

Temperature-dependent reproduction of the spruce bark beetle *Ips typographus*, and analysis of the potential population growth

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Abstract. 1. The spruce bark beetle *Ips typographus* (L.) is one of the most important forest pests in Central Europe, but despite this the effects of temperature on life history and population growth are largely unknown. This study examines the effects of temperature on reproduction and intrinsic demographic statistics.

2. Laboratory experiments on oviposition were carried out at six temperatures in the range 12–33 °C, using the so-called sandwich rearing technique for bark beetles.

3. A linear relationship between oviposition rates and temperatures in the range 15–25 °C was used to estimate the lower temperature threshold for oviposition as 11.4 °C. With a nonlinear model fitted to the data across the whole range of experimental temperatures, the lower and upper limiting temperatures and optimum temperature were found to be 7.9, 33.7, and 28.9 °C, respectively. A model for daily oviposition rate was fitted, which describes the pattern of oviposition over the entire oviposition period.

4. The analysis of life tables, combining developmental rates, reproduction, mortality, and sex ratio, suggests maximum population growth (r_m) at near 30 °C.

5. After generating a first brood, spruce bark beetles often re-emerge from the tree and produce other *sister* broods. The effects of temperature and number of sister broods on demography were evaluated using age-specific life-table analyses. It is hypothesized that sister broods play an important role in regions where *I. typographus* is monovoltine, but have only moderate significance where this species has more than one generation per season.

Key words. Demographic statistics, life-table analysis, oviposition, population dynamics, sister broods.

Introduction

The eight-spined spruce bark beetle *Ips typographus* (L.) has for centuries been recognized as one of the most important forest pests in Central Europe (Christiansen & Bakke, 1988). Despite its importance, significant gaps in the knowledge of its basic biology remain. Data on temperature effects on demographic parameters of bark beetles are sparse in the literature. They refer either to species other than *I. typographus* (e.g. Wagner *et al.*, 1981; Bentz *et al.*, 1991; Ye, 1994; Coeln *et al.*, 1996) or exclusively to its larval development (Annala,

1969; Coeln *et al.*, 1996; Wermelinger & Seifert, 1998). In terms of reproduction, most quantitative investigations on *I. typographus* under controlled conditions have been carried out to estimate the effect of breeding density (Anderbrant, 1990) or on sister-brood production (Anderbrant & Löfqvist, 1988). Some field data on these aspects also exist (Thalenhorst, 1958; Mills, 1986), but they are largely insufficient. No study has evaluated specifically the effect of temperature on reproduction, and hence a first goal of the present investigation was to quantify this and to assess the temperature effects on population growth rates using life-table analyses.

The reproductive period of this bark beetle can be divided into several phases. After mating, the female deposits a first brood. It may then re-emerge and, after some regeneration feeding, re-enter the same or a different tree to produce one or

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more so-called sister broods. This phenomenon is well documented for *I. typographus* (Thalenhurst, 1958; Annala, 1969; Simon, 1982; Bakke, 1983; Anderbrant & Löfqvist, 1988; Anderbrant, 1986, 1988, 1989, 1990), and also occurs in other bark beetle species (Wagner *et al.*, 1981, 1988; Gagne *et al.*, 1982; Flamm *et al.*, 1987; Sauvard, 1993). The second objective of this study was to assess the significance of sister broods on the demographic statistics of spruce bark beetle populations. This was accomplished by means of life-table analyses at different temperatures with different numbers of sister broods.

Materials and methods

The methods used in this study have been described in detail by Wermelinger & Seifert (1998). Briefly, observations of the cryptically living bark beetles were made possible by the widely used sandwich technique. In this technique, phloem pieces of cut spruce trees are clamped between two Plexiglas panes. Beetles taken from a mass reared colony (bolt rearing method) were sexed (Schlyter & Cederholm, 1981), and males were introduced singly to each sandwich to excavate the nuptial chamber. After 2 days, two or three females were added to each sandwich for mating and subsequent oviposition. Groups of sandwiches were exposed to temperatures of 12, 15, 20, 25, 30, and 33 °C in controlled-temperature cabinets at 60–75% RH. The day of female introduction was defined as day zero. The number of eggs deposited by each female was recorded daily (twice a day at 33 °C). Using an overhead transparency placed on the pane over the galleries, maternal and larval galleries were traced with different coloured pens. Not all eggs were visible through the Plexiglas pane, but after the larvae hatched their galleries became visible and were traced back to the maternal gallery. Such progeny were assigned to the increment of the maternal gallery they intersected. Female bark beetles were observed until death or disappearance from the sandwich. The experiments were repeated until a sufficient number of replicates was obtained for each temperature regime.

In the analysis, only females that lived 5 days or more and produced a minimum of one egg were included. Mean total fecundity, oviposition rate (eggs per female per day of their oviposition period), and preoviposition and oviposition periods were calculated. The temperature thresholds for oviposition were computed using the maximum daily oviposition rates at each temperature. Maximum rather than mean oviposition rates were used because temperature effects are more distinct at peak productivity than when including oviposition in the senescence phase. A weighted linear regression analysis was used for regimes 15–25 °C. The weights for the regression were obtained by fitting an exponential function relating the variances of the oviposition rates to temperature. The linear oviposition threshold temperature (T_{Lin}) is the zero intercept of the regression line on the x-axis. In addition, a nonlinear model proposed by Logan *et al.* (1976) and modified by Lactin *et al.* (1995) to model developmental rates, was fitted to the

oviposition rates across temperature using weighted least square regression. The equation is:

$$MOR(T) = e^{\alpha T} - e^{[\alpha T_{max} - (T_{max} - T)/\beta]} + \gamma \quad (1)$$

where $MOR(T)$ is the temperature dependent maximum daily oviposition rate, T is temperature, and α , β , γ and T_{max} are fitting parameters. This model allows the estimation of the lower (T_L) and upper (T_U) temperature thresholds, and the optimum temperature (T_O) for oviposition.

Two sets of data were utilized in developing the life tables. In the first analysis, a small data set for beetles with continuous records of individual development from the egg stage to the end of oviposition was used (limited data set). Many individuals had gaps in their developmental history (e.g. without known date of birth), and hence in the second set the common life-table parameters (r_m , R_0 , G , and DT , cf. Laughlin, 1965) were computed using the oviposition data from all individuals and in combination with random development times drawn from beetles observed at the same temperature (Wermelinger & Seifert, 1998) (complete data set). The intrinsic rate of natural increase (r_m) is the population growth rate per time unit (1 day), the net reproductive rate R_0 is the number of multiplications per generation, generation time (G) is the mean age (starting from egg stage) of the females at the birth of female offspring (when 0.5 R_0 is reached), and DT the doubling time ($\ln 2/r_m$) (cf. Laughlin, 1965; Southwood, 1978). Based on data from the literature, immature mortality was assumed to be 20% in the analyses (Thalenhurst, 1958; Mills, 1986). Sex ratios were taken from the present study. A jackknife technique (cf. Meyer *et al.*, 1986; Hulting *et al.*, 1990; Wermelinger *et al.*, 1991) was used to estimate variances for all parameters. In this technique, pseudovalues for the life-table parameters are computed by recalculating n times the parameters using only $n-1$ of the replicates each time. Each of the original n observations was left out of the calculations only once. Means and variances of these treatment pseudovalues at each temperature were calculated and the means analysed using ANOVA and Bonferroni *post hoc* test.

To evaluate the impact of sister broods on life-table parameters, life tables were compiled from this study's results and the literature data listed in Table 1. Egg production in each sister brood was assumed to be distributed according to the relative oviposition pattern shown in Fig. 1. A 3-day lag was used between broods to simulate the host-finding and adult-feeding period.

Results

Ips typographus females oviposited successfully in the temperature range 12–33 °C. In preliminary experiments outside this range no substantial oviposition activity was observed. Below 12 °C, daily increments of maternal galleries were very short and only scattered eggs were deposited. At 35 °C, females survived only a few days and no oviposition occurred. In the range 12–33 °C, reproduction was dependent

Table 1. Parameter values used for life-table analyses evaluating the effect of sister broods and temperature based on corresponding literature data (exclusively on *Ips typographus*). Second brood=first sister brood, third brood=second sister brood.

Parameter	Values	Literature data	Reference
Developmental time (days) (at 20, 25, 30 °C)	29, 20, 17	29, 20, 17	Wermelinger & Seifert, 1998
Immature mortality (%)	20	10–15 (eggs) 15 (larvae) 7 (eggs)	Thalenhorst, 1958 Mills, 1996
Maturation feeding (days) (at 20, 25, 30 °C)	17, 13, 11	17, 13, 11	Wermelinger & Seifert, 1998
Sex ratio (at 20, 25, 30 °C)	0.6, 0.6, 0.5	0.6, 0.6, 0.5	Table 2, this publication
Offspring 1st brood (eggs/♀) (at 20, 25, 30 °C)	14, 23, 24	14, 23, 24 92 42–58	Table 2, this publication Mills, 1986 Anderbrant & Löfqvist, 1988
Oviposition period 1st brood (days) (at 20, 25, 30 °C)	6, 5, 4	6, 5, 4	Table 2, this publication
Proportion of females producing 2nd brood (re-emergence) (%)	60	45 60–85 60 94	Simon, 1982 Bakke, 1983 Anderbrant, 1988 Anderbrant & Löfqvist, 1988
Offspring 2nd brood (eggs/♀) (at 20, 25, 30 °C)	10, 17, 18	33 75% of 1st brood	Anderbrant, 1989 Anderbrant & Löfqvist, 1988
Oviposition period 2nd brood (at 20, 25, 30 °C)	6, 5, 4	80–150% of 1st brood	Anderbrant & Löfqvist, 1988
Proportion of females producing 3rd brood* (%)	40	38 45	Martinek, 1956 Simon, 1982
Offspring 3rd brood (eggs/♀) (at 20, 25, 30 °C)	7, 11, 12 (50% of 1st brood)	—	
Oviposition period 3rd brood (at 20, 25, 30 °C)	6, 5, 4	—	
Regeneration feeding (days) (for all broods, at 20, 25, 30 °C)	4, 3, 2	—	

*Relative to females producing 1st brood.

on temperature (Table 2). Total fecundity increased almost sixfold over this range of temperatures, dropping rapidly at 33 °C. The same behaviour was found for the oviposition rate, peaking at 30 °C. The oviposition rates in Table 2 represent mean egg production per day over the whole oviposition period at the different temperatures. Productivity is low compared to egg production in the field (cf. Table 1). Pre-oviposition and oviposition periods declined gradually with temperature. Pre-oviposition period is the time that elapses from introduction of the females into the nuptial chamber to the production of the first egg. The sex ratios of the offspring suggest that females are favoured over males at low temperatures, but the differences were not significant (χ^2 test).

To describe the time-specific oviposition pattern of *I. typographus* (e.g. for modelling purposes), the relative cumulative oviposition data were plotted against relative oviposition time (time divided by maximum oviposition period at each temperature) and a logistic function was fitted (Fig. 1a). This model is used to estimate the fraction of total progeny deposited at a relative time in the oviposition period. From this function the real number of accumulated eggs at time t within the oviposition period

(OP) may be calculated by substituting t/OP for the variable x in the model (Fig. 1a) and multiplying this proportion by total fecundity (F). The first derivative of this cumulative function is the relative oviposition rate y_2 at each relative time in the oviposition period (Fig. 1b). The absolute oviposition rate $OR(t)$ at time t can be calculated by multiplying y_2 in Fig. 1b by F and dividing it by OP :

$$OR(t) = [0.244x^{-3.30}/(0.096x^{-2.30} + 1)^2] * (F/OP) \quad (2)$$

where x again is t/OP . Oviposition period and time may be expressed as chronological or physiological time. The proportion of a female's reproduction at a given physiological age is temperature independent (cf. Curry & Feldman, 1987).

The impact of temperature on egg production was analysed in an analogous way, as for developmental data (Wermelinger & Seifert, 1998). Dependency of egg production on environmental factors was considered to be represented best by the maxima of the daily production rates (peak in Fig. 1b) when females are reproducing at their highest possible rate. On the one hand, a linear regression was fitted to the temperature-

dependent oviposition maxima (cf. Fig. 2). The corresponding parameters are listed in Table 3. The resulting oviposition threshold temperature was 11.2 °C. On the other hand, the Logan/Lactin model (eqn 1) was fitted to these oviposition rates; the fitting parameters are also listed in Table 3. The model described the data very well. With this model, the lower oviposition threshold was at 7.9 °C, as expected, a lower value than with the linear model. The optimum temperature, i.e. the temperature where the oviposition rate reached its maximum, was estimated at ≈ 29 °C. Temperatures at or above 34 °C are limiting.

In order to evaluate the role of temperature in the overall propagation potential of *I. typographus* populations, life tables were compiled and analysed (Table 4). Both the limited and complete data sets (cf. Materials and methods) gave similar results, hence the discussion is focused on the complete set. R_0 (i.e. the number of multiplications per generation) tended to be elevated at 25 °C, although the differences were not significant. The other population parameters r_m , G , and DT were significantly higher at 25 and 30 °C than at 20 °C. As a result of high fecundity and short generation time at 25 °C, r_m doubled relative to 20 °C. There was no difference in

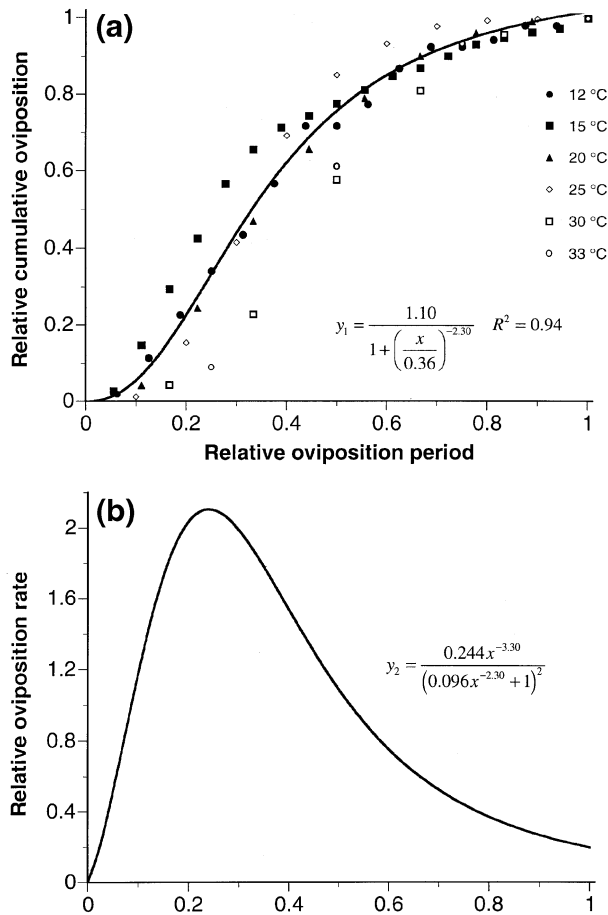


Fig. 1. Relative oviposition of *Ips typographus* vs. relative time: (a) cumulative oviposition, (b) daily oviposition rate ($y_2 = y_1$).

Table 2. Reproductive parameters and sex ratio of *Ips typographus* at various temperatures. Sex ratio is calculated as the proportion of females in the offspring (replicate = one sandwich), SE = standard error.

Temperature (°C)	Fecundity (eggs/♀)	Oviposition rate (eggs/♀/day)			Oviposition period (days)			Pre-oviposition period (days)			Sex ratio		
		SE	n	rate	SE	n	period	SE	n	period		SE	n
12	4.1	1.24	13	0.45	0.07	13	7.6	1.20	13	2.5	0.43	13	—
15	9.5	1.99	22	1.17	0.13	22	8.6	0.99	22	2.1	0.48	22	0.82
20	14.5	1.96	19	2.64	0.25	18	5.6	0.49	18	1.0	0.20	18	0.61
25	23.3	3.14	22	4.34	0.43	21	5.4	0.38	21	1.3	0.17	21	0.62
30	23.6	4.49	8	5.33	0.82	8	4.4	0.53	8	1.1	0.23	8	0.48
33	6.4	1.05	14	2.28	0.25	14	2.7	0.27	14	0.7	0.13	14	—

population performance between 25 and 30 °C. It has to be stressed that this analysis assumes temperature-independent intrinsic mortalities. This may be reasonable in the uncritical range of temperatures (cf. Curry & Feldman, 1987). The effect of these life-table parameter values on a multiseasonal base (winter mortality) is discussed in the context of sister broods below.

The above life-table analyses are based on a single reproductive phase (first brood) of the spruce bark beetle. Because bark beetles often re-emerge after the first brood and produce sister broods (cf. Introduction), the quantitative role of sister broods in population growth was assessed. The analysis was based on life-history parameters of the present experiments for the first brood and on sister brood data from the literature (see Table 1). Most results in the literature are not temperature-specific. Re-emergence time (i.e. oviposition period) was defined relative to the temperature-dependent oviposition periods found in the present experiments. A fixed figure for average, temperature-specific re-emergence time was applied because the pattern (not time!) of re-emergence is reported to be temperature independent (Anderbrant, 1989). Life tables were compiled

at 20, 25, and 30 °C with zero, one, and two sister broods each.

Estimates of r_m given different brood numbers are shown in Fig. 3. First, a marked increase of r_m was visible in the temperature range under study. Second, the contribution of sister broods to population growth was moderate, at least at high temperatures. At 25 °C the growth rate increased by only 10% with two sister broods, at 20 °C it increased by 15%. The absolute r_m values may appear to be low, because the data on fecundity and oviposition period used in this analysis are low compared to observations in the field (cf. Table 1). However, in Fig. 3 emphasis is put on the relative significance of sister broods. Unlike r_m , the net reproductive rate R_0 increased by more than 60% with three broods (two sister broods), irrespective of temperature. As an example, R_0 values at 25 °C are indicated in Fig. 3. The effect of sister broods on R_0 outstripped even that of temperature. It is obvious that generation time also increased, though only moderately ($\approx 8\%$).

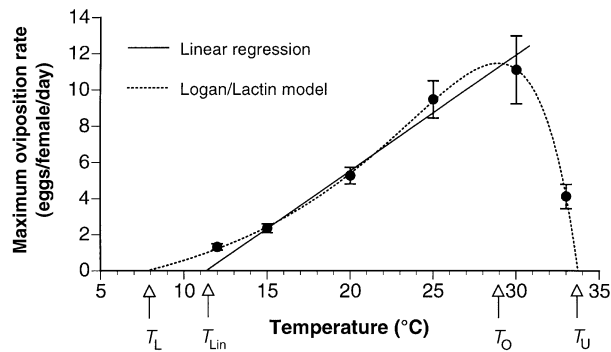


Fig. 2. Temperature-specific maximum oviposition rates of *Ips typographus*. Bars = SE.

Table 3. Parameters of the linear model and the Logan/Lactin model, respectively, for maximum oviposition rates of *Ips typographus*, and resulting temperature characteristics for oviposition. a = slope, b = intercept, r^2 = adjusted correlation coefficient, T_{Lin} = linear temperature threshold (minimum temperature for oviposition), SE = standard error; α , β , γ , T_{max} cf. text, T_L and T_U = lower and upper temperature threshold, respectively, T_O = optimum temperature; cf. Fig. 3.

Model parameters			Results		
Linear model					
a	b	r^2	T_{Lin}	SE	
0.641	-7.27	0.54	11.4 °C	1.1 °C	
Logan/Lactin model					
α	β	γ	T_{max}	r^2	T_L T_O T_U
1.04E-1	3.05	-2.24	34.04	0.99	7.9 °C 28.9 °C 33.7 °C

Table 4. Life-table analysis for *Ips typographus* based on a limited data set and on the complete data set (see text), respectively, at various temperatures. R_0 = net reproductive rate, r_m = intrinsic rate of natural increase, n = number of replicates, SE = standard error.

Temperature (°C)	R_0		r_m (day ⁻¹)		Generation time G (days)		Doubling time DT (days)		n
	R_0	SE	r_m	SE	SE	SE	SE		
Limited data set									
20	7.5 ^a	1.81	0.039 ^a	0.0047	52.5 ^a	0.98	17.5 ^a	2.33	7
25	13.5 ^a	2.54	0.068 ^b	0.0068	38.5 ^b	3.06	10.1 ^b	1.07	7
30	5.7 ^a	1.88	0.052 ^{ab}	0.0091	34.4 ^b	5.29	12.9 ^{ab}	2.53	4
Complete data set									
20	7.1 ^a	1.02	0.039 ^a	0.0029	50.2 ^a	2.05	17.6 ^a	1.36	18
25	12.0 ^a	1.82	0.078 ^b	0.0056	32.1 ^b	1.33	8.9 ^b	0.66	21
30	9.1 ^a	1.72	0.072 ^b	0.0064	30.7 ^b	0.87	9.5 ^b	0.89	8

Within each data set, means followed by different letters differ significantly at $P < 0.05$.

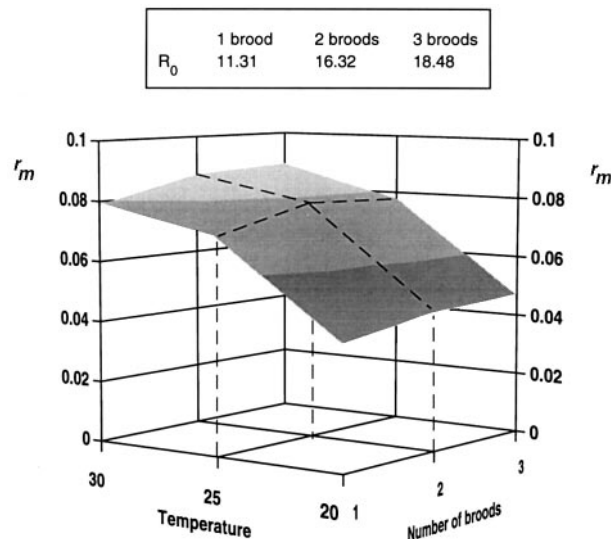


Fig. 3. Intrinsic rate of natural increase (r_m) of *Ips typographus* at different temperatures and with different number of broods; the superimposed numbers indicate the net reproductive rates R_0 at 25 °C.

Discussion

The sandwich method allowed easy monitoring of the developmental and reproductive processes, however this technique does not exactly reproduce the situation in the field. For example, offspring production in the sandwiches was smaller than that reported in the literature and observed in the field. A single female under field conditions produces a first brood of up to sixty eggs (Anderbrant & Löfqvist, 1988). Likewise, the oviposition period appears shorter. Many females left the sandwiches, possibly to start other broods, but failed because no uninfested bark was available in the sandwiches. The low fecundity reduces the relative contribution of reproduction to population dynamics and puts more emphasis on developmental aspects. Mortality in the sandwiches also differed from the natural situation. Nevertheless, the sandwich method allows a reliable assessment of the response pattern of *I. typographus* population dynamics to temperature. The temperature relevant for bark dwelling organisms is the phloem temperature, which may differ markedly from the ambient temperature due to radiation or insulation effects. The temperature regimes used in this study represent phloem temperatures.

The responses of immature development (see Wermelinger & Seifert, 1998) to extreme temperatures and that of adult oviposition are not consistent. The lower temperature threshold is notably higher for egg production than for development. This contradicts the findings that at the experimental temperature of 12 °C, oviposition but no development could be observed (except for eggs). This may be attributed to excessive mortality at very low temperatures, although development is possible in principle. Oviposition seems to be more sensitive to extreme temperatures (stenothermic) than is immature development.

Population growth is determined not only by egg production but also by development, sex ratio, and mortality. These factors may be merged in life tables. Temperatures between 25 and 30 °C resulted in the fastest population growth as indicated by r_m as an overall population growth estimator. Up to 30 °C, the speed of development and fecundity did increase, but the sex ratio tended to decline. In view of the non-significance of the sex ratio pattern, a temperature slightly below 30 °C may be concluded to be optimal for the performance of *I. typographus*. Above this level, a rapid deterioration of population growth sets in. These results confirmed *a posteriori* the temperature of 28 °C used for mass rearing the beetles (Wermelinger & Seifert, 1998).

Bark beetles often re-emerge from the first gallery and produce a second or even a third brood. The females of *I. typographus* can produce sister broods without further mating (Anderbrant & Löfqvist, 1988). This contrasts with the traditional view that females have to mate at regular intervals (e.g. Chararas, 1962). The moment of re-emergence is reported to depend on density (Bakke, 1983; Anderbrant & Löfqvist, 1988; Anderbrant, 1989) and temperature (Anderbrant, 1986, 1989), while re-emergence distribution is independent thereof. The number of progeny in the sister broods depends neither on the size of the first brood nor on its density (Anderbrant & Löfqvist, 1988). Information on the percentage of re-emerging parents, however, is greatly divergent (cf. Table 1). In addition, only a fraction of the re-emergers produces a sister brood (Annala, 1969; Anderbrant, 1989). The present analysis of the significance of sister broods revealed that in terms of the population increase rate (r_m) sister broods appear to play a minor role. The impact of sister broods on this rate is outstripped markedly by that of temperature.

Population performance must be evaluated on a multi-seasonal basis, taking into consideration voltinism and mortality during overwintering. If all developmental stages were capable of overwintering successfully, the propagation of a population would continue in the spring where it ceased at the beginning of the previous winter. This means that, over several years, a higher r_m would actually result in a faster population growth. If, in contrast, mortality of immature stages in winter is substantial or even complete, the effect of a higher r_m resulting in an unfinished generation entering winter as immatures is almost nil. This statement is only valid for one complete generation per season and for fatal immature mortality in the winter as in most of Scandinavia (Annala, 1969; Bakke, 1983). Because in the present analysis the effect of sister broods on r_m turned out to be minor, their contribution to population growth would be moderate. On the other hand, the analysis also indicated a distinct increase of R_0 with more sister broods (cf. Fig. 3), meaning a higher multiplication rate in monovoltine populations and thus a higher multiseasonal net growth.

The question arises whether it is a better strategy to deposit total offspring in one brood, thus avoiding significant mortality of the parents (cf. Sauvard, 1993) while seeking another host tree. The main advantage of sister broods over a single large brood is presumably that the offspring escape from crowding mortality caused by intraspecific competition at high brood

densities in the first host tree (cf. Kirkendall, 1983). In the case of two or even three generations per year and modest winter mortality, as in the lower elevations of Central Europe, differences in r_m would actually result in different multi-seasonal population growth. This analysis did not indicate substantial differences in r_m with different numbers of sister broods. Hence, the contribution of sister broods (which are progeny produced late in a female's life) to overall population growth is limited. Fatal winter mortality of immatures as postulated by Coeln *et al.* (1996) would question this statement, but many observations indicate that as a rule survival of larvae and pupae during winter is possible. The admittedly higher mortality of these stages compared to that of overwintering adults remains to be quantified.

The present analyses suggest that in Scandinavia and in higher elevations in Europe with only one successful generation per year and possibly fatal winter mortality of immature stages, sister broods can contribute substantially to the propagation of the spruce bark beetle. For Scandinavia, this is confirmed by the observations of Bakke (1983). Sister broods are also important in other bark beetle species that are monovoltine (see for example Sauvard, 1993). At lower elevations with two or even three generations of *I. typographus* and only moderate winter mortality, sister broods are hypothesized to have only moderate impact on overall population growth.

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