# Biological differences reflect host preference in two parasitoids attacking the bark beetle *Ips typographus* (Coleoptera: Scolytidae) in Belgium

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## Abstract

The basic reproductive biology of two ectoparasitoids developing on the late larval instars of the scolytid *Ips typographus* Linnaeus, a pest of spruce forests in Eurasia, was studied with the purpose of explaining which biological features allow the two species to share the same host. The anautogenous braconid *Coeloides bostrichorum* Giraud had a longer pre-oviposition period (5.1 vs. 3.3 days), a greater egg load (8.1 vs. 6.1 eggs), survived longer and emerged later than the pteromalid *Rhopalicus tutela* (Walker). In contrast, *R. tutela* was autogenous and tended to be more fecund under constrained conditions (9.7 vs. 5.1 total offspring per female). The longer pre-oviposition period of the specialist *C. bostrichorum*, coupled with its greater longevity, afforded the opportunity of better synchronization of ovipositing females with late instar larvae of *I. typographus*. By contrast, the polyphagous *R. tutela* matured rapidly, allowing parasitism of both younger and older larval instars of *I. typographus* in addition to other species. These small differences favoured the co-occurrence of the two parasitoid species on the same attacked trees.

## Introduction

The braconid *Coeloides bostrichorum* Giraud and the pteromalid *Rhopalicus tutela* (Walker) are two solitary ectoparasitoids of *Ips typographus* Linnaeus (Coleoptera: Scolytidae) (Mills, 1983). This bark beetle is one of the most damaging pests of spruce *Picea abies* L. Karst (Pinaceae) in Europe and Asia (Christiansen & Bakke, 1988; Grégoire & Evans, 2004). In Belgium for example, 250,000 m$^3$ of spruce were killed by *Ips typographus* in 1992 following the 1990 storms, at a total cost of 6200,000 euros (Grégoire *et al.*, 1995). Beetles breed in the phloem and are associated with pathogenic fungi (mostly *Ophiostoma* spp.) which they

transfer allowing them to infect and kill healthy trees as a result of pheromone-mediated mass-attack. *Ips typographus* adults overwinter under the bark of attacked trees, or in the forest litter. The first flight period occurs in April to May and a second protracted flight period occurs during the summer (Chararas, 1962; Christiansen & Bakke, 1988). A third period of flight activity may occur if climatic conditions are mild enough (Chararas, 1962). A range of control methods is regularly applied against bark-beetle pests (preventive thinning and felling, peeling and removal of infested material, pheromone trapping) that can successfully limit the spread and damage of *I. typographus* (Abgrall & Schvester, 1987; Raty *et al.*, 1995). Bark-beetle parasitoids have been surveyed in many countries (Mills, 1983; Kenis *et al.*, 2004) and there are many indications in the literature that their role in the population dynamics of bark beetles can be important (Mills, 1983; 1986, Weslien & Regnander, 1992; Stephen *et al.*, 1997). However, the selection of efficient biological control agents for importation and release, or for developing strategies for the biological conservation of

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native natural enemies requires a profound knowledge of their biology and ecology (Pimentel, 1963; Pschorn-Walcher, 1977) and, so far, parasitoids have never been seriously included in bark-beetle management strategies (Kenis *et al.* 2004).

*Rhopalicus tutela* is an holarctic species with a very wide distribution in Europe, USA and Canada (Chararas, 1962; Graham, 1969) while *C. bostrichorum* is confined in the Palaearctic region, and mainly distributed in northern and central Europe (Nuorteva, 1957).

Both species are idiobionts and oviposit on late bark-beetle larvae by boring through the bark with their ovipositor. Host specificity differs between the two species. *Rhopalicus tutela* has a broad host range, attacking numerous scolytids on both pine and spruce (Graham, 1969; Mills, 1983; Kenis *et al.*, 2004) while *C. bostrichorum* appears more particularly associated with *I. typographus* (Krüger & Mills, 1990; Hedqvist, 1998; Kenis *et al.*, 2004). However, the two species are frequently found together on trees attacked by *I. typographus* (Hougardy & Grégoire, unpublished). Kleptoparasitism has been described as one of the possible mechanisms used to mediate competition between *R. tutela* and *C. bostrichorum* (Hougardy & Gregoire, 2003). The present study was designed to characterize the basic reproductive biology of the two species with the purpose of exploring which other features could play a role in their coexistence strategies. Several features such as survival, fecundity, phenology and size were examined. Both species are synovigenic and fecundity was assessed by looking at the interval between emergence and the deposition of the first egg (the pre-oviposition period; Doutt, 1964), the ability to mature and lay eggs without first feeding (autogeny), and age-specific potential fecundity. All observations and experiments, except those dealing with phenological syn-chronization with the host, were undertaken in the laboratory.

## Materials and methods

### Insects

Laboratory experiments were undertaken at the Université Libre de Bruxelles between 1998 and 2001. *Rhopalicus tutela* individuals came from a culture maintained in the laboratory on spruce logs infested with *I. typographus*. The insects originally came from spruce bark infested with *I. typographus* collected in Bertrix, southern Belgium in 1997. The culture was provisioned with new individuals from field-infested bark collected in Bertrix or Resteigne (southern Belgium) twice a year (i.e. every eight generations approximately). *Coeloides bostrichorum* was reared from the same *I. typographus*-infested bark, except that the bark containing the braconid cocoons was stored at 2°C until needed. *Coeloides bostrichorum* adults started to emerge after 10 to 25 days at room temperature, depending on the time spent in diapause at 2°C. *Ips typographus* adults came from the same pieces of field-collected bark and from cultures.

### Longevity

Freshly-emerged individuals of both parasitoid species were held at 21°C and a 16:8 h (light:dark) photoperiod in 14 cm diameter Petri dishes (a maximum of four males and four females per species per dish) with water, and for those

which were fed, with honey gelose (agar, sucrose and honey in a 1:50:20 ratio). Each group (combination of treatment and sex) comprised 24–40 individuals. Dead insects were removed daily and sexed. Resulting survivorship curves were compared using the Kolmogorov-Smirnov test (Siegel & Castellan, 1998). Body length, not including the ovipositor, was measured using a WILD 18 binocular with a WILD MMS 235 micrometer (± 0.01 mm) in order to establish the relationship, if any, between parasitoid size and survival.

### Fecundity

The length of the pre-oviposition period was investigated using 'phloem sandwiches' that permit the observation of the bark beetle and parasitoid brood within the phloem (Hougardy & Grégoire, 2003). The phloem sandwiches were each made of a 20 cm square piece of bark (phloem + outer bark) taken from a freshly felled spruce tree and pressed between a Plexiglas plate (phloem) and a wooden frame (outer bark), both the same size as the bark square and held together with bolts and nuts. Sandwich edges were covered with parafilm to prevent water loss. Observations of the sub-cortical medium could be made through the transparent Plexiglas sheet. To colonize the phloem sandwich, one male *I. typographus* bark-beetle was placed in a shaft drilled in the centre of each bark square. After the male had bored a mating chamber (24 h later), three females were introduced into the same shaft with an interval of 12 h between each female in order to avoid crowding in the mating chamber. Once most of the offspring had reached the late larval stage (about 16 days at 21°C), one freshly-emerged (< 24 h) fertilized parasitoid female was released onto the bark surface and confined there by a glass plate placed over the wooden frame. Fourteen individual *C. bostrichorum* and 29 individual *R. tutela* were tested in separate phloem sandwiches.

The parasitoids had access to water (moistened cotton) and food (honey gelose). Each sandwich was checked every 24 h by visually searching for parasitized host larvae detected by their immobility, and for the presence of a parasitoid egg. As soon as the majority of hosts within a set-up had reached the pupal stage (after three to four days), the parasitoid females were carefully moved to another phloem sandwich containing younger stages. The experiment was stopped as soon as the female had laid an egg or, if no egg was observed, after eight days for *R. tutela* and 15 days for *C. bostrichorum*. These delays were chosen based on the results of Krüger & Mills (1990). These authors reported a pre-oviposition period of 8–10 days in *C. bostrichorum* while *R. tutela* was observed to search for hosts immediately after mating which occurs just after the female emerges. The experiment was run at 21.5 ± 0.5°C.

Autogeny was assessed by inducing females, left unfed since emergence, to oviposit on *I. typographus* infested spruce logs (30–40 cm long, 10–15 cm diameter). The control treatment consisted of rearing fed females on similar spruce logs. The mean host density was similar between treatments: 355 ± 110 (SD) hosts per log ($n$ = 5) for unfed *C. bostrichorum*, 265 ± 119 hosts per log ($n$ = 5) for unfed *R. tutela*, 293 ± 89 hosts per log ($n$ = 6) for fed *C. bostrichorum*, and 319 ± 89 hosts per log ($n$ = 8) for fed *R. tutela* (one-way ANOVA, F = 0.715, $P$ = 0.555 with 3 and 20 df). Offspring production was calculated by adding the number of parasitoid adults that emerged from the logs and, after peeling back the bark, the

number of parasitoid larvae and adults present under the bark. The control treatment (fed females) was used to estimate the constrained realized fecundity, i.e. the fecundity of females provided with hosts for a limited 6-day period, which correspond to the window of availability of final instar larvae of *I. typographus* populations reared on spruce logs at room temperature.

Age-specific potential fecundity of both parasitoids was assessed by ovariole dissections. Batches of one freshly-emerged female were placed with one male in 8.5 cm diameter Petri dishes, provisioned with water and honey until dissection. Each day, from day 1 to day 15, an average of eight females was killed and dissected in 70% ethanol. Acetocarmine staining, prepared from carmine powder (1% solution) was added to distinguish mature from immature oocytes (Jervis & Copland, 1996). Numbers of mature eggs in ovarioles were recorded. Body length was measured before the dissection in order to establish the relationship, if any, between parasitoid size and fecundity.

### Emergence pattern in the spring

Bark infested with *I. typographus* and sheltering parasitoids was collected in southern Belgium (Bertrix) in February 2000 and 2001 and kept at 2°C until March. Then the bark was placed in cages outdoors in a sheltered position in a private garden located 15 km south of Brussels. Cages were checked three to four times a week and emerged insects were identified.

### Parasitoid size

Body length and ovipositor length were measured on a number of males and females of both species (see table 1 for the sample size). Adult sizes were compared between and within species and sexes using t-tests. The relationships between adult size and survival or fecundity were investigated using the data collected in the longevity test and in the ovariole dissections (only the data corresponding to the plateau period in the ovarioles vs. time curve were considered). The significance of the relationships was assessed by linear regression analyses (SPSS, 2001).

### Results

#### Longevity

Survival in both species of parasitoid was reduced in the absence of food: unfed parasitoids never survived more than 10 days, while in the presence of food, adults lived up to 49–72 days (fig. 1). When the insects were left unfed, the survival of males and females of each species was the same (*C. bostrichorum*: Z = 0.842, P = 0.478 and *R. tutela*: Z = 0.857, P = 0.454). A comparison indicated that males of *C. bostrichorum* survived better than those of *R. tutela* (fig. 1, Z = 1.997, P = 0.001) but no difference was detected among females (Z = 0.887, P = 0.411).

When fed, the survival of males and females of *C. bostrichorum* was the same while, in *R. tutela*, females exhibited better survivorship (*C. bostrichorum*: Z = 1.227, P = 0.099 and *R. tutela*: Z = 3.324, P < 0.001). When comparing the two species, there were differences in both sexes: *C. bostrichorum* generally survived longer than *R. tutela* (fig. 1, males: Z = 3.367, P < 0.001 and females: Z = 1.588, P = 0.013), although 50% survival was the same for females of both species (fig. 1).

#### Fecundity

The pre-oviposition period of *C. bostrichorum* lasted 5.1 ± 1.3 days (n =10) while *R. tutela* had a significantly shorter pre-oviposition period of 3.3 ± 1.0 days (n = 4) (t = −2.578, P = 0.024 with 12 df). No oviposition was recorded in four of the *C. bostrichorum* and 25 of the *R. tutela* tests.

*Rhopalicus tutela* is an autogenous species: unfed females produced on average 2.9 ± 2.1 offspring per individual. However their reproductive success without food was lower than when they were provided with food (9.7 ± 6.5 offspring per female; t = −2.690, P = 0.024 with 9.2 df). In contrast, unfed *C. bostrichorum* females were unable to lay any eggs.

The constrained realized fecundity, when the females had access to hosts for about six days differed between the two species, but not significantly: 5.1 ± 3.0 offspring per female (max = 9.4) in *C. bostrichorum* compared to 9.7 ± 6.5 offspring per female (max = 18.0) in *R. tutela* (t-test: t = 1.764, P = 0.107 with 10.3 df) (fig. 2).

The number of mature eggs per female was plotted against time after emergence in fig. 3. Egg maturation lasted five days in *C. bostrichorum*, thereafter the egg load remained constant until day 15 ($R^2$ = 0.030, P = 0.109, n = 88). By comparison, mature eggs were readily available in *R. tutela* and the egg load remained relatively constant for eight days ($R^2$ = 0.001, P = 0.794, n = 64) before showing a slight decrease ($R^2$ = 0.259, P < 0.001, n = 43).

When all the age classes were taken together, *C. bostrichorum* was found to carry significantly more mature eggs in its ovarioles than *R. tutela*, i.e. 6.9 ± 3.9 eggs (n = 104) vs. 5.2 ± 3.3 eggs (n = 91) respectively (t = 3.178, P = 0.002 with 193 df). The result showed that over the plateau period when egg numbers were stable (i.e. days 5–14 for *C. bostrichorum* and days 2–8 for *R. tutela*, fig. 3), *C. bostrichorum* carried 8.1 ± 2.8 mature eggs (n = 88) and *R. tutela* 6.1 ± 3.3 mature eggs (n = 64) (t = 3.926, P < 0.001 with 124 df).

#### Emergence pattern in the spring

In the spring 2000, *R. tutela* and *C. bostrichorum* started to emerge seven days and 19 days respectively after *I.*

Table 1. Body and ovipositor length in mm of *Coeloides bostrichorum* and *Rhopalicus tutela*.

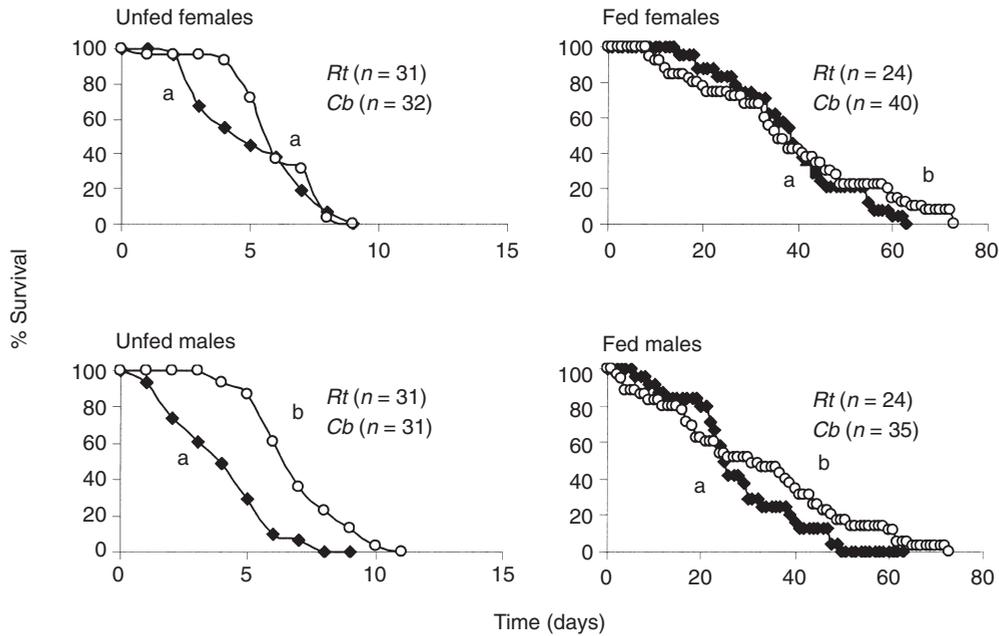| Species | Sex | n | Body length | | Ovipositor length |
|---|---|---|---|---|---|
| | | | Mean ± S.D. | Range | Mean ± S.D. |
| *C. bostrichorum* | Males | 52 | 3.92 ± 0.53 | 2.48–5.30 | |
| | Females | 142 | 4.23 ± 0.48 | 3.09–5.35 | 4.39 ± 0.51 |
| *R. tutela* | Males | 148 | 3.76 ± 0.90 | 1.89–5.22 | |
| | Females | 130 | 4.03 ± 0.72 | 2.50–5.26 | 2.01 ± 0.37 |

Fig. 1. Survivorship curves for *Coeloides bostrichorum* (○, *Cb*) and *Rhopalicus tutela* (◆, *Rt*), males and females, provided with or without food. Curves with different letter differ significantly (*P* < 0.05, Kolmogorov-Smirnov tests).
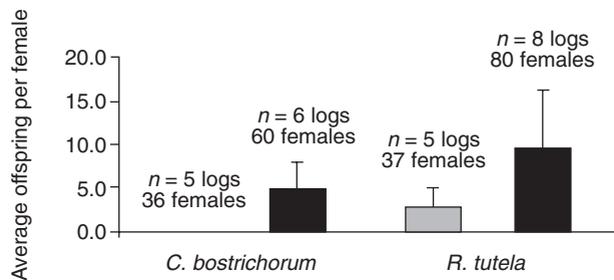


Fig. 2. Ability of newly-emerged *Coeloides bostrichorum* and *Rhopalicus tutela* females to produce offspring for a limited 6-day period (i.e. the window of availability of final instars in *Ips typographus* populations reared on spruce at 21°C) when kept unfed (■) since their emergence or provided with food (■).

*typographus* (fig. 4). The following year, both species emerged at the same time, 10–11 days after their host, though *R. tutela* emerged at a faster rate, with 60% of the individuals emerging after one day while this level of emergence was reached only after 12 days in *C. bostrichorum*.

### Parasitoid size

*Rhopalicus tutela* showed a wider range of sizes than *C. bostrichorum* (table 1). Females of *C. bostrichorum* were larger than those of *R. tutela* (t = −2.735, *P* = 0.007, 219 df) while no difference was detected between males (t = −1.466, *P* = 0.145 with 154 df). Within species, females were significantly larger than males (*C. bostrichorum*, t = −4.009, *P* < 0.001 with 202 df and *R. tutela*, t = −2.739, *P* = 0.007 with 274 df).

In *C. bostrichorum*, survival was independent of body length and whether insects were fed or not (table 2). Larger individuals in *R. tutela* survived longer when unfed but body length had no influence on survival when the insects

were fed. A significant positive linear relationship between body length and number of mature eggs in the ovarioles was detected in both species but the relationship was stronger in *C. bostrichorum* (table 2).

### Discussion

*Rhopalicus tutela* is a polyphagous species with a broad host range including numerous bark beetles on both pine, i.e. *Tomicus piniperda* (Linnaeus), *Ips acuminatus* (Gyllenhall), *Ips sexdentatus* (Boerner), and spruce, i.e. *Pityogenes chalcographus* Linnaeus (all Scolytidae), as well as *Pissodes* species (Curculionidae) (Graham, 1969; Kenis *et al.*, 2004 for a full review). *Coeloides bostrichorum* appears to be more particularly associated with bark-beetle species developing on spruce, especially *I. typographus* and *I. amitinus* Eichhoff (Kenis *et al.*, 2004). When occurring on the host *I. typographus*, the two parasitoid species mainly attack the final instar larvae of the bark beetle, but occasionally *R. tutela* has been reported to oviposit on younger larvae and on pupae (Krüger & Mills, 1990). Most of the biological differences between *C. bostrichorum* and *R. tutela* detected in this study reflect these specific host-species and host-age preferences.

There was a tendency for *C. bostrichorum* to show slightly better survival than *R. tutela* when food sources were available, which is probably the case in the field (Hougardy & Grégoire, 2000). Prolonged longevity increases lifetime fecundity but also helps females to face any temporal variations in host availability, probably more often encountered by *C. bostrichorum* owing to its more restricted host age and host species preferences.

The longer pre-oviposition period of *C. bostrichorum* offers the opportunity of a better synchronization of the ovipositing females with the appearance of final larvae instars of *I. typographus*. Krüger & Mills (1990) reported a pre-oviposition period of 8–10 days for *C. bostrichorum*,
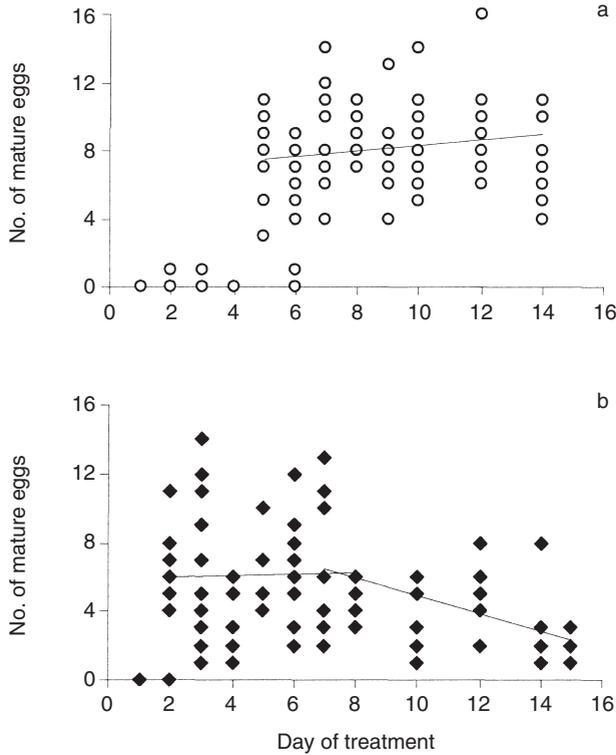
Fig. 3. Age-specific potential fecundity (number of mature eggs present in the ovarioles) in fed (a) *Coeloides bostrichorum* and (b) *Rhopalicus tutela* when females have no access to hosts. In *C. bostrichorum*, egg load remained constant from day 5 onward (days 5–15: $R^2 = 0.030$, $P = 0.109$, N = 88) while in *R. tutela* it remained constant from days 2 to 8 ($R^2 = 0.001$, $P = 0.794$, N = 64) before showing a slight decrease from days 8 to 15 ($R^2 = 0.259$, $P < 0.001$, N = 43).



Fig. 4. Spring emergence of *Ips typographus* (-), *Coeloides bostrichorum* (●) and *Rhopalicus tutela* (△) from bark collected in Bertrix, southern Belgium, in February 2000(a) and 2001(b). Bark was kept at 2°C until March and then placed in cages outdoors in a private garden 15 km south of Brussels. (- - - -, maximum temperature.)

slightly longer than in the present study, which could be explained by a lower rearing temperature (20°C vs. 21.5°C). These authors mention that *R. tutela* was searching for hosts immediately after emergence, but it is not clear whether they actually observed them ovipositing at that age.

The egg-load dynamics of both species showed divergent patterns just after emergence. Females of *R. tutela* rapidly developed mature eggs while *C. bostrichorum* required several additional days, according to the results of the pre-oviposition period experiment. The interpretation of the second part of fig. 3 (after day 8) is more ambiguous. In
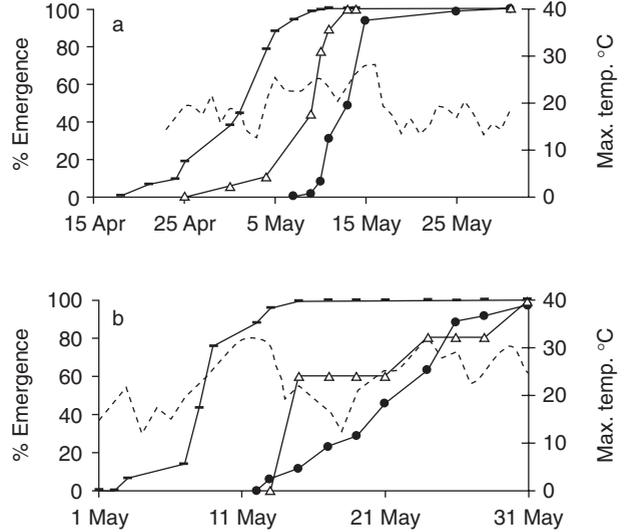
synovigenic parasitoids, females are able to resorb their eggs and, thus, the egg load depends on the relative rates of oogenesis and resorption (King, 1963). Both rates could be affected by factors such as access to food or access to hosts. In these experiments, females had never experienced access to hosts except during development and emergence from the spruce bark (insects were collected a maximum of 24 h after emergence). The decreasing trend observed in the *R. tutela* egg load suggests that the lack of hosts might affect oogenesis in this species more significantly whereas *C. bostrichorum* might be able to balance resorption of old eggs and production of new eggs more adequately. This hypothesis needs to be confirmed by further experiments but, if true, suggests that *C. bostrichorum* might be able to exploit hosts as soon as they become available.

Although females of *R. tutela* carried fewer eggs at any given time in their ovarioles, they were able to lay more eggs than *C. bostrichorum* in a given period of time in the laboratory. Egg production and egg renewal might be faster in this species in the presence of hosts.

*Rhopalicus tutela* does not need to feed before starting its reproductive life (autogeny), in contrast to *C. bostrichorum*.

Table 2. Relationships between body length and survival or potential fecundity, in unfed or fed *Coeloides bostrichorum* (Cb) and *Rhopalicus tutela* (Rt).

| Parameter | Treatment | Species | Sex | $n$ | $R^2$ | $P$ |
|---|---|---|---|---|---|---|
| Survival | Unfed | Cb | Males | 31 | 0.025 | 0.394 |
| | | | Females | 32 | 0.003 | 0.763 |
| | | Rt | Males | 31 | 0.487 | **<0.001** |
| | | | Females | 31 | 0.379 | **<0.001** |
| | Fed | Cb | Males | 35 | 0.069 | 0.126 |
| | | | Females | 40 | 0.067 | 0.107 |
| | | Rt | Males | 24 | 0.004 | 0.765 |
| | | | Females | 23 | 0.006 | 0.713 |
| Potential fecundity | Fed | Cb | | 88 | 0.220 | **<0.001** |
| | | Rt | | 89 | 0.072 | **0.032** |

Bold type indicates significant positive linear relationship.

Host feeding is rare in bark-beetle parasitoids (Mendel, 1988) and females most probably feed on nectar, pollen or honeydew. Flowers and honeydew are available within, or close to, spruce stands (Hougardy & Grégoire, 2000). Bark-beetle parasitoids do not need to disperse far from the native tree to find potential food resources. Furthermore, no specific food searching behaviour was observed in *C. bostrichorum* (Hougardy & Grégoire, 2000) and in parasitoids of another scolytid, *Dendroctonus frontalis* Zimmerman (Drumtra & Stephen, 1999) suggesting that these females probably find their food easily and rather passively. The search for food is probably more a time-consuming than energy-consuming process and again delays the reproductive activity of *C. bostrichorum*.

*Rhopalicus tutela* tended to emerge ten days earlier in the spring than *C. bostrichorum*. The parasitoids of *I. typographus* usually produce two generations a year, similar to their host at low elevations (Krüger & Mills, 1990). The difference in development time between the two species is small (about 20 days at 22°C for *R. tutela* and 18 days at 24°C for *C. bostrichorum* at constant temperature in the laboratory, unpublished data) but the cumulative effect of late emergence and the longer pre-oviposition period in *C. bostrichorum* might accentuate the differences in emergence patterns between the two species in the second, mid-summer generation.

The ability of *R. tutela* to develop on smaller (younger larvae) or larger (pupae) hosts is reflected by its wider range of body size. Females were larger than males in both species, suggesting that the females manipulate their offspring sex ratio in response to host size. This is in agreement with the model of Charnov *et al.* (1981) who predicted more investment in large females than in large males. Two *Coeloides* spp., *Coeloides brunneri* Viereck (Hymenoptera: Braconidae) on the Douglas-fir beetle *Dendroctonus pseudotsugae* Hopkins (Ryan & Rudinsky, 1962) and *C. sordidator* (Ratz.) (Braconidae) on the pine weevil *Pissodes castaneus* De Geer (Coleoptera: Curculionidae) have already been shown to lay more female eggs on larger or older hosts (Kenis, 1996). However a higher mortality of females developing on small hosts could not be excluded (Wellings *et al.*, 1986). The relationship between size and female fitness was examined in order to examine pressures that could be selecting for size-dependent sex allocation. Fitness in females is largely correlated with the number of hosts attacked, and the size of the adult female could influence fitness by affecting longevity, fecundity or host finding abilities (Godfray, 1994; Visser, 1994). The relationship between size and female fitness characteristics (longevity, egg load, realized fecundity) tended to be positive in many studies (see Visser, 1994; Jervis & Copland, 1996 and references therein). In this study, parasitoid size had a positive influence on the fecundity of both species and on the survival of unfed *R. tutela*, but no obvious impact on the survival of *C. bostrichorum*.

Altogether, the delay in emergence, the longer pre-oviposition period, the requirement for feeding before egg laying and the longer survival may benefit *C. bostrichorum*. These features provide a better synchronization with the late instar larvae of *I. typographus*, allowing freshly emerged parasitoid adults to feed and mature eggs while the host offspring mature. On the other hand, *R. tutela* shows a rapid oviposition activity according to its more flexible host stage preference as well as its wider host species range. Thus *R. tutela* could attack the first *I. typographus* hosts that become available during the season or attack alternative hosts if *I. typographus* is absent or present at very low density.

*Coeloides bostrichorum* and *R. tutela* are frequently found together on trees attacked by *I. typographus* in Belgium. These infestations provide limited numbers of bark-beetle hosts because they are generally restricted to groups of 1–4 spruce trees. Parasitism rates on these trees vary between 17–60% (Hougardy & Grégoire, unpublished). A variable proportion of the host population is probably invulnerable to attack by either species (e.g. buried too deeply in the phloem) and thus the parasitoids would probably have shared fewer hosts than revealed by the bark sampling used to quantify parasitism. These relatively high parasitism rates suggest that competition for hosts is important. Because they apparently exploit the same niche, *C. bostrichorum* and *R. tutela* might face intense competition for hosts when resources are limited. According to the competitive exclusion principle, they are unlikely to coexist for long if they share exactly the same niche (Price, 1997). However, the wider host range of *R. tutela* favours the coexistence of the two species within the same spruce stands and on the same *I. typographus* attacked trees. By comparison, *C. bostrichorum* often outnumbers *R. tutela* in the field, suggesting that it is capable of successfully exploiting *I. typographus*. Other mechanisms of host resource partitioning might also favour the coexistence of the two species, based on bark thickness and ovipositor length.

This study has contributed to a better understanding of the two parasitoids species attacking *I. typographus* and offers the practical suggestion that mixed stands of pine and spruce should favour control of this pest by both *R. tutela* and *C. bostrichorum*. Increasing tree species diversity in forest stands should promote the occurrence of *R. tutela* within the stand by providing alternative host bark beetles such as *I. sexdentatus* on *Pinus sylvestris* Linnaeus and *P. nigra* Arnold, *T. piniperda* or *I. acuminatus* on *Pinus* spp. (based on Chararas, 1962 and Kenis *et al.*, 2004). The availability of alternative hosts for *R. tutela* should also promote its coexistence with *C. bostrichorum* when *I. typographus* are scarce, providing a refuge from intense competition with this specialist species. Stand diversity should also favour the survival of both parasitoids if it encourages increased colonization of herbaceous plant species on the forest floor that provide parasitoid adult food resources such as nectar, pollen and honeydew. This study suggests that mixed planting of conifers may offer advantages in terms of pest control and should be investigated further.

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