

# Life-history traits promoting outbreaks of the pine bark beetle *Ips acuminatus* (Coleoptera: Curculionidae, Scolytinae) in the south-eastern Alps

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**Abstract** The pine bark beetle *Ips acuminatus* has recently increased frequency and intensity of outbreaks in *Pinus sylvestris* stands in the Alps. During a 3-year period, we investigated life-history traits of the species that may have adaptive value. In the south-eastern Alps, *I. acuminatus* becomes active in early spring when the air temperature reaches 14°C, suggesting the presence of a local population adapted to low temperature. Such an early emergence allows the complete development of a second generation, even if only a portion of the population is truly bivoltine. As a consequence, there are two main attack periods, the first in early spring and the second in summer, resulting in different trees being colonised each time. Irrespective of the generation, a large part of the beetles leaves the breeding substrate before hibernation, and this is interpreted as an escape from natural enemies associated with the bark. These findings suggest that the populations of *I. acuminatus* of the south-eastern Alps may benefit from climate warming as they have more opportunities to complete the second generation and to escape from mortality factors associated with a long permanence in the bark. In addition, the extended period of tree colonisation offers more possibilities to locate suitable hosts and to build up outbreak densities.

**Keywords** Pine bark beetle · Voltinism · Colonisation density · Mortality · Temperature

## Introduction

Many insect populations, including bark beetles, are known to respond to the recent climate change (Dobbertin et al. 2005, 2007; Berg et al. 2006; Bigler et al. 2006; Lange et al. 2006; Jönsson et al. 2007; Faccoli 2009), promoting a progressive forest decline, especially in the alpine regions. In the last years, high temperature coinciding with periods of drought has resulted in a global-change-type drought (Breshears et al. 2005), which reduces developmental time, increases voltinism and the infestation pressure of bark beetles (Wermelinger and Seifert 1998). This effect, however, interacts with the regulation of the life cycle by the photoperiod, which varies with latitude and is known to affect the diapause mechanism in bark beetles (Gehrken 1985; Baier et al. 2007).

Outbreaks of the pine engraver beetle *Ips acuminatus* (Gyllenhal) (Coleoptera: Curculionidae, Scolytinae) have been recently reported in many Scots pine (*Pinus sylvestris* L.) forests in the western (Lozzia and Rigamonti 2002; Wermelinger et al. 2008) and eastern Alps (Dolomites, NE Italy) (Colombari et al. 2008). *I. acuminatus* is a polygamous species with phloemycetophagous larvae, colonising the upper part of the trunk and the branches with a bark thickness of 2–3 mm (Bakke 1968). For many years *I. acuminatus* has been reported as a species of minor economic importance (Bakke 1968), causing damage mainly by transmitting blue-stain fungi to saw-logs, but in the last decades, it has been included among the ten most damaging wood-boring insect in Europe as a result of the increasing tree mortality caused by this species (Grégoire

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and Evans 2004). As low temperature is known to be a limiting factor for *I. acuminatus* flight activities and brood development (Bakke 1968), it is likely that climate change may aggravate the threat to pine forest health, either with the beetle alone or in combination with secondary pathogens (Rebetez and Dobbertin 2004; Rigling et al. 2007). This could explain the increasing importance of *I. acuminatus* in the Scots pine decline recently observed in the Alps (Wermelinger et al. 2008).

The life history of *I. acuminatus* varies according to study sites. Literature reports *I. acuminatus* as monovoltine in Scandinavia (Bakke 1968) and bivoltine in southern Europe (Chararas 1962; Hernández et al. 2004), although this information is rather fragmentary and does not concern alpine populations. Overwintering occurs as an adult mainly under the bark of the infested trees (Bakke 1968; Lekander et al. 1977; Hernández et al. 2004; Wermelinger et al. 2008), but overwintering in the litter has been considered possible in central Europe and Scandinavia (Francke-Grosmann 1963; Lekander et al. 1977). Spring emergence begins slowly when air temperature reaches 14°–16°C (Bakke 1968), but the real mass flight occurs when temperature exceeds 18°C (Bakke 1968; Lekander et al. 1977; Hernández et al. 2004, 2007). The above mentioned aspects are still unclear for the alpine populations and need to be clarified. In addition, as far as we know, no earlier studies were conducted on mating systems and competition of *I. acuminatus* in living trees under natural conditions or on the relationships between colonisation densities and brood performance over generations and years.

During an outbreak of *I. acuminatus* that has spread in the south-eastern Alps since 2006, we investigated voltinism, phenology and breeding performance in relation to both temperature and colonisation density over a 3-year period, in order to determine how these factors may affect insect performance and population dynamics.

## Materials and methods

### Study area

The study area is located in the Cadore Valley (46°27'N, 12°12'E, altitude 900–1,300 m) in northern Italy, on dolomite and limestone bedrock covered by shallow soils on south-western facing slopes. The climate is continental with annual mean temperature of 7.2°C and annual precipitation of 1,100 mm. The stands of Scots pine have a mean density of about 300 stems per hectare and are composed of mature trees (>100 years) with a poor annual growth because of nutrient and water limitations. The main ecological functions of these stands are reducing soil erosion and improving the scenic value of the landscape, as

the valley is one of the major tourist attractions in the Alps. Since 2006, *I. acuminatus* outbreak has killed thousands of pines in the valley. The killed trees are clumped in multiple-tree spots, very different in size and distributed over an area of about 2,000 ha. Rainfall and temperature data of the study area were collected from a weather station of the Padova University located inside the outbreak area at an altitude of 1,100 m a.s.l.

### Population survey

Phenology and voltinism of *I. acuminatus* were monitored by multi-funnel traps (Witasek®) set in active spots of *I. acuminatus* killed trees (colonised in the previous year) in early spring 2007 (36 traps), 2008 (9 traps) and 2009 (5 traps). Traps were baited with a species-specific pheromone lure (Acuwit®, Witasek) and checked daily in the early afternoon from mid-March until the first *I. acuminatus* was caught. Traps were emptied twice a month until no beetles were caught. The pheromone dispensers were replaced 2 months after trap activation except in 2009 when traps were removed at the end of the spring flight period. All trapped adults of *I. acuminatus* were counted and sexed.

Colonisation and breeding performance of *I. acuminatus* was studied in 21 randomly selected spots ranging in size from 2 to 350 killed trees (mean 43.5, SE 16.1). Mean distance between studied spots of the same year varied between 0.8 and 3.5 km. The sampling was conducted in April and June in 2007 and 2008 ( $N = 6$  in April 2007, June 2007 and April 2008;  $N = 3$  in June 2008). The spots selected in April resulted from trees attacked in the summer of the previous year, whereas those selected in June consisted of trees colonised in the spring of the current year. Three colonised trees were felled in each spot, summing up to a total of 63 trees. For each one of these trees, diameter at breast height, total tree height, height and diameter at the beginning and at the end of the *I. acuminatus* colonisation points were recorded. The relative infested bole height (RIBH) was computed for all felled trees as: (infested bole height)/(total tree height) (Fargo et al. 1979). In addition in 2007, on one tree per spot (summing up to thirteen trees, because in addition to the twelve trees an isolated infested pine was cut), the total colonised bark surface (TCBS) was calculated as the sum of the infested bole area (IBA) and the infested branch area (IBRA). IBA was computed as:

$$\text{IBA} = \text{diameter} \times \text{length of the attacked trunk portion},$$

where the diameter value was calculated as the mean of the trunk diameters at the beginning and end of the insect colonisation points.

IBRA of each  $n$ -whorl was computed as:

$$\text{IBRA}_n = (\text{diameter} \times \text{length of the attacked portion} \\ \text{of one branch per whorl}) \times \text{number } (n) \\ \text{of colonised branches in the whorl,}$$

where the diameter value was calculated as the mean of the branch diameters at the beginning and the end of the insect colonisation.

Hence, the TCBS was equal to:

$$\text{TCBS} = \text{IBA} + \sum_n^1 \text{IBRA}_n.$$

From each one of the 63 felled trees, ten colonised branch samples (approximately 45 cm long and 5 cm in diameter) were randomly selected. The branch samples were cut and transported to the campus of the Agriculture Faculty of the Padova University in the same day. The ten branch samples from each tree were caged together in plastic pipe cages (diameter 40 cm, length 50 cm) closed at both ends by a fine wire mesh and placed under outdoor conditions. Temperature was recorded on site. Cages were checked daily, and all emerging *I. acuminatus* adults were counted and sexed.

At the end of the *I. acuminatus* emergence from the cages (first half of June and first half of September for second and first generation, respectively), branches were debarked and all dead or alive *I. acuminatus* recorded. On one randomly chosen branch per cage (i.e., per tree), all mating systems were analysed in order to estimate the density of colonising males (i.e., number of nuptial chambers), females (i.e., number of egg galleries) and, consequently, total colonisation density (i.e., number of males and females). Furthermore, for one mating system per branch, the length of egg galleries was measured, and the number of egg niches, larval galleries, pupal cells and galleries resulting from maturation feeding by the new generation adults was recorded. It was assumed that each egg niche had contained one egg. The number of young larvae was estimated from the number of larval galleries starting from the egg niches, whereas the number of mature larvae was estimated from the larval galleries ending with a slight enlargement in diameter. The number of pupal cells was considered as the number of pupae, and the number of pre-emerging adults was estimated from the number of irregular galleries of maturation feeding starting from the pupal cells. Lastly, the percentage of beetles that have emerged to hibernate outside the breeding material was assessed considering the number of maturation feedings on the branches and the number of emerging adults from the branches. Only on branches collected in 2007 (36 trees, 12 spots) were also measured size of nuptial chambers, initial egg-free part of the maternal galleries and distance between eggs along the galleries.

Statistical analysis

The thermal sums needed for the beginning and peak of spring flight (calculated for the period from January 1st to the event considered) and for brood development (calculated for the period between the observed flight peaks in 2007 and 2008) were obtained by testing a set of threshold temperatures ranging between 0 and 10°C for the spring flight and between 9 and 15°C for the brood development. The temperature that minimised the standard deviation of the mean thermal sum calculated over the 3 years was chosen as threshold temperature.

Values of all variables recorded from each tree were averaged within the spot ( $N = 21$ ). All mean values are reported  $\pm$ standard deviation (SD), unless otherwise specified. Two independent factors, generation and year, and their interactions, were tested by a two-way ANOVA for each variable (density of parent beetles and preimaginal stages, percentage of mortality). To fit the assumptions of the ANOVA, density and proportion data were log and arcsine-square root transformed when needed. Visual inspection of model residuals was used to check the assumption of homogeneity of variance. Significance was determined at  $P < 0.05$ .

Statistical analyses were performed using the software programs R (version 2.7.0) and Statistica 8 (Statsoft, Inc 1993).

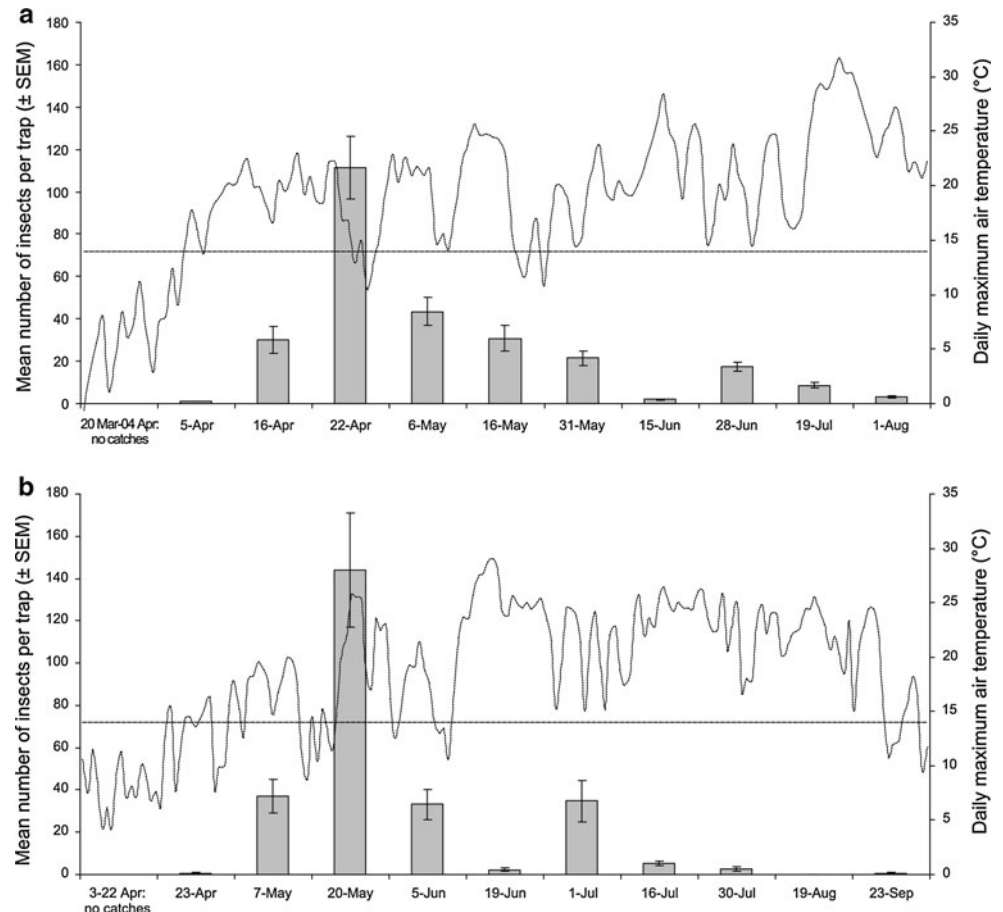
## Results

### Phenology and voltinism

The first adults of *I. acuminatus* were caught after daily maximum air temperatures reached 14°C (April 5th in 2007, April 23rd in 2008 and April 12th in 2009). In both 2007 and 2008, trap captures showed two peaks, the first very clear in spring and the second one much less evident in summer (Fig. 1). The first peak occurred 17, 27 and 31 days after the beginning of flights in 2007, 2008 and 2009, respectively (mean of  $25.0 \pm 7.2$ ). Spring flight started at a thermal sum of  $15.2 \pm 1.6$  DD (degree days), calculated from January 1st above the threshold of 6°C, whereas flight peak occurred at a thermal sum of  $98.5 \pm 2.2$  DD (Table 1).

Considering mean trap catches of the entire flight period, beetles swarmed in summer corresponded to 19.6 and 14.0% of those swarmed in spring of 2007 and 2008, respectively. Spring and summer peaks were separated by 67 days in 2007 and 42 days in 2008. The thermal sum of the two peaks, calculated above the threshold of 14°C, amounted to  $72.8 \pm 5.2$  DD. In rearing cages, the insect emergence recorded from branches collected in spring and

**Fig. 1** Mean number of *I. acuminatus* caught per trap ( $\pm$ SEM) and daily maximum air temperature (dashed line) in 2007 (a) and 2008 (b). Horizontal line corresponds to 14°C. On the X axis are reported the dates of trap emptying and the period of trap checking before the beginning of flights



**Table 1** Thermal sums calculated in each year from January 1st to the date of the spring flight peak considering thermal thresholds ranging between 0 and 10°C

Spring flight peak	Year	Thermal sum of daily mean temperature above 0–10°C										
		0	1	2	3	4	5	6	7	8	9	10
April 22nd	2007	423	338	268	211	164	129	100	74	54	39	26
May 20th	2008	483	389	309	241	184	136	96	64	37	19	7
May 13th	2009	400	333	273	220	173	133	99	71	48	34	20
	Mean	435.32	353.25	283.36	224.10	173.53	132.70	98.51	69.61	46.15	30.46	17.53
	$\pm$ SD	42.96	31.17	22.76	15.01	9.71	3.24	2.19	5.20	8.61	10.33	9.32

summer had a pattern similar to that observed in the field, with two distinct peaks and a lower number of adults swarming in summer (from 5.8 to 40.1%).

The emergence data from branches collected in June and colonised in the same spring demonstrated that about half of the offspring of the first generation (50.5 and 55.5% in 2007 and 2008, respectively) did not emerge in summer. Moreover, only 15.7 and 4.8% (in 2007 and 2008, respectively) of the overwintering adults were effectively

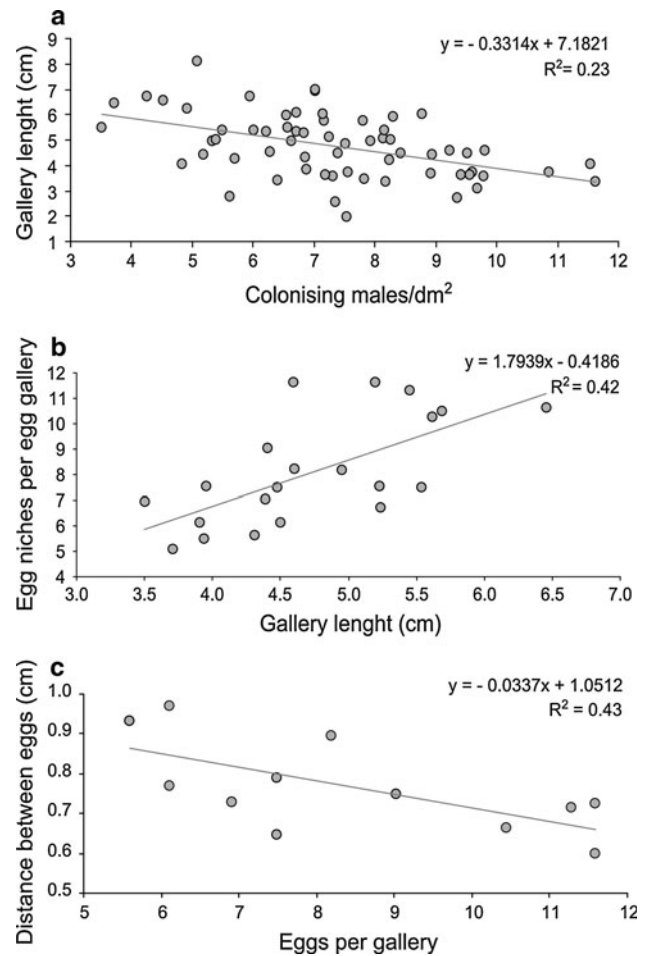
found hibernating under the bark in the following spring, as the rest had evidently left the tree before collection.

#### Tree infestation pattern

*I. acuminatus* colonisation generally occurred in the medium-upper part of the tree starting at a mean diameter of  $14.1 \pm 2.0$  cm ( $N = 21$ ). The mean RIBH was  $0.5 \pm 0.1$  ( $N = 21$ ), with a total tree height varying from 5.5 to

14.5 m ( $9.8 \pm 1.8$ ,  $N = 21$ ). The TCBS ranged from 1.5 to  $8.4 \text{ m}^2$  per tree and it was related significantly to tree diameter at breast height (TCBS =  $0.387 \times$  diameter at breast height - 3.55,  $N = 13$ ) ( $R^2 = 0.71$ ,  $F_{(1, 11)} = 27.51$ ,  $P < 0.001$ ). It was thus estimated that the infested pines were colonised by  $10,947 \pm 3,948$  beetles ( $N = 21$ ), depending on their size (mean breast height diameter  $20.2 \pm 3.6$  cm,  $N = 21$ ).

Whereas male density (nuptial chambers) showed a significant interaction between year and generation, female density (egg galleries) was similar between and within years (Table 2). Nuptial chambers were always free of frass, and their size ( $0.23 \pm 0.02 \text{ cm}^2$ ,  $N = 12$ ) did not vary with colonisation density. Harem size ranged from 1 to 7 ( $2.6 \pm 0.3$ ,  $N = 21$ ) females per male. Galleries shorter than 1 cm did not contain egg niches and ranged from 0 to 4 per harem ( $1.8 \pm 0.5$ ,  $N = 21$ ), increasing linearly with colonisation density ( $R^2 = 0.36$ ,  $F_{(1, 19)} = 10.67$ ,  $P < 0.005$ ). Differently, the mean number of egg galleries per mating system (harem size) and their length ( $4.7 \pm 0.8$  cm, range 1–11 cm,  $N = 21$ ), decreased with increasing density of colonising males ( $R^2 = 0.43$ ,  $F_{(1, 19)} = 14.55$ ,  $P < 0.005$  and  $R^2 = 0.23$ ,  $F_{(1, 61)} = 18.40$ ,  $P < 0.0001$ , respectively) (Fig. 2a). The number of eggs in each harem ( $26.7 \pm 8.0$ ,  $N = 21$ ) was strongly correlated with both harem size ( $P < 0.05$ ) and egg gallery length ( $P < 0.01$ ). Female fecundity (eggs per gallery) varied from 4.2 to 16.7 ( $8.1 \pm 2.1$ ,  $N = 21$ ) according to gallery length ( $R^2 = 0.42$ ,  $F_{(1, 19)} = 14.04$ ,  $P < 0.005$ ) (Fig. 2b). The distance between eggs along the gallery ( $0.76 \text{ cm} \pm 0.12$ ,  $N = 12$ ) was inversely related to the female fecundity ( $1.8 \text{ egg/cm} \pm 0.4$ ,  $N = 12$ ) ( $R^2 = 0.43$ ,  $F_{(1, 10)} = 7.55$ ,  $P < 0.05$ ) (Fig. 2c). Lastly, the mean length



**Fig. 2** Relationships between length of egg galleries and density of colonising males (mating systems per  $\text{dm}^2$ ) ( $N = 63$ ) (a), number of eggs and gallery length ( $N = 21$ ) (b), distance between eggs and eggs per egg gallery ( $N = 12$ ) (c)

**Table 2** Mean density ( $\pm$ SD) per  $\text{dm}^2$  of parent beetles and preimaginal stages observed in the four sampled generations ( $N = 21$ )

	Density/ $\text{dm}^2$				Two-way ANOVA		
	2006/2007 generations		2007/2008 generations		P-value		
	$F_2$ 2006	$F_1$ 2007	$F_2$ 2007	$F_1$ 2008	Generation	Year	Interaction Gen*Year
Nuptial chambers (males)	$6.7 \pm 1.4$	$8.5 \pm 0.8$	$7.3 \pm 0.9$	$6.5 \pm 1.0$	ns	ns	<0.05
Egg galleries (females)	$17.0 \pm 2.0$	$20.2 \pm 1.5$	$17.8 \pm 1.7$	$17.9 \pm 4.0$	ns	ns	ns
Colonisation density (males plus females)	$23.7 \pm 3.4$	$28.7 \pm 1.5$	$25.1 \pm 2.6$	$24.4 \pm 5.0$	ns	ns	ns
Harem size (females per male)	$2.6 \pm 0.3$	$2.5 \pm 0.4$	$2.5 \pm 0.2$	$2.8 \pm 0.2$	ns	ns	ns
Eggs	$170.9 \pm 36.1$	$136.0 \pm 26.6$	$145.7 \pm 15.8$	$102.3 \pm 33.5$	<0.005	<0.05	ns
Young larvae	$138.3 \pm 29.7$	$115.6 \pm 23.6$	$123.6 \pm 17.1$	$87.6 \pm 32.0$	<0.05	ns	ns
Mature larvae	$121.0 \pm 28.1$	$99.0 \pm 14.9$	$110.3 \pm 13.6$	$78.3 \pm 31.3$	<0.01	ns	ns
Pupae	$95.3 \pm 27.6$	$63.0 \pm 15.7$	$82.5 \pm 21.6$	$55.8 \pm 18.5$	<0.01	ns	ns
Pre-emerging adults	$45.7 \pm 17.9$	$16.0 \pm 6.4$	$34.9 \pm 11.5$	$15.8 \pm 6.3$	<0.01	ns	ns

Generation, year, and their interactions were tested by a two-way ANOVA for each variable

ns not significant



( $0.76 \pm 0.13$  cm,  $N = 12$ ) of the egg-free part of the gallery was not correlated with any density variable.

#### Breeding performance and brood mortality

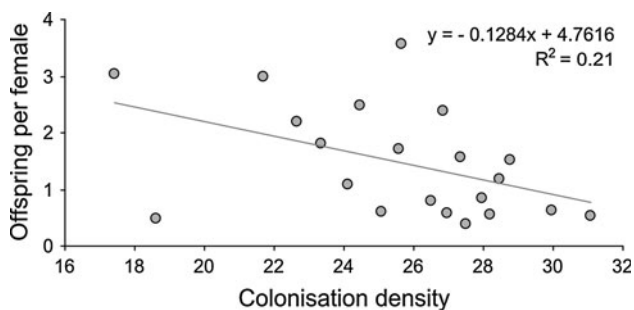
The mean breeding performance, calculated as percentage of eggs giving emerging adults, was higher in the second than in the first generation ( $F_{(1, 19)} = 19.20$ ,  $P < 0.005$ ), with a mean of 16.5% per spot ( $\pm 8.0$ ,  $N = 21$ ). The offspring production, ranging from 0.003 to 5.55 new adults per female ( $1.47 \pm 0.97$ ,  $N = 21$ ), was negatively correlated with colonisation density ( $R^2 = 0.21$ ,  $F_{(1, 19)} = 4.98$ ,  $P < 0.05$ ) (Fig. 3). The sex ratio of the adults emerged from the sampled branches ranged from 1 to 1.45 females per male. The density of all preimaginal instars was higher in the second than in the first generation and, with the exception of the number of eggs, did not show significant variations among years (Table 2). Preimaginal mortality strongly reduced the number of individuals, as  $47.7\% \pm 11.5\%$  ( $N = 21$ ) of the offspring died before pupation (Fig. 4). Egg mortality ( $16.7\% \pm 5.4\%$ ,  $N = 21$ ) and young larvae mortality ( $12.2\% \pm 5.4\%$ ,  $N = 21$ ) were not affected by colonisation density. Mortality increased in mature larvae ( $29.0\% \pm 13.1\%$ ,  $N = 21$ ) and especially

in pupae ( $62.5\% \pm 17.1\%$ ,  $N = 21$ ): values were higher in the first than in the second generation ( $F_{(1, 17)} = 6.23$ ;  $P < 0.05$ ) and positively related to colonisation density ( $R^2 = 0.25$ ,  $F_{(1, 19)} = 6.47$ ,  $P < 0.05$ ). Lastly, the mortality of the pre-emerging callow adults ranged from 0 to 90.9% ( $22.2\% \pm 13.2\%$ ,  $N = 21$ ).

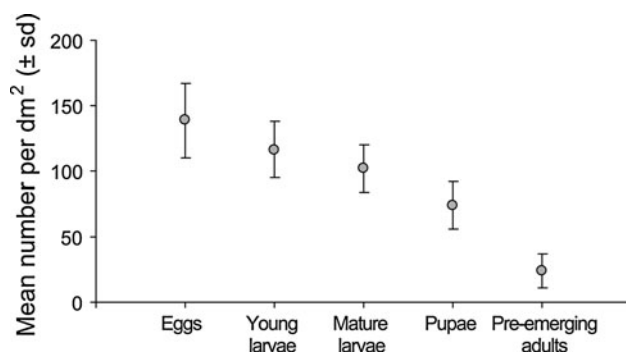
#### Discussion

The life-history traits of *I. acuminatus* in the new outbreak area in the south-eastern Alps reveal a number of adaptations to local abiotic and biotic factors that may increase the frequency and intensity of outbreaks in the future. First, the early spring emergence allows the beetles to complete a second generation, resulting in an extension of the period during which trees are challenged by colonising adults. As summer in the southern slope of the Alps is characterised by irregular drought events, trees will be thus more exposed to beetle attacks (Wermelinger et al. 2008). With increasing temperatures, the proportion of new generation beetles reproducing before hibernation may increase, causing a higher risk of tree mortality. Second, a high proportion of the beetles overwinter away from the infested tree, possibly in the litter (Francke-Grosmann 1963; Lekander et al. 1977), and thus escape natural enemies occurring under the bark of their breeding material, especially when high temperature allows a longer period of activity of predators and parasitoids (Faccoli 2002).

Alpine populations appear to emerge earlier than other known populations in both northern and southern Europe. In Norway, *I. acuminatus* is included among the ‘late-swarming bark beetles on pine’ as the earliest trap collections has been observed in mid-May (in June at the northern sites) and the mass flight takes place only when air temperature is greater than  $18^\circ\text{C}$ , even if few beetles can fly at a temperature of  $14\text{--}16^\circ\text{C}$  (Bakke 1968). We identified the thresholds of 6 and  $14^\circ\text{C}$  for spring emergence and brood development, respectively. While there are no comparable data for the spring emergence threshold, the second one appears to be slightly higher than the minimum level for brood development ( $12^\circ\text{C}$ ) assumed by Bakke (1968) for Scandinavian populations. As this author obtained 5 larvae and 3 pupae out of 120 females in 114 days, we think that the threshold could be underestimated. In addition, southern population could differ in their reaction norms from the northern ones (Bentz et al. 2011). The flight activity lasts for 1 or 2 months, depending on locations in Norway, and a second generation is excluded (Bakke 1968). In southern areas, such as Spain, *I. acuminatus* flight starts in May, when the maximum air temperature also exceeds  $18^\circ\text{C}$  (Hernández et al. 2004; Pérez and Sierra 2006). Further, the flight period in Spain is



**Fig. 3** Offspring production per female at different colonisation density (males and females per  $\text{dm}^2$  of bark) ( $N = 21$ )



**Fig. 4** Mean density ( $\pm$ SD) of individuals of each instar per  $\text{dm}^2$  ( $N = 21$ )

prolonged and without a clear peak, so a second generation seems possible only when unusually warm temperatures allow beetles to breed until very late in the season (Hernández et al. 2004; Pérez and Sierra 2006). On the contrary, in our field site the beetles swarm when temperature is 14°C only. These findings lead to hypothesise the existence of local specific developmental thresholds in the studied population, regulating both the early start of the flight period and the precise synchronisation in emergence; these factors allow the occurrence of a partial second generation in the year and a longer exposure of trees to beetle attack (Logan and Powell 2003; Ayres et al. 2009). The model fits well with predictions made by Bentz et al. (2010) that temperature influences bark beetle population dynamics predominately through effects on life traits, facilitating the maintenance of adaptive developmental timing.

*I. acuminatus* has been hypothesised to have mono or bivoltine populations according to latitude and altitude (Chararas 1962; Bakke 1968; Forster and Zuber 2001; Hernández et al. 2004), but precise information is lacking and it is not clear whether the two generations may occur in the same tree. In our study, we show that different host trees are attacked in spring and summer by beetles of two distinct swarming flights, as demonstrated by the appearance twice a year of new infested trees about 2 months after the flight peaks recorded by traps. The long period between the spring and summer emergence peaks (about 50 days) excludes the possibility that the second peak is the result of re-emerging parent beetles trying to establish a sister brood (Pérez and Sierra 2006). The beetle population in the study area, however, is only partly bivoltine and this suggests the possible existence of a regulatory mechanism of voltinism such as a facultative diapause, already shown by Gehrken (1985) for northern populations. This regulatory mechanism could be affected by abiotic factors, such as the photoperiod as shown by Baier et al. (2007) for *I. typographus*, or by seasonal fluctuations in some factors that regulate individual fitness such as host-plant quality, food limitation, or natural enemies (Sota 1988). Unfortunately, there are no historical data on the outbreak occurrence of *I. acuminatus* in the area. A survey of old spots and interviews with local stakeholders were attempted and revealed that some old attacks did occur, although at much lower intensity. The voltinism in former time is unknown, but considering the temperature pattern, it seems unlikely that a second generation could have occurred in the past. We analysed the temperature measured in the study site in the last 40 years and found that it has slightly increased, as shown for other sites of the Alps (Battisti et al. 2006).

Our results indicate that beetles hibernate both under the bark of the infested trees and outside of the breeding material. Branches sampled in early spring, before insect

emergence, contained only about 10% of the expected adults. This small number of beetles could not explain the occurrence of successful attacks in spring on a large number of trees, because attack densities known to be lethal to Scots pine are very high (Guérard et al. 2000), as it has been confirmed by our data. Wermelinger et al. (2008) also observed that the number of overwintering adults (0.35/dm<sup>2</sup>) found during a study carried out in south-western Switzerland (Rhône valley) was lower than expected based on the number of infested trees. The most plausible explanation is that the missing beetles emerged before the winter of the previous year. Traps did not detect this flight because beetles looking for hibernation sites—such as bark or forest litter—are probably not responding to pheromones. Although in northern Scandinavia most of the *I. acuminatus* population spend the winter under the bark of trees where they have developed (Bakke 1968), some authors (Francke-Grosmann 1963; Lekander et al. 1977) reported the possible hibernation of *I. acuminatus* adults in the forest litter. There is no precise information, however, about this behaviour and how it could affect beetle survival. *I. acuminatus* is a freezing-susceptible species, but newly emerged adults freeze at a temperature of −19°C and hibernating adults can tolerate temperature down to about −34°C (Bakke 1968; Gehrken 1984, 1989). It is thus unlikely that adults leave the tree to find less extreme conditions than those provided by pine bark (Bakke 1968; Lombardero et al. 2000). We hypothesise instead that migration to different overwintering sites can be considered as an escape from unfavourable conditions (overcrowding) and from high concentration of natural enemies, known to be important factors that could impact the breeding performance of *I. acuminatus* in Europe (Kenis et al. 2004) and also in our study site (unpublished data). As warmer and wetter winters are generally predicted by climate-change scenarios (Rosenzweig et al. 2007), it is likely that there will be a higher activity of predators, parasitoids and pathogens associated with beetles under the bark (Bentz et al. 2010), whereas individuals dispersed elsewhere will be less exposed.

Synchronised early colonisation and enemy escape can be important factors for the reproductive success of a species that is characterised by very high attack density in our (7.25/dm<sup>2</sup> resulting in 100% killed trees) as well in other studies (8.5/dm<sup>2</sup> resulting in 95% killed trees, Guérard et al. 2000). Increasing bark colonisation density has been associated with increasing mortality due to intraspecific competition (Beaver 1974; Kirkendall 1989) and our results confirm this general trend. High density of colonising males and within-harem crowding lead gallery length to reduce noticeably, but the newly observed strategy of density-dependent regulation of egg population (fewer, well-spaced eggs in short galleries) cannot help

reducing space and resources for the brood. Spreading the reproductive effort over two generations may allow the beetle to reduce the risk of intraspecific competition, as there is a higher probability to find susceptible trees that can be killed with a lower attack density, releasing space to the colonizers. The contrasting values of attack density observed across generations and years may reveal the plasticity of the system, tending to optimise attack densities in relation to tree susceptibility and to limit mortality associated with overcrowding of broods.

Insects adapt their thermal responses to the habitat (Taylor 1981) adjusting phenology to maintain favourable match between themselves and the environment. For this reason, it is expected that a significant impact of global warming may affect bark beetles performance both directly and indirectly, through the effects on community associates (symbiotic microorganisms and natural enemies) and host-tree vigour (Bale et al. 2002; Bentz et al. 2010). As the studied population becomes active at rather low temperature and has developed an appropriate matching with availability of susceptible hosts, this may lead to an increase in frequency and severity of outbreaks. Furthermore, the early emergence combined with the overwintering of many beetles outside of the breeding material may reduce the exposure to natural enemies associated with the bark, enhancing survival and allowing the population to achieve the high density required to successfully colonise trees.

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