

Development and distribution of predators and parasitoids during two consecutive years of an *Ips typographus* (Col., Scolytidae) infestation

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Abstract: The development of the natural enemy complex, its within-tree distribution and the resulting mortalities imposed on bark beetles were investigated during two consecutive years (1994, 1995) at the peak of an *Ips typographus* infestation. For this reason bolts from infested spruce trees were incubated until the inhabiting insects had emerged. Some 17 000 antagonists were identified and found to belong to 16 predatory and 14 parasitic insect species. Among the predators the Dolichopodidae (Dip.) were most abundant, while among the parasitoids the Pteromalidae (Hym.) ranked first. Parasitoids preferred the upper tree parts, while predators were more abundant in the lower parts. Total bark beetle mortality was assessed based on the literature data on the *per capita* consumption of the antagonistic larvae. In the first year, the most destructive group were the dolichopodid flies, killing three to seven times more bark beetle larvae than the second ranking Lonchaeidae (Dip.) and the Pteromalidae. In the second year, the pteromalid parasitoids killed 2.5 times more larvae than the dolichopodids. Total bark beetle survival was assessed to decrease from 46 to 18% in the course of the 2 years.

1 Introduction

The last decade of the 20th century experienced two exceptionally violent gale disasters in Central Europe, namely 'Vivian/Wiebke' in 1990 and 'Lothar' in 1999. 'Vivian' felled more than 110 million m³ (Switzerland: 4.9 million) of timber, while 'Lothar' uprooted or broke trees of an estimated volume of 180 million m³ (Switzerland: 12.7 million). Since in Switzerland the majority of the fallen trees were spruce trees (*Picea abies* (L.) Karst.), these storms gave rise to exceptionally large outbreaks of the European spruce bark beetle (*Ips typographus* L.) (WERMELINGER et al., 1999; ENGESSER et al., 2002).

Although the efficiency of the so-called clean management ('saubere Wirtschaft') is generally acknowledged in the literature, the sense and purpose of these measures are increasingly being questioned. This is even more so as forest protection measures had not been able to prevent huge outbreaks, mainly because they were incomplete due to limited manpower. It was argued that outbreaks are more efficiently and inexpensively regulated by natural agents and that phytosanitary measures may even prolong outbreaks by interfering with these agents.

A number of studies have been carried out on the biology and prey consumption of specific predatory insects such as the clerid beetle *Thanasimus* spp. (e.g. MILLS, 1985; HEIDGER, 1994; REEVE et al., 1995; YE HUI and BAKKE, 1997; SCHROEDER, 1999b), predatory Diptera (e.g. HOPPING, 1947; NUORTEVA, 1957; MILLS, 1985; DIPPEL

et al., 1997) and parasitic wasps (e.g. REID, 1957; BERISFORD et al., 1970; ECK, 1990a,b; KRÜGER and MILLS, 1990). Some studies have provided inventories of antagonistic species and/or discussed their effects on bark beetle populations (BUSHING, 1965; MILLS, 1983, 1986; ECK, 1990b; HERARD and MERCADIER, 1996; WESLIEN and SCHROEDER, 1999). Others have dealt with the sequential arrival of natural enemies after bark beetle attack (STEPHEN and DAHLSTEN, 1976; LAWSON et al., 1997). Only few investigations have been concerned with the multi-generation dynamics of natural enemies of bark beetles (e.g. MOORE, 1972; LANGOR and RASKE, 1988; HERARD and MERCADIER, 1996; SCHROEDER, 1999a), none of them with *I. typographus*.

In 1994 and 1995 a 100-ha area of contiguous *I. typographus* infestations in Central Switzerland provided the opportunity to examine the temporal succession of natural enemies during two consecutive years in the last phase of an outbreak and to assess their impact on bark beetles. Besides investigating species composition and densities special emphasis was put on the assessment of the resulting bark beetle mortality and the significance of the predatory and parasitic guilds.

2 Material and methods

2.1 Experimental procedure

The study site was situated on a north exposed slope in the Sernftal valley near Schwanden, Canton Glarus. It consisted

of an approx. 120-year-old spruce forest of some 100-ha. Bark beetle attack of living trees in this stand started in 1993, presumably as a consequence of some scattered trees felled by Vivian. In 1994 widespread attack was observed and by 1995 almost all the trees in this forest had been killed. Ten spruce trees distributed across a horizontal line of approx. 500 m at an elevation of 1250–1350 m a.s.l. were selected. The criteria were: (i) they had been infested during 1994, (ii) their diameter at breast height was between 25 and 40 cm and (iii) their bark was still attached to the stem. In April 1995, as soon as the stand became accessible after the spring thaw, they were cut. They contained the 1994 insect community that had overwintered in the galleries. After delimiting the trunks they were transported to a truck-accessible forest road by helicopter. Two 1.5 m densely colonized bolts were cut from every stem, one from the stem base (lowermost 4 m) and one from the upper tree third (beginning of the crown). These were transferred to the institute.

The same procedure was repeated in late July 1995 with trees that had become newly infested with *I. typographus*. At the time of harvesting the trees, the beetle population was in the pupal/teneral beetle stage. Thus, there were samples from two consecutive generations during the outbreak, i.e. 20 bolts from each infestation year 1994 and 1995.

The bolts from both samplings were kept in so-called photo-electors. These installations were constructed from metal cabinets, with a tube at both the bottom and the top that ended in transparent plastic box traps. The boxes contained water, some detergent and fungicide. Upon emerging in the darkened cabinets the phototactic insects head for the daylight coming in from the eclector boxes and get trapped inside (emergence traps). Species like *Rhizophagus* spp. or *Thanasimus formicarius* whose larvae may leave the trees for overwintering were thus not completely covered by this procedure. The photo-electors were arranged in a glasshouse under semi-natural conditions (near ambient temperatures). Bolts were sprayed with water one to two times per week to prevent the bark from desiccating. The conditions inside the eclector cabinets during the emergence period ranged from 7–31°C and from 40–100% relative humidity (RH).

The emerging insects trapped in the eclector boxes were stored in alcohol until processing. At the end of the sampling period (end of 1995), they were separated into different taxonomic groups and identified by specialists (see Acknowledgements). The insect counts were converted into densities, i.e. insects per square metre of bark surface.

2.2 Data analysis

The mean values and standard errors of densities and consumption rates were calculated on a per bolt basis ($n = 20$ each year). To assess the number of killed bark beetles the densities of antagonists were multiplied by the literature-based consumption rates of the respective species (cf. table 3). The sum of actually emerged and calculated killed bark beetles then allowed an assessment of the total initial bark beetle population. This figure provided the base for calculating the mortality rates imposed by predators and parasitoids. The insect densities in the tree bases and tops as well as yearly densities, prey consumption and mortalities were analysed by submitting the square root transformed values to a t-test. The square roots of the mortality rates within the same year (fig. 3) were arcsine transformed (ZAR, 1999) and subsequently subjected to an analysis of variance, followed by the *post hoc* Scheffé test.

3 Results

3.1 Species composition

Table 1 summarizes the abundance of 16 species from eight predatory families and 13 species (plus *Roptrocerus brevicornis*, see below) from three parasitic families found in this study. Additionally, bark beetle numbers are listed. A total of 29 716 individual bark beetles and 17 071 antagonists were identified. *Ips typographus* accounted for 89% of the bark beetles. The listed insects emerged from a total bark surface of 30.38 m² in 1994 and 25.78 m² in 1995. The most numerous family among the predators were the

Table 1. Species composition and abundance of natural enemies of bark beetles emerging from spruce trees that were killed by *Ips typographus* in 1994 and 1995

	1994	1995
Predators		
Cleridae (Col.)		
<i>Thanasimus formicarius</i>	34	9
<i>Thanasimus rufipes</i>	2	–
Rhizophagidae (Col.)		
<i>Rhizophagus dispar</i>	1	–
Salpingidae (Col.)		
<i>Rabocerus foveolatus</i>	1	–
<i>Rabocerus gabrieli</i>	1	–
Dolichopodidae (Dip.)		
<i>Medetera breviseta</i>	1	–
<i>Medetera excellens</i>	232	1
<i>Medetera pinicola</i>	240	–
<i>Medetera signaticornis</i>	3039	551
Lonchaeidae (Dip.)		
<i>Lonchaea bruggeri</i>	1065	10
<i>Lonchaea helvetica</i>	3	–
<i>Lonchaea scutellaris</i>	–	10
<i>Lonchaea zetterstedti</i>	–	1
Pallopteridae (Dip.)		
<i>Palloptera usta</i>	1	–
Chrysopidae (Neur.)		
<i>Chrysoperla carnea</i>	1	–
Raphidiidae (Raph.)		
<i>Puncha ratzeburgi</i>	2	–
Total predators	4621	582
Parasitoids		
Braconidae (Hym.)		
<i>Cosmophorus klugii</i>	5	–
<i>Dendrosoter middendorffii</i>	20	87
<i>Helconidea dentator</i>	17	–
<i>Ropalophorus clavicornis</i>	450	2
Eurytomidae (Hym.)		
<i>Eurytoma arctica</i> *	–	13
Pteromalidae (Hym.)		
<i>Anognmus hohenheimensis</i>	1	–
<i>Dinotiscus eupterus</i> *	244	37
<i>Mesopolobus typographi</i> *	75	19
<i>Rhopalicus quadratus</i>	1	–
<i>Rhopalicus tutela</i>	23	319
<i>Roptrocerus mirus</i>	679	6823
<i>Roptrocerus xylophagorum</i>	2068	661
<i>Tomicobia seitneri</i>	203	74
Total parasitoids	3827	8041
Bark beetles		
<i>Ips typographus</i>	23822	2556
Other Scolytidae	3211	127
Total bark beetles	27033	2683
* Obligatory or facultative hyperparasitoid.		

Dolichopodidae (long-legged flies). In the first year *Medetera signaticornis* clearly outnumbered the other predatory species as well as the parasitic species. In the second year, it was still the most abundant predator, but it was outstripped by parasitic *Roptrocerus* species. From the other predatory groups Lonchaeidae (lance flies), another dipteran family, ranked second, and was dominated by *Lonchaea bruggeri*. The lonchaeid *L. helvetica* was found to be new to science (MAC-GOWAN, 2001). A third dipteran family, i.e. Pallopteridae, as well as Chrysopidae (lace wings) and Raphidiidae (snakeflies), played only an insignificant role. Among Coleoptera, the well known clerid beetles *Thanasimus* spp. were present only in moderate numbers and mainly in the first year. It is conspicuous that the density of predators in the first year of investigation was approx. 8 times higher than in the second year.

Among the parasitic groups, Pteromalidae reached the highest numbers. The genus *Roptrocerus* was dominant with *Roptrocerus xylophagorum* as the most frequent species in the first year. This species was replaced by *Roptrocerus mirus* in the second year. It has to be noted that *R. brevicornis* was also present. This species is very similar to *R. xylophagorum* and the males especially are not easily discriminated. For this reason, it was not recognized as a separate species at the beginning of the identifications. For reasons of consistency, the numbers of this species were allotted to those of *R. xylophagorum*. Braconid wasps (Braconidae) were notably less numerous than the pteromalids. *Ropalophorus clavicornis*, an adult parasitoid, was the most frequent species in this family. Unlike the other parasitoids, braconids were mainly observed in the first year of investigation. Twenty five per cent of all emerging insects were parasitoids, whereas only 11% were predators.

Obviously, bark beetles also emerged from the bolts. In the second year, the frequency of the main species, i.e. *I. typographus*, dropped to 13% of that in the first year. The abundance of the other bark beetle species decreased as well. These were mainly *Polygraphus poligraphus*, *Hylurgops palliatus*, *Xyloterus lineatus* and *Crypturgus pusillus*.

Not included in this synopsis are species that are carnivorous, but not specifically associated with bark beetle. Nor are species included whose feeding behaviour is unknown. Among these were, for instance, a few Carabidae (Col.), Aphelinidae, Bethyidae, Diapriidae, Eucoilidae, Eulophidae, Ibalidae, Platygastriidae, Trichogrammatidae, Ichneumonidae (all Hym.), Coniopterygidae (Neur.) and Tachinidae (Dip.). Two frequent families of uncertain feeding behaviour were the Phoridae (Dip., 555 individuals) and the Mymaridae (Hym., 898 individuals). At least one phorid species does live in a parasitic way (DISNEY, 1994) but the species found in this study are most probably saprophagous (PRESCHER, pers. comm.) and were thus discarded from this analysis. The Mymaridae were also excluded because of their uncertain feeding ecology, although some species may be carnivorous (egg parasitoids) as well (J. HUBER, pers. comm.).

3.2 Within-tree distribution

The abundance of the different taxonomic groups of natural enemies turned out to depend on the position within the stem (fig. 1). While bark beetle density exhibited no significant difference between the upper and lower parts of the stems, the parasitic Pteromalidae were clearly more abundant in the stem tops than in the bases. This applied particularly to *R. xylophagorum* that was over four times more abundant in the upper tree parts. As far as the predatory flies, i.e. Dolichopodidae and Lonchaeidae, are concerned, there was at least a strong tendency for a preference for developing in the lower tree half. Among the most frequent species, it was primarily *L. bruggeri* that occurred in numbers almost six times higher in the lower than in the upper bolts.

No significant preference for within-stem position was found for the clerid beetles and braconid wasps, while the Eurytomidae almost exclusively inhabited the upper tree parts.

3.3 Yearly densities and prey/host consumption

Table 2a lists the yearly densities of the most frequent insect groups. Emerging bark beetles were more than eight times more abundant in 1994 than in 1995. As already evident from table 1, pteromalid and dolichopodid density ranked first in both years, overall the pteromalids were the most frequent group. All antagonistic groups except Pteromalidae were less abundant in the second year, as indeed were the bark beetles. Parasitoids were the most frequent group in both years. However, density figures do not reflect the impact predators and parasitoids exert on bark beetle populations. By definition, a predator consumes more than one prey during its immature development whereas a parasitoid basically just kills one host. From the literature, data were collected on prey consumption of the species concerned (table 3). Obviously, the larger species consume more prey than the smaller ones. It has to be stressed that these data are

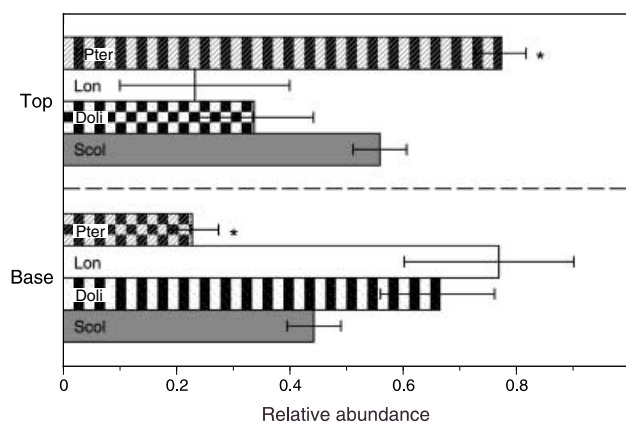


Fig. 1. Relative within-tree distribution of bark beetles and their predatory and parasitic associates (mean \pm SE). Doli = Dolichopodidae, Lon = Lonchaeidae, Pter = Pteromalidae, Scol = Scolytidae. Bars marked with * differ between position ($P < 0.05$)

	1994	1995
(a) Density		
Bark beetles	859.3 ± 102.6	103.4 ± 17.1
Predators		
Cleridae	1.1 ± 0.40	0.3 ± 0.12
Dolichopodidae	113.0 ± 23.3	20.5 ± 6.0
Lonchaeidae	30.6 ± 10.5	0.7 ± 0.4
Total predators	144.8 ± 29.3	21.5 ± 6.0
Parasitoids		
Braconidae*	1.3 ± 0.38	3.5 ± 0.69
Pteromalidae*	101.3 ± 30.2	310.3 ± 35.8
Total parasitoids*	102.6 ± 30.2	313.8 ± 35.9
(b) Bark beetle consumption		
Predators		
Cleridae	53.8 ± 19.0	15.6 ± 5.4
Dolichopodidae	678.2 ± 139.8	123.2 ± 35.8
Lonchaeidae	183.6 ± 63.0	3.9 ± 2.6
Total predators	915.6 ± 172.9	142.7 ± 36.7
Parasitoids		
Braconidae*	1.3 ± 0.38	3.5 ± 0.69
Pteromalidae*	101.3 ± 30.2	310.3 ± 35.8
Total parasitoids*	102.6 ± 30.2	313.8 ± 35.9

* Hyperparasitic *Mesopolobus typographi* and adult parasitoids *Tomicobia seitneri*, *Cosmophorus klugii* and *Ropalophorus clavicornis* excluded.

Table 2. (a) Density (number per m² bark surface) of emerged bark beetles (*Scolytidae*), predatory and parasitic insects, and (b) calculated total bark beetle consumption (number of killed scolytid larvae per m²) from two infestation years; mean values (± SE) differ between years except for the Cleridae ($P < 0.05$)

Table 3. Literature-based consumption rates (number of scolytid larvae) of predators and parasitoids during their juvenile development. These values were used for the assessment of the antagonists' impact

Organisms	Consumption rate	References
<i>Thanasimus</i> spp. (Cleridae)	47 (44–57)	GAUß, 1954; MILLS, 1985; HEIDGER, 1994; HERARD and MERCADIER, 1996; DIPPEL et al., 1997
<i>Medetera</i> spp. (Dolichopodidae)	6 (5–10)	HOPPING, 1947; NUORTEVA, 1959; DIPPEL et al., 1997
<i>Lonchaea</i> spp. (Lonchaeidae)	6	HERARD and MERCADIER, 1996
Parasitoids	1	–

approximate values as they originate from studies under different conditions, with different scolytid prey species. For the Lonchaeidae the data are even just rough estimates: *Lonchaea* and *Medetera* are known to have the same consumption rate (HERARD and MERCADIER, 1996) and were assumed to have a comparable developmental time. Thus, the Lonchaeidae were assigned the same prey consumption rate as the Dolichopodidae.

As the parasitic larvae kill only one host *per capita* (host feeding is not known among these species), the number of hosts they devour is equal to the number of parasitoids. The pteromalid *Mesopolobus typographi* is – contrary to what its name suggests – a hyperparasitoid of *Tomicobia seitneri*, and was therefore excluded from this analysis. *T. seitneri* and the braconids *Cosmophorus klugii* and *R. clavicornis* are parasitoids of adult bark beetles and were excluded as well because they do not contribute to larval mortality. The total consumption of bark beetles was assessed on the basis of the densities and consumption rates of their antagonists (table 2b). Therefore, the predators consumed in 1994 eight times more bark beetle larvae during their development than the parasitoids, although they were only slightly more numerous than the parasitoids. In the following beetle generation, the parasitoids killed more than twice as many beetles as the predators.

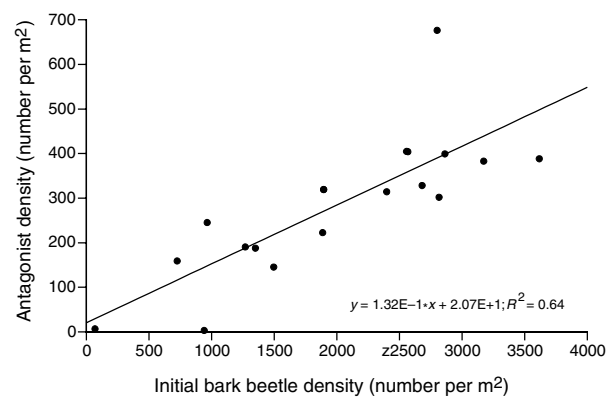


Fig. 2. Relationship between densities (individuals per m² bark) of bark beetles and antagonists in 1994. Each dot represents one bolt ($P < 0.01$)

To investigate the relationship between bark beetles and antagonists, the densities of predators and parasitoids were plotted against each other (fig. 2). Note that the x-axis represents the calculated bark beetle density, i.e. the sum of emerged and killed beetles. There was a significant increase in antagonist density with increasing bark beetle density. As a result of low beetle densities in 1995, this relationship was only true for 1994. The trees were not homogeneously colonized

by either the bark beetles or their antagonists, which is reflected in the large standard errors in table 2. Some trees were very poorly colonized as a whole, but many showed a distinct 'preference' for either predators or parasitoids.

3.4 Bark beetle mortality

For explorative reasons bark beetle mortality inflicted by predators and parasitoids was assessed. Based on surviving bark beetles, emerged antagonists and their estimated consumption (table 2b), the mortalities of the scolytid population was calculated for each year (fig. 3). On this basis, a little less than half (46%) of the total bark beetle broods survived in 1994 to the adult stage and emerged from the bolts. Almost half of the scolytid populations died from predation, whereas only a few beetle larvae were killed by parasitism. Scolytid survival and predation rates did not differ. However, the parasitism rate in 1994 was significantly ($P < 0.01$) lower than both survival and predation rates. This pattern completely changed in the following year. In 1995 bark beetle survival collapsed because of the parasitoids, while the impact of predators markedly declined compared with that in 1994. Again, calculated predation and parasitism rates, as well as scolytid survival and parasitism, differed significantly ($P < 0.01$), whereas scolytid survival and the predation rate did not. The changes in the rates from 1994 to 1995 were statistically significant. Thus, based on the consumption rates assessed from the literature, total bark beetle mortality imposed by natural enemies markedly increased during two beetle generations.

4 Discussion

The species of natural enemies found in this study have often been reported in earlier investigations on *I. typographus* associates (e.g. SACHTLEBEN, 1952; PETTERSEN, 1976a; ECK, 1990b; WESLIEN, 1992; SCHOPF and KÖHLER, 1995). Many of the genera have also been described with other bark beetle species from other countries and zoogeographical regions (REID, 1957; BUSHING, 1965; PETTERSEN, 1976b; LAWSON et al., 1997). Species diversity in the present study, however, is poorer than in some of these investigations. This may

be attributed to the unfavourable climatic conditions resulting from the high elevation and the northern aspect of the study site. *Coeloides bostrichorum*, for example, a well-known braconid wasp that attacks bark beetles, was completely lacking in our samples. It has already been reported as locally or temporally absent in other studies (THALENHORST, 1958; SCHOPF and KÖHLER, 1995).

Predators and parasitoids preferred different development sites. This behaviour may avoid competition. The predatory Dolichopodidae, as the most important predator group, were more frequent at the stem base. The female flies lay their eggs in bark crevices (HOPPING, 1947; NUORTEVA, 1959) and the hatched larvae are able to bore through even thick bark. On the other hand, many parasitic wasps have to penetrate the bark with their ovipositors (e.g. *Rhopalicus*, SACHTLEBEN, 1952; KRÜGER and MILLS, 1990). For this reason they prefer the thinner bark in the upper tree parts. *Roptrocercus* species, being the most frequent genus in this study, access their hosts through the entrance holes of the bark beetles (SAMSON, 1984), which should make them independent of bark thickness. Nevertheless, they also preferred the thinner bark of the upper tree parts. Similar behaviour was noted by GARGIULLO and BERISFORD (1981). MILLS (1986) demonstrated a positive correlation between the parasitic braconids and tree height, BALL and DAHLSTEN (1973) reported decreasing parasitism rates with increasing tree diameter. A similar relationship ($R^2 = 0.39$, $P < 0.05$) could also be found in our data.

When considering both the years under study, Pteromalidae were the most numerous antagonistic group and the predatory Dolichopodidae ranked second. However, the impact natural enemies exert on a bark beetle population does not solely depend on their density. Indeed, their consumption rates are also very important. In this study, it was therefore the dipteran family Dolichopodidae that contributed most to bark beetle mortality. The significance of the *Medetera* species has been acknowledged in previous studies (HOPPING, 1947; WESLIEN and REGNANDER, 1992; LAWSON et al., 1996). Assessing the impact of antagonists from literature data and the densities obtained in this study, Dolichopodidae together with Pteromalidae accounted for more than 80% of the bark beetle mortality. The clerid beetles (*Thanasimus* spp.) are generally recognized to be very important predators (e.g. MOORE, 1972; HEIDGER, 1994; WESLIEN, 1994; REEVE, 1997; WESLIEN and SCHROEDER, 1999). As they are reported to overwinter outside the infested trees in Sweden (FORSSLUND, 1947, cited in WESLIEN, 1992), the density reported in the present study is likely to be an underestimate because some individuals may have left the trees prior to cutting the 1994 sample logs.

The 2 years under study revealed a clear shift in the relative abundance of predators and parasitoids and therefore also in their effects on bark beetle mortality (table 2, fig. 3). While in the first year, the predator-inflicted mortality predominated, parasitoids caused the most bark beetle mortality in the second year. Predators are often generalists, feeding on a number of different prey species. For this reason they may always

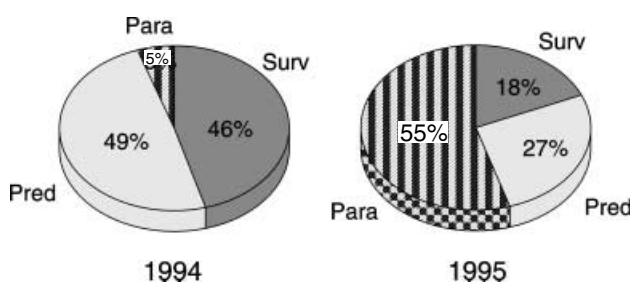


Fig. 3. Calculated mortality rates of *Ips typographus* by predators (Pred) and parasitoids (Para) and corresponding survival rate (Surv). Rates differ significantly ($P < 0.05$) between years

be present in the ecosystem in relatively high densities. This means they can react to any new food resources fairly rapidly. In contrast to predators, many parasitoids depend on a limited range of host species. It takes these populations some time to reach effective densities (table 2). The temporal succession of these different antagonistic guilds may explain the sometimes contradicting relevance assigned to predators and parasitoids in the literature. It is obvious that their impact, i.e. the mortality inflicted on bark beetles, depends to a great extent on the phase of a bark beetle infestation. Recently, TURCHIN et al. (1999) have shown that, in an oscillating bark beetle/antagonist system, antagonist-imposed mortality is most significant at the beginning of the decline of a bark beetle outbreak. It may be hypothesized that predators are important at low bark beetle levels and at the beginning of outbreaks (progradation), and that their role is taken over by parasitoids in a later phase of the outbreak (culmination, retrogradation). This assumption needs to be verified in long-term studies of infestations. As a rule, endophytically living hosts – such as bark beetles – seem to be more subject to parasitism than to predation (HAWKINS et al., 1997). For both predators and parasitoids density-dependent responses are known (fig. 2; MOORE, 1972; GARGIULLO and BERISFORD, 1981; LAWSON et al., 1996).

In this study, all bark beetle mortality was attributed to insect predators and parasitoids. It is understood that other factors, such as abiotic factors, intraspecific competition, mites, nematodes, fungi and other pathogens, may influence mortality as well. The results emphasize the considerable regulatory capacity of natural enemies. However three points need to be stressed: (i) the mortalities calculated in this study have explorative character as they rely on literature data partly obtained from laboratory conditions. Moreover, some predators overwintering outside the trees may have been missed; (ii) the high mortalities observed in this study occurred in a late infestation phase. The 2-year study did not cover the beginning of the bark beetle outbreak. The investigation could not be continued because there were no more living spruce trees left to be attacked, and (iii) the results refer to a single large infestation spot. On a regional scale, however, the development of bark beetle outbreaks depends on many additional factors such as beetle dispersal and, in particular, the susceptibility of the neighbouring stands.

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