.2c	12	98.0±11.8a	12	147.7±25.0a	3	11.7±2.3b	19	59.5±5.8b	17	80.1±7.1ab	13	100.1±11.2ab	9

NOTE: Means followed by the same letter within the same column are not different (Ryan-Einot-Gabriel-Welsch multiple range test,  $P > 0.05$ ).

**TABLE 8.** Lengths of eggs produced by *Dendroctonus rufipennis* adults identified as univoltine, semivoltine, or re-emerged parents from two collection dates.

	Egg length (mm) in June 2001		Egg length (mm) in November 2001	
	Mean $\pm$ SE	<i>n</i>	Mean $\pm$ SE	<i>n</i>
Univoltine	1.103 $\pm$ 0.011 <i>a</i>	39	1.163 $\pm$ 0.013 <i>a</i>	47
Semivoltine	1.163 $\pm$ 0.010 <i>b</i>	50	1.168 $\pm$ 0.014 <i>a</i>	38
Re-emerged parents	1.162 $\pm$ 0.010 <i>b</i>	50	—	—

NOTE: Means followed by the same letter within the same column are not different (Ryan–Einot–Gabriel–Welsch multiple range test,  $P > 0.05$ ).

### Brood survival

There was no difference among parent groups in the total surviving brood per 15  $\times$  25 cm phloem section ( $F_{2,25} = 0.22$ ,  $P = 0.8074$ ; univoltine: least squares mean = 51.7 live brood, SE = 4.4,  $n = 16$ ; semivoltine: least squares mean = 48.5 live brood, SE = 8.7,  $n = 4$ ; re-emerged: least squares mean = 46.9 live brood, SE = 6.2,  $n = 8$ ). Poor success with establishing galleries resulted in small sample sizes for the semivoltine and re-emerged parent groups.

### Flight capability of re-emerged parent beetles

Marked beetles, both blue and pink, were captured in the funnel trap, indicating that at least some re-emerged parent beetles are capable of flight. About 2.5% of all spruce beetles caught in the trap were marked. Peak capture of re-emerged parent beetles was 1 week earlier than the peak for all beetles caught, the latter group included new adult beetles as well as re-emerged parents (Fig. 1).

## Discussion

We were confident, although not certain, that re-emerged parent beetles were correctly distinguished from potential univoltine hibernators. Indeed, the differences in the parameters of the two classes validated our classification. Future investigators should find the guidelines described in Table 1 to be useful, although host characters may be different for trees other than Engelmann spruce. In particular, these guidelines ensure proper distinction between univoltine and semivoltine new adults. It should be noted, however, that despite our results indicating correct identification of re-emerged parents, beetles in this group can be difficult to correctly distinguish if hibernating univoltine adults are present. This is especially true if a substantial proportion of univoltine broods hibernate, which is typical in south-central Alaska.

The most obvious differences among the three groups pertained to the parent dry weight and lipid content. Our results showed that univoltine beetles were lighter, which is consistent with a decrease in body size corresponding to a shorter life cycle (Mousseau and Roff 1989) or faster development rate (Bentz *et al.* 2001). June-collected re-emerged parents had reduced lipid content, presumably because of previous dispersal and brood production. For new adults of both univoltine and semivoltine cycles, lipid content of beetles collected in June (post winter) was greater than lipid content of beetles collected in November (pre-winter), and semivoltine and univoltine females had similar amounts of lipids post winter, but not pre-winter. Many species of *Dendroctonus* benefit nutritionally from associated fungi (Coppedge *et al.* 1995; Six and Paine 1998; Ayres *et al.* 2000), especially in pupal chambers where fungal growth becomes highly sporogeneous (Six 2003) and can contain high amounts of lipids

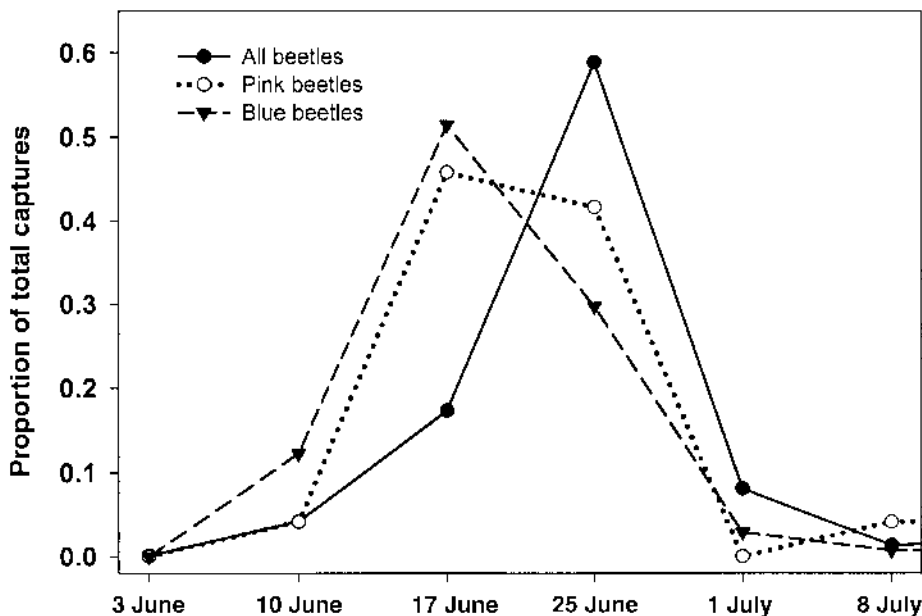


FIGURE 1. Weekly proportions of total *Dendroctonus rufipennis* captures in a baited funnel trap, Fishlake National Forest, Utah. "Blue" beetles ( $n = 138$ ) were re-emerged parents from 8 trees marked with blue fluorescent powder that were  $<50$  m from the trap. "Pink" beetles ( $n = 24$ ) were re-emerged parents from 6 trees marked with pink fluorescent powder that were 50–100 m from the trap. "All" beetles ( $n = 6327$ ) include all marked and unmarked beetles caught in the trap, with new adult beetles included in the latter category. No attempt was made to estimate the total number of re-emerged parent beetles that were marked.

(Deacon 1997). For individuals not hibernating (*i.e.*, the univoltine and semivoltine beetles collected for this study), teneral adults of both univoltine and semivoltine life cycles overwinter in their pupal chambers where they can feed on lipid-rich fungi prior to emergence in June. Potentially, the beetles we collected in November had not yet fed on pupal chamber fungi, resulting in the overall lower lipid content. For beetles collected in November, semivoltine beetles passed the summer in a nonfeeding stage, whereas the univoltine beetles fed on phloem during the summer, resulting in a greater lipid content in univoltine females than in semivoltine females. These results suggest that univoltine and semivoltine beetles do not necessarily have different lipid contents, depending on the time of year, and that new adults emerging in the spring have significantly more lipids than adults entering the winter.

Overall, we found no important differences in reproductive capacity among univoltine, semivoltine, and re-emerged parent spruce beetles. Re-emerged beetles were found to have more eggs at the first sample date than either univoltine or semivoltine new adults, but the latter two parent groups increased oviposition by later sample intervals, resulting in no overall difference. The difference at the first sample date is correlated to the egg-free gallery lengths, which were shortest for re-emerged parents. Sahota and Thomson (1979) proposed that relatively long egg-free gallery lengths are indicative of "poorer quality" beetles, but our results found no apparent relationship between distance to first egg and egg production 30 days after introduction. Semivoltine beetles from the November collection had poor success with establishing galleries, relatively short total gallery lengths, and relatively low egg production in successfully established

galleries; however, we have repeatedly reared broods from semivoltine beetles in our laboratory with high success over several years. We believe that the measured performance of semivoltine beetles in the November collection is unusual, possibly because of the lack of fungal feeding as described above, and does not represent the true potential of spruce beetles with that life cycle. Regardless, we found no evidence that univoltine females are less fecund than either semivoltine or re-emerged parent females.

Perhaps even more importantly, brood survival was similar for each parent group. Laboratory observations show that intraspecific competition (*i.e.*, cannibalism) is a major limiting factor in the density of the surviving brood (see also Safranyik and Linton 1999). For example, we found that most female beetles are capable of producing 100–150 eggs each, whereas brood survival in the 15 × 25 cm phloem sections averaged about 50 individuals. Conceivably, one parent group would need to show at least a 50% reduction in egg production, relative to the other groups, to result in detectable differences in the density of the surviving mature brood. Our results indicate that no such differences exist. Furthermore, densities of the surviving mature brood are considerably smaller under field conditions than what we measured in the laboratory (for comparison see Knight 1960 and Safranyik and Linton 1999). Almost certainly, the net replacement rate for females,  $R_0$ , is not greater among semivoltine parents than among univoltine parents.

For the parameters measured, brood characteristics were generally similar among the three parent groups, the exception being that eggs were smaller from univoltine parents collected in June. Our results showing no brood development rate differences among parent groups are contrary to the hypothesis that life-cycle duration is genetically determined. If voltinism is genetically based, then the brood from univoltine parents should have exhibited accelerated development relative to the phenology of the brood from semivoltine parents. That is, under equivalent conditions, individuals predisposed to a shorter life cycle would need to exhibit shorter developmental durations. Instead, all evidence supports flexible voltinism that is regulated by temperature (Massey and Wygant 1954; Dyer 1969; Dyer 1970; Dyer and Hall 1977; Werner and Holsten 1985; Hansen *et al.* 2001a).

The implication of these findings is that univoltine populations will have accelerated population growth relative to semivoltine populations. This effect may be even more dramatic because the shorter life cycle reduces exposure to mortality agents such as adverse weather and predation. In other words, the net replacement rate for females,  $R_0$ , may actually be greater for univoltine parents than for semivoltine parents. Of course, warm weather and the resulting univoltine brood alone will not result in a spruce beetle outbreak. The primary prerequisite conditions for an outbreak are stand hazard, availability of windthrow, and current beetle population size (Reynolds and Holsten 1994). Given suitable host material and an existing population, however, univoltine broods can substantially increase the risk of an outbreak or result in dramatically accelerated spruce mortality in established outbreaks. Continued warming trends, as predicted by global climate-change modeling, will increase the risk of spruce beetle outbreaks throughout the host's range (Logan *et al.* 2003).

Although all studied species of *Dendroctonus* have exhibited re-emergence (Coulson 1979), little work has been done on the significance of this phenomenon for western North American species. New adults combine with re-emerged parents to form the population that infests new hosts. Understanding the numerical relationship between the two groups, therefore, is critical to understanding a species' population dynamic (Coulson 1979). Gray and Dyer (1972) found that the primary flight muscles of spruce beetle were degenerated following flight and host attack, suggesting that flight capability and subsequent re-attack may be compromised for such beetles. Reid (1958) found

similar reduction in both flight muscles and lipid volume during the egg-laying phase for mountain pine beetle females. Following gallery completion, however, mountain pine beetle females had regenerated both flight muscles and fat bodies, appearing similar to new adults (Reid 1958). Apparently, this is due to the female's ingestion of phloem during gallery construction. Furthermore, Amman and Bartos (1991) found similar egg production for re-emerged and fresh mountain pine beetle females.

Massey and Wygant (1954) found that nearly 20% of re-emerged parents immediately begin a second egg gallery, and an additional 70% were found to hibernate at the bases of infested or green hosts. Our results show that these hibernating, re-emerged parent beetles are capable of both dispersal and oviposition and, therefore, can substantially influence the population dynamics of this species. For example, if new adult and re-emerged parent beetle population sizes are equivalent, then about 40% of a new generation will have come from re-emerged females (assuming 67% gallery success for re-emerged females and 100% success for fresh females). Furthermore, because overwintered re-emerged parents are among the first beetles to fly at the beginning of the summer (Fig. 1), they may play a primary role in the selection of new hosts.

Forest entomologists and managers can increase treatment success if they consider these findings in implementing suppression actions. Univoltine broods pose an additional risk of outbreak populations and subsequent acceleration of spruce mortality. Moreover, the time frame for suppression action is substantially reduced relative to that for semivoltine broods. Also, the reproductive potential of re-emerged parents implies that sanitation/salvage operations as a suppression technique may have limited success because a single residual stump may contain many hundreds of re-emerged parent beetles, as well as hibernating new adults depending on the brood life cycle and timing of the sanitation treatment. This underscores the need to treat stumps when removing infested trees to maximize treatment success.

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## References

- Amman GD. 1972. Some factors affecting oviposition behavior of the mountain pine beetle. *Environmental Entomology* **1**: 691–5
- Amman GD, Bartos DL. 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.
- Ayres MP, Wilkens RT, Ruel JJ, Lombardero MJ, Vallery E. 2000. Nitrogen budgets of phloem-feeding bark beetles with and without symbiotic fungi (Coleoptera: Scolytidae). *Ecology* **81**: 2198–210
- Bentz BJ, Logan JA, Vandygriff JC. 2001. Latitudinal variation in *Dendroctonus ponderosae* (Coleoptera: Scolytidae) development time and adult size. *The Canadian Entomologist* **133**: 375–87
- Cole LC. 1954. The population consequences of life history phenomena. *Quarterly Review of Biology* **29**: 103–37

- Coppedge BR, Stephen FM, Felton FW. 1995. Variation in female southern pine beetle size and lipid content in relation to fungal associates. *The Canadian Entomologist* **127**: 145–54
- Coulson RN. 1979. Population dynamics of bark beetles. *Annual Review of Entomology* **24**: 417–47
- Deacon JW. 1997. *Modern mycology*. 3rd edition. Malden, Massachusetts: Blackwell Science Ltd
- Dodds KJ, Ross DW. 2002. Sampling range and range of attraction of *Dendroctonus pseudotsugae* pheromone-baited traps. *The Canadian Entomologist* **134**: 343–55
- Dyer EDA. 1969. Influence of temperature inversion on development of spruce beetle, *Dendroctonus obesus* (Mannerheim)(Coleoptera: Scolytidae). *Journal of the Entomological Society of British Columbia* **66**: 41–5
- . 1970. Larval diapause in *Dendroctonus obesus* (Mannerheim) (Coleoptera: Scolytidae). *Journal of the Entomological Society of British Columbia* **67**: 18–21
- . 1973. Spruce beetle aggregated by the synthetic pheromone frontalin. *Canadian Journal of Forest Research* **3**: 486–94
- Dyer EDA, Hall PM. 1977. Factors affecting larval diapause in *Dendroctonus rufipennis* (Mannerheim) (Coleoptera: Scolytidae). *The Canadian Entomologist* **109**: 1485–90
- Gray TG, Dyer EDA. 1972. Flight-muscle degeneration in spruce beetles, *Dendroctonus rufipennis* (Coleoptera: Scolytidae). *Journal of the Entomological Society of British Columbia* **69**: 41–3
- Hagen BW, Atkins MD. 1975. Between generation variability in the fat content and behavior of *Ips paraconfusus* Lanier. *Journal of Applied Entomology* **79**:169–72
- Hansen EM, Bentz BJ, Turner DL. 2001a. Temperature-based model for predicting univoltine brood proportions in spruce beetle (Coleoptera: Scolytidae). *The Canadian Entomologist* **133**: 827–41
- . 2001b. Physiological basis for flexible voltinism in the spruce beetle (Coleoptera: Scolytidae). *The Canadian Entomologist* **133**: 805–17
- Holsten EH, Thier RW, Munson AS, Gibson KE. 1999. The spruce beetle. *US Forest Service Forest Insect and Disease Leaflet* **127**
- Knight FB. 1960. Measurement of Engelmann spruce beetle populations. *Ecology* **41**: 249–52
- . 1961. Variations in the life history of Engelmann spruce beetle. *Annals of the Entomological Society of America* **54**: 209–14
- . 1969. Egg production by the Engelmann spruce beetle, *Dendroctonus obesus*, in relation to status of infestation. *Annals of the Entomological Society of America* **62**: 448
- Linton DA, Safranyik L, Whitney HS, Spanier OJ. 1984. Possible genetic control of color morphs of spruce beetles. *Canadian Forestry Service Research Notes* **4**: 52–3
- Logan JA, Régnière J, Powell JA. 2003. Assessing the impacts of global warming on forest pest dynamics. *Frontiers in Ecology and the Environment* **1**: 130–7
- Lyon RL. 1958. A useful secondary sex character in *Dendroctonus* bark beetles. *The Canadian Entomologist* **90**: 582–4
- Massey CL, Wygant ND. 1954. Biology and control of the Engelmann spruce beetle in Colorado. *US Department of Agriculture Circular* **944**
- McCambridge WF, Knight FB. 1972. Factors affecting spruce beetles during a small outbreak. *Ecology* **53**: 830–9
- Mousseau TA, Roff DA. 1989. Adaptation to seasonality in a cricket: patterns of phenotypic and genotypic variance in body size and diapause expression along a cline in season length. *Evolution* **43**: 1483–96
- Price PW. 1997. *Insect ecology*. New York: John Wiley and Sons, Inc
- Reid RW. 1958. Internal changes in the female mountain pine beetle, *Dendroctonus monticolae* Hopk., associated with egg laying and flight. *The Canadian Entomologist* **90**: 464–8
- . 1962. Biology of the mountain pine beetle, *Dendroctonus monticolae* Hopkins, in the East Kootenay region of British Columbia. II. Behaviour in the host, fecundity, and internal changes in the female. *The Canadian Entomologist* **94**: 605–13
- Reynolds KM, Holsten EH. 1994. Relative importance of risk factors for spruce beetle outbreaks. *Canadian Journal of Forest Research* **24**: 2089–95
- Safranyik L, Linton DA. 1999. Spruce beetle (Coleoptera: Scolytidae) survival in stumps and windfall. *The Canadian Entomologist* **131**: 107–13
- Safranyik L, Simmons C, Barclay HJ. 1990. A conceptual model of spruce beetle population dynamics. *Canadian Forestry Service Pacific Forest Research Centre Report* **BC-X-316**
- Sahota TS, Thomson AJ. 1979. Temperature induced variation in the rates of reproductive processes in *Dendroctonus rufipennis* (Coleoptera: Scolytidae): a new approach to detecting changes in population quality. *The Canadian Entomologist* **111**: 1069–78
- SAS Institute Inc. 1989. *SAS/STAT user's guide*. Version 6, 4th edition, volume 1. Cary, North Carolina: SAS Institute Inc
- Schmid JM, Beckwith RC. 1975. The spruce beetle. *US Forest Service Forest Pest Leaflet* **127**
- Six DL. 2003. Bark beetle–fungus symbioses. pp 99–116 in K Bourtzis, T Miller (Eds), *Insect symbioses*. Boca Raton, Florida: CRC Press

- Six DL, Paine TD. 1998. Effects of mycangial fungi and host tree species on progeny survival and emergence of *Dendroctonus ponderosae* (Coleoptera: Scolytidae). *Environmental Entomologist* **27**: 1393–401
- Werner RA, Holsten EH. 1985. Factors influencing generation times of spruce beetles in Alaska. *Canadian Journal of Forest Research* **15**: 438–43
- Zar JH. 1996. *Biostatistical analysis*. Upper Saddle River, New Jersey: Prentice-Hall, Inc

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