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Cleptoparasitism increases the host finding ability of a polyphagous parasitoid species, *Rhopalicus tutela* (Hymenoptera: Pteromalidae)

Received: 23 June 2003 / Accepted: 28 August 2003 / Published online: 1 October 2003
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Abstract Host finding abilities were investigated in the braconid *Coeloides bostrichorum* and the pteromalid *Rhopalicus tutela*, two ectoparasitoid wasps attacking the late instar of the bark beetle *Ips typographus*. Under laboratory conditions, important differences in the host-searching behaviour of these species were found, *R. tutela* being highly mobile as compared to *C. bostrichorum*. In the presence of *C. bostrichorum*, *R. tutela* behaved as a cleptoparasitoid, displacing the females from their oviposition sites and stealing the hosts previously located by the braconid. This behaviour facilitated host finding in *R. tutela* and could partly explain the relative success of the polyphagous *R. tutela* when occurring with the more specialised *C. bostrichorum*.

Keywords *Coeloides bostrichorum* · *Rhopalicus tutela* · Host-searching behaviour · Host-finding efficiency · Cleptoparasitism

Introduction

Cleptoparasitism has been reported among insect parasitoids when one species develops at the expense of another species, through being able to steal the food supply (the primary host) provided by the first attacking species for its offspring (Eggleton and Belshaw 1992). Cleptoparasitism, as a way of life, has been observed in

several parasitoid–host systems with various levels of specialisation, from an obligate interaction to a more facultative interaction between species. *Pseudorhyssa sternata* Merrill is an ichneumonid parasitoid that lacks a boring ovipositor and which can only attack siricid woodwasps parasitised by *Rhyssa* spp. (Spradbery 1969). Similarly, *Eurytoma waachtli* (Eurytomidae) only attacks *Pissodes* weevil larvae after they have been paralysed by ichneumonids of the genus *Scambus* (Roques 1976). In contrast, *Temelucha interruptor* (Grav.) (Ichneumonidae) shows poor success in locating its host *Rhyacionia buoliana* (Schiff.) (Tortricidae) but shows greater success in finding hosts that had already been parasitised by the braconid *Orgilus obscurator* (Nees) (Arthur et al. 1964). In each case, however, successful parasitism by the cleptoparasitoid is dependent on being able to consistently kill the egg or young larva of the previously attacking species.

Antagonistic interactions that induce cleptoparasitism have also been reported in bark beetle parasitoid complexes, when females forage for host larvae at the bark surface. *Eurytoma conica* Provancher, an eurytomid attacking the scolytid *Dendroctonus brevicomis* Le Conte has been observed to steal the oviposition site of *Coeloides sympitis* (Braconidae) (Dahlsten 1982). Similarly, the pteromalid *Cheirpachus quadrum* (F.) and the eurytomid *Eurytoma morio* Boheman—two species in the parasitoid complex associated to the scolytid *Leperisinus varius* (F.)—have been observed to aggressively displace the braconid *Coeloides filiformis* Ratzeburg, from the bark surface where it was probing for host larvae (Mills 1991).

Coeloides bostrichorum Giraud (Braconidae) and *Rhopalicus tutela* Walker (Pteromalidae) are two sympatric solitary ectoparasitoids attacking the late instar of the Eurasian spruce pest *Ips typographus* L. (Coleoptera: Scolytidae). *R. tutela* is a polyphagous species attacking numerous bark beetles on both pine and spruce (Mills 1983) as well as *Pissodes* species (Curculionidae) (Graham 1969). Parasitism rates on *I. typographus* vary from 4% to 20–25% (Mills 1983 and references therein). *C.*

Communicated by R.F.A. Moritz

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bostrichorum has a narrow host range restricted to bark beetle species developing on spruce (Mills 1983; Hedqvist 1998) and has been reported as the most efficient parasitoid of *I. typographus* (up to 50–95% parasitism on *I. typographus*, Mills 1983 and references therein).

The aim of this study was to investigate the oviposition success of *R. tutela* and *C. bostrichorum* when present alone and together, in order to reveal cleptoparasitic habits and to better understand the specific strategies allowing the coexistence of the two species. This is the first study exploring the feasibility of cleptoparasitism as a mechanism to mediate competition between two parasitoid species.

Methods

Insects

R. tutela came from a culture maintained in the laboratory on *I. typographus* for approximately 50 generations. Original insects came from bark infested with *I. typographus* collected in southern Belgium in the winter of 1998. *C. bostrichorum* was reared from *I. typographus*-infested bark collected on November 2001 in Resteigne (southern Belgium). The bark was stored at 2°C until needed. *C. bostrichorum* adults started to emerge after 10–25 days at room temperature, depending on the time spent in diapause at 2°C. *I. typographus* adults came from the same pieces of field-collected bark and from cultures in the laboratory.

Experimental procedures

The host-searching behaviour of parasitoids was studied in “phloem sandwiches”, that permit the observation of the bark beetle and parasitoid brood within the phloem (Kinn and Miller 1981). The phloem sandwiches were each made of a 20-cm square piece of bark (phloem + outer bark) taken from a freshly felled spruce 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 (Fig. 1). 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 colonise the phloem sandwich, one male bark beetle was placed in a shaft made in the centre of each bark square. After the male had bored a mating chamber (24 h later), three females were introduced in 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), naive parasitoid females were released onto the bark surface and confined there by a glass plate placed over the wooden frame. We

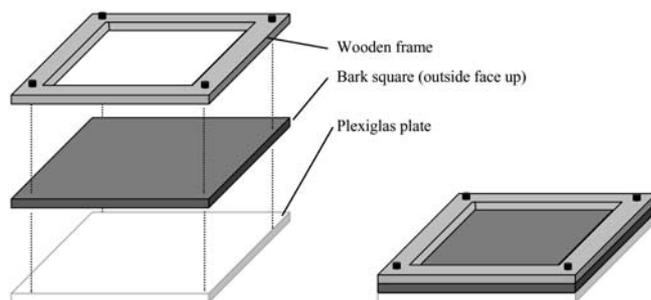


Fig. 1 The components of a phloem sandwich

consider as naive, parasitoid females that had no experience with hosts except during development and emergence from spruce bark or logs (parasitoids were collected a maximum of 24 h after their emergence). Beetle abundance was measured within each sandwich, and before the parasitoids were released, the positions of the host larvae were recorded on a transparent plastic sheet. The position of each host under the bark could easily be verified during the observations by placing the plastic sheet on top of the glass observation plate. The phloem sandwiches were held at 21±1°C with a 16:8 (light:dark) photoperiod, and observations were carried out under the same conditions. However, as light seemed to negatively affect the response of *C. bostrichorum* to the infested bark, observations were undertaken without direct light.

A total of ten pairs of one *R. tutela* (8±3 days old) and one *C. bostrichorum* (14±3 days old), were released onto separate phloem sandwiches. As controls, ten individual *R. tutela* (10±3 days old) and nine individual *C. bostrichorum* (6±2 days old) were released alone onto separate phloem sandwiches for the same period of time (in total 29 observations). All females had completed their preoviposition period (the interval needed between emergence and the deposition of the first egg) as determined from previous results (pre-oviposition period lasted 5.1±1.3 days in *C. bostrichorum* and 3.3±1.0 days in *R. tutela*; Hougardy and Grégoire, unpublished research).

Parasitoid searching behaviour and interactions

Only parasitoids showing an immediate (within 10 min) interest in the bark by exhibiting obvious searching behaviour were observed continuously for a period of 2 h. The general searching behaviour was noted and the following information was recorded from 100 interactions between the two species: the challenging species, the activity of challenged species before the interaction and the outcome of the interaction (= the species displaced and the activity of both species after the interaction).

Host-searching success

For each parasitoid species, the number of females locating a host and a “productive” host (a successfully parasitised host) within the 2-h observation period was recorded. We made the distinction between finding a first host and finding a first productive host, because the location of a host was not always followed by successful parasitism and because the interaction between females could lead to the loss of a potential oviposition site. For each female, the number of hosts located, the number of probes undertaken above a host, the number of eggs laid and the number of wrong locations (when females probed through the bark at sites with no host beneath) were recorded. The hosts probed by the females were marked and checked at the end of the observation period for the presence of a parasitoid egg and to detect the incidence of superparasitism (the laying of an egg on a host previously parasitised by the same species) and multiparasitism (the laying of an egg on a host previously parasitised by another species). Sometimes, dissection of the bark was necessary for this purpose. The eggs of the two species could easily be distinguished as *C. bostrichorum* has larger and more elongated eggs than *R. tutela*. The exact location of ovipositor probes (above uninfested bark, maternal gallery, larval gallery, bark beetle larva, prepupa or pupa) was recorded during the first four periods of observation for *R. tutela* (75 observations) and the first eight periods of observation for *C. bostrichorum* (47 observations). These observations were confined to sandwiches where the parasitoids were searching together. During the further observation, only the sites probed above a host were marked and checked at the end of the observation period.

Statistical analyses

Differences in the number of females locating a host within the 2-h observation period were determined using nonparametric Fisher Exact Tests (Siegel and Castellan 1998). Differences in the numbers of hosts, probes or eggs between species and treatments (alone or together with the other species) were tested using two-way ANOVA. For all tests, the significance level was set at 0.05. All statistical analyses were performed using SPSS (2001). When needed, data were log transformed in order to achieve homoscedasticity among the measurements.

Results

Parasitoid searching behaviour and interactions

The searching behaviour of *C. bostrichorum* was characterised by long pauses on the bark surface interrupted by walking periods, sometimes coupled with a rotating movement of the body on a horizontal plane. Antennae were held out at right angles and parallel to the bark surface. Occasionally, the females swept their antennae from side to side. When a suitable site was located, pauses followed rotating movements just above the host. Finally the females attempted to insert their long ovipositor through the bark. In contrast, *R. tutela* was highly mobile, walking continuously with the elbowed antennae pointing downwards, their tips drumming the bark surface. When a potential oviposition site was detected, the females suddenly stopped and the site was intensively inspected with the antennae. If the site was accepted, the females moved forward and put their ovipositor tip precisely on a point previously selected by the converging antennae.

When the two species were released simultaneously on the bark surface, the mobile *R. tutela* frequently encountered *C. bostrichorum* searching for hosts. Both females seemed unaware of each other until physical contact occurred. The pteromalid then behaved very aggressively towards the braconid through wing beating and lateral thrusts of the abdomen. If *C. bostrichorum* was ovipositing, *R. tutela* moved closely around it, inspected the bark with its antennae and finally displaced *C. bostrichorum* by bumping into it, or by biting its legs, antennae or sometimes even its ovipositor. Most of the time, *C. bostrichorum* rapidly moved away. After displacing the braconid, *R. tutela* inspected the freshly acquired site with its antennae, also frequently probing with its ovipositor. These interactions lasted on average 2.1 ± 3.7 s ($n=100$).

R. tutela was the species that challenged most (83% of the interactions, $n=100$). Encounters with *C. bostrichorum* occurred most frequently (61%) while the braconid was standing near an oviposition site from which it had previously been displaced (Fig. 2A). In 95% of the interactions, *R. tutela* displayed an aggressive behaviour, displacing *C. bostrichorum*. *R. tutela* was not aggressive in 5% of the encounters and moved away. This occurred when *C. bostrichorum* was ovipositing, and in the majority of the cases (three of four) *R. tutela* had already laid an egg on that host. *C. bostrichorum* was never observed displacing *R. tutela*. The frequency with which displacement of *C.*

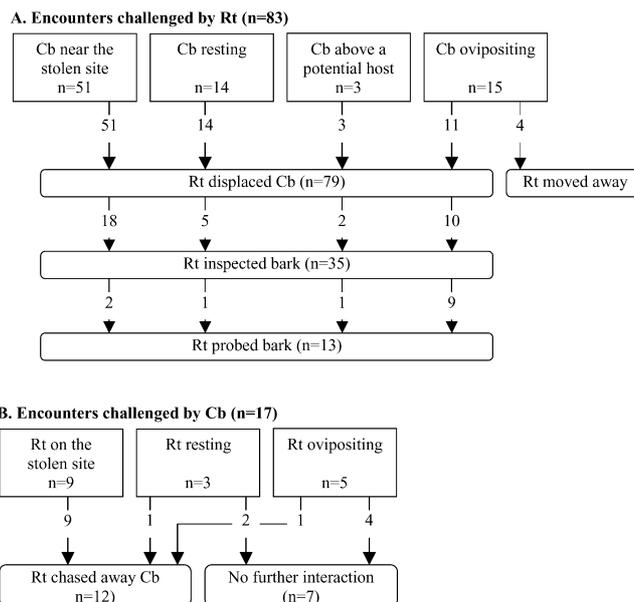


Fig. 2 Behavioural sequences following encounters between *Coeloides bostrichorum* (*Cb*) and *Rhopalicus tutela* (*Rt*) (7 pairs, 100 interactions observed), when the challenging species is *R. tutela* (A) or *C. bostrichorum* (B)

bostrichorum was followed by bark inspection and probing by *R. tutela* increased with the chance of finding a susceptible host. The chances were low when *C. bostrichorum* was resting on the bark and increased when *C. bostrichorum* was resting above a potential host or ovipositing (Fig. 2A). *C. bostrichorum* initiated an encounter with *R. tutela* in 17% of the interactions (Fig. 2B), while returning to a stolen oviposition site (76%), while meeting *R. tutela* resting on the bark surface (18%) or while bumping into an ovipositing *R. tutela* (6%). In most of the cases (70%), *R. tutela* reacted by chasing away *C. bostrichorum*. In the other 30%, no aggression was observed and both species moved away. Generally, only one very aggressive encounter was necessary. Later, just a rapid approach of *R. tutela* was sufficient to intimidate and displace *C. bostrichorum*. The frequency of such interactions tended to increase with time as *C. bostrichorum* tended to stay near the stolen oviposition site.

Host-searching success

The mean number of host larvae in the phloem sandwiches was similar between treatments: 21 ± 9 hosts/sandwich when the two species were released together, 20 ± 8 hosts/sandwich when *C. bostrichorum* was alone and 20 ± 9 hosts/sandwich when *R. tutela* was alone (one-way ANOVA: $F_{2,28}=0.70$, $P=0.93$).

No significant difference in the number of females that were able to locate a host within 2 h was detected between both species when released alone (Table 1, *Rt* alone vs *Cb* alone, Fisher Exact Test: $P=0.12$) or when released together (*Rt* alone vs *Rt* with *Cb*: $P=0.11$ and *Cb* alone

Table 1 Numbers of females locating at least one host and one “productive” host (= a successfully parasitized host) during a 2-h observation period for *Rhopalicus tutela* (*Rt*) and *Coeloides bostrichorum* (*Cb*) either alone or together with the other species

Species	Treatment	<i>n</i>	Locating a host <2 h	Locating a productive host <2 h
<i>Rt</i>	Alone	10	7	2
	With <i>Cb</i>	10	10	7
<i>Cb</i>	Alone	9	9	8
	With <i>Rt</i>	10	10	8

Table 2 Average number (\pm SD) of hosts located (productive or not), number of probes undertaken above hosts (productive and not), duration of oviposition, number of eggs laid per female and number of wrong locations probed during a 2-h observation period for *R. tutela* (*Rt*) and *C. bostrichorum* (*Cb*) either alone or together with the other species

Species	Treatment	No. of hosts located	No. of probes on located hosts		Duration of oviposition (s)	No. of eggs laid	No. of wrong locations
			Non productive	Productive			
<i>Rt</i>	Alone (<i>n</i>)	2.2 \pm 2.4 (10)	12.4 \pm 9.0 (7)	6.0 \pm 1.0 (3)	418 \pm 170 (3)	0.3 \pm 0.7 (10)	2.0 \pm 1.6 (10)
	With <i>Cb</i> (<i>n</i>)	4.2 \pm 3.0 (10)	10.0 \pm 9.1 (10)	5.6 \pm 3.8 (11)	456 \pm 186 (11)	1.1 \pm 1.1 (10)	2.5 \pm 2.1 (10)
<i>Cb</i>	Alone (<i>n</i>)	3.4 \pm 1.7 (9)	0.3 \pm 0.5 (9)	2.9 \pm 1.8 (23)	1030 \pm 448 (23)	2.6 \pm 1.7 (9)	– (9)
	With <i>Rt</i> (<i>n</i>)	4.7 \pm 1.9 (10)	3.4 \pm 5.4 (10)	1.6 \pm 0.7 (19)	837 \pm 390 (19)	1.9 \pm 1.7 (10)	0.1 \pm 0.3 (10)

Table 3 Percentage of probes undertaken by *R. tutela* (four females, *n*=75 observations) and *C. bostrichorum* (eight females, *n*=47 observations) at different locations on the bark surface;

BARK=uncolonised bark, *LGAL*=larval galleries, *MGAL*=maternal galleries, *LL*=late instar larvae, *PP*=pre-pupae and *PU*=pupae

Species	BARK	LGAL	MGAL	LL	PP	PU	Total
<i>R. tutela</i>	1	16	12	39	21	11	100
<i>C. bostrichorum</i>	7			70	23		100

vs *Cb* with *Rt*: $P=1.00$). However, fewer *R. tutela* were able to locate a productive host as compared to *C. bostrichorum* (Table 1, *Rt* alone vs *Cb* alone: $P=0.004$). The presence of *C. bostrichorum* increased the ability of *R. tutela* in locating a productive host (*Rt* alone vs *Rt* with *Cb*: $P=0.04$). On the other hand, the presence of *R. tutela* did not change the efficiency of *C. bostrichorum* (*Cb* alone vs *Cb* with *Rt*: $P=0.54$).

The average numbers of hosts (productive or not) located by parasitoid females did not differ between the two species (Table 2, two-way ANOVA, $F_{1,35}=1.38$, $P=0.25$). However there was a treatment effect ($F_{1,35}=4.81$, $P=0.04$): females of both species found a greater number of hosts in the presence of the other species than when released alone. No interaction between species and treatment was detected ($F_{1,35}=0.25$, $P=0.62$). *R. tutela* increased its host-finding ability in the presence of *C. bostrichorum* while for *C. bostrichorum*, this result was due to the fact that females were forced to locate more hosts as some of them were stolen and lost.

R. tutela probed more above a host than *C. bostrichorum*, considering nonproductive hosts (Table 2, two-way ANOVA, $F_{1,32}=28.83$, $P<0.001$) or productive hosts ($F_{1,52}=22.67$, $P<0.001$). The number of probes was not influenced by a treatment effect (nonproductive hosts: $F_{1,32}=0.70$, $P=0.41$; productive hosts: $F_{1,52}=1.20$, $P=0.28$) and no interaction between species and treatment was detected (nonproductive hosts: $F_{1,32}=4.34$, $P=0.05$; productive hosts: $F_{1,52}=0.38$, $P=0.54$). The probe of longest

duration, often the last one undertaken on a host, was considered here as the oviposition per se. *R. tutela* took less time for oviposition than *C. bostrichorum* (two-way ANOVA, $F_{1,52}=13.08$, $P<0.001$; no effect of treatment: $F_{1,52}=0.33$, $P=0.57$; no interaction: $F_{1,52}=0.70$, $P=0.41$).

C. bostrichorum laid significantly more eggs than *R. tutela* (Table 2, two-way ANOVA, $F_{1,35}=12.40$, $P=0.001$) but there was no treatment effect ($F_{1,35}=0.03$, $P=0.87$). No interaction between species and treatment was detected ($F_{1,35}=2.81$, $P=0.10$). In the presence of *C. bostrichorum*, *R. tutela* was not more successful, although there was a slight tendency towards more eggs laid. However, all the ovipositions recorded for *R. tutela* occurred after interactions with *C. bostrichorum* females. For *C. bostrichorum*, the presence of *R. tutela* had no significant effect on oviposition success.

Several females probed through the bark at sites with no host beneath. Such wrong host locations were more frequent in *R. tutela* than in *C. bostrichorum* (Table 2, two-way ANOVA, $F_{1,35}=26.00$, $P<0.001$) but there was no significant difference in the average numbers of wrong locations between females released alone or in the presence of the other species ($F_{1,35}=0.48$, $P=0.49$). No interaction between species and treatment was detected ($F_{1,35}=0.21$, $P=0.65$). *C. bostrichorum* rarely probed at a wrong location and did so only in the presence of *R. tutela*. Seventy-one percent of probes were located above a potential host for *R. tutela* and 93% for *C. bostrichorum* (Table 3). When wrong, *R. tutela* probed above host

galleries, 2–6 cm away from the host larva. One female probed several times along the course of a larval gallery, each time probing closer to the host larva at the end of the larval gallery.

No superparasitism was observed while multiparasitism was observed with a frequency of 11% (3 multiparasitised hosts from a total of 27 hosts parasitised in the ten sets of phloem sandwiches with paired releases). In one case was *R. tutela* the first ovipositing species. This occurred on a host, which *C. bostrichorum* had been probing just before being displaced by *R. tutela*. For the two other cases, the second egg in the sequence was laid by *R. tutela*. We were not able to establish the outcome of multiparasitism because parasitoid larvae died prematurely.

Discussion

A highly mobile searching strategy, as observed for *R. tutela* in the present study, seems a characteristic feature of cleptoparasitic bark beetle parasitoids, increasing their encounter rates with other parasitoids foraging at the bark surface (Mills 1991). This author suggested that such behaviour allows species with poor host-searching abilities to compete successfully with species that have better host-searching abilities but poor fighting abilities (the “counter-balanced” competition described by Zwölfer 1971 and Schröder 1974). The present study provides evidence that facultative cleptoparasitism facilitated the host-finding success of the pteromalid *R. tutela*. In the presence of *C. bostrichorum*, a greater number of *R. tutela* females were able to locate and parasitise a host, and, they located a greater average number of hosts during the 2-h observation period, than when they searched alone on the bark surface. In contrast, *C. bostrichorum* is obviously better able to locate and exploit hosts beneath the bark: all females tested were able to find a productive host within the 2-h observation period and to lay a greater number of eggs than *R. tutela*. Surprisingly, the success of host location and parasitism by *C. bostrichorum* did not seem to be affected by the antagonistic interactions with *R. tutela*. However, *C. bostrichorum* only probed at wrong locations on the bark when *R. tutela* was present, suggesting that the interactions must have had a disturbing influence. Moreover, after several acts of aggression, *C. bostrichorum* was observed to fly away from the bark, and would probably have definitively left the area if they had not been confined on the phloem sandwiches.

C. bostrichorum and *R. tutela* can probably discriminate between healthy hosts and hosts it has already parasitised as superparasitism was not observed. No evidence of interspecific discrimination was observed for either species. Multiparasitism is not rare in these cleptoparasitoid species as the egg is often laid on a previously parasitised host. However only one individual can successfully develop on a single host larva. The cleptoparasitoid larvae must have good fighting abilities or, especially for obligate cleptoparasitoids, the adult

female might first kill the primary parasitoid egg or young larva before laying its own egg. We observed 11% multiparasitism in the present laboratory study, but unfortunately, we were not able to assess the outcome of the larval competition. Krüger and Mills (1990) observed 5% multiparasitism for the same species in the field in Austria.

Chemicals are the main cues used in host detection by bark beetle parasitoids (Richerson and Borden 1972a, 1972b, Mills et al. 1991; Pettersson 2001a, 2001b; Pettersson et al. 2001). However, the obvious differences between *C. bostrichorum* and *R. tutela* in host-searching behaviour suggest that, in addition to chemical cues, females may use different additional signals for short-range detection. The behaviour of *R. tutela*, drumming continuously on the bark surface with its antennae, suggests that this species might also use vibrational sounding to find their hosts (producing pulses of sound by tapping the substrate with their antennae and detecting the echoes with specific receptors, see Broad and Quicke 2000; Fischer et al. 2001; Vilhelmsen et al. 2001). Inexperienced females were observed to probe above larval galleries but not always just above a host larva, suggesting that they probably find their hosts by first detecting galleries. However, scanning electron micrographs of the antennae of *R. tutela* (Pettersson et al. 2001) do not show the morphological adaptations to vibrational sounding described in Broad and Quicke (2000) and Vilhelmsen et al. (2001), and so far, vibrational sounding has not been demonstrated in this species. In addition, *R. tutela* most probably uses its ovipositor in host detection and host acceptance, as suggested by the large number of probes and the frequency of sites incorrectly probed.

The observed cleptoparasitic behaviour could partly explain the success of the polyphagous *R. tutela* when coexisting with the more successful and more specialised *C. bostrichorum*. In southern Belgium, *C. bostrichorum* dominated in heavily parasitised infestations of *I. typographus* (up to 56% parasitism per tree, Hougardy and Grégoire, unpublished data). In the present study, the braconid was observed to exploit the host patch almost systematically, moving from a host they have just parasitised to the next nearest one suggesting that it must have very efficient host-location mechanisms. Although less numerous (0–13% parasitism per tree), *R. tutela* has been observed to coexist with *C. bostrichorum* in the upper sections of trees (Hougardy and Grégoire, unpublished data). According to the “counter-balanced strategies” theory described by Zwölfer (1971) and Schröder (1974), coexistence with a superior species in host exploitation (extrinsic competition) is possible if counterbalanced by a species with superiority in other attributes such as larval competitive ability (intrinsic competition). Here two mechanisms should be considered in relation to the competitive ability of *R. tutela*: a presumed ability to kill eggs/young larvae of *Coeloides* (stealing) and an ability to displace rivals from oviposition sites (interference competition). Our system obviously needs further investigations, notably on the

outcome of multiparasitism and the impact of cleptoparasitism on *C. bostrychorum*.

Acknowledgements The authors thank Nick Mills, Jacques Pasteels, Guy Boivin and two anonymous reviewers for their valuable comments on an earlier version of the manuscript. Special thanks to Marius Gilbert and Pierre Herman for technical and field assistance. Evelyne Hougardy was supported by Fonds pour la Formation à la Recherche dans l'Industrie et dans l'Agriculture (FRIA).

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