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Generalist cuckoo bees (Hymenoptera: Apoidea: *Sphecodes*) are species-specialist at the individual level

Abstract Intensive and incessant arms races between a parasite and its host are generally expected to lead to parasite specialization. Nevertheless, some parasitic species still successfully attack wide spectra of hosts. One of the solutions to the evolutionary enigma of the long-term existence of generalist parasites is their specialization at an individual level, a phenomenon well known, e.g., in European common cuckoo. Over its range, it parasitizes a number of bird species; however, individual females are mostly specialists possessing adaptations to a particular host species. In this study, we test the possibility of individual specialization in generalist cuckoo bees, the insect counterparts of avian cuckoos. Females of cuckoo bees lay each egg into a single brood cell in the nests of other bee species. The host's offspring is destroyed by the parasitic female or later by her larvae, which feed on pollen supplies accumulated by the host. Both studied cleptoparasitic bees (*Sphecodes ephippius* and *Sphecodes monilicornis*) are widely distributed in Europe, where they have been reported to use broad host spectra. We recorded several host species (including some previously unknown) for both cuckoo bee species, and confirmed that these parasites are indeed generalist even at a small local scale. However, we demonstrate that exactly as in the avian cuckoos, each female in both species of generalist bee parasites tends to attack just one host species.

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Introduction

Parasitism is defined as a symbiosis in which one member (the parasite) benefits from the use of resources gathered by the other member (the host). As the host suffers the fitness cost from the parasite, we can expect that it evolves some, e.g., immunological defense or behavioral avoidance of the parasite. The parasite, dependent on the resources acquisition from its host, is then selected to overcome the host defensive strategy (Poulin et al. 2000). As a result, the continuous interactions between the parasite and its host lead to arms race. One of the often-suggested results of such arms race is the specialization of the parasite to just one host species. Specialization and long-term host specificity during the evolutionary history of the parasite–host system can be demonstrated by rigorous tests of cospeciation (Legendre et al. 2002).

Nevertheless, not all species of parasites are specialists. To give an example, some popular parasitic birds—cuckoos and cowbirds—are generalists at a specific level. There are huge differences between generalist species, whether every member of given species is a generalist or a specialist to a particular host. The brown-headed cowbird [*Molothrus ater* (Boddaert,1783)] is, for instance, a generalist at the level of both species and individuals (Winfree 1999. On the other hand, the common cuckoo (*Cuculus canorus* Linnaeus, 1758) uses more than 100 species of birds over its range, but individual cuckoo females often use only one host species (Marchetti et al. 1998). All cuckoo females parasitizing one host species (the so-called "gens"), usually share the same adaptation enabling them to overcome the defense of their particular hosts—e.g., they have mimetic eggs resembling those of their hosts (Aviles and Møller 2004). Generalist parasites are also not rare among invertebrates. However, even among some invertebrate generalist parasites, there is strong genetic evidence of the coexistence of sympatric

specialized host races (e.g., McCoy et al. 2001). Therefore, without careful examination, we cannot decide how many parasitic species with several known hosts are in fact specialists in the sense of the "cuckoo" system, i.e., at an individual or subpopulational level.

In this study, we explore an interesting system of the cleptoparasitic bees, the obligatory parasites of another bee species. Within the taxon Apoidea, the cleptoparasitic bees form a special ecological group. Owing to their way of life, they are commonly called the "cuckoo bees". Females of these bees do not build a nest. They lay eggs into nests of other solitary bee species. Brood (larvae) feed on pollen supplies collected by the owner of the nest (a host) for its offspring. Eggs are laid strictly into the brood cells and the host's offspring is destroyed by the cleptoparasitic female (e.g., genus *Sphecodes* Latreille, 1805) or by young larvae (e.g., *Coelioxys* Latreille, 1809, *Nomada* Scopoli, 1770). Especially the first larval instars of the majority of cuckoo bees possess elongate, pincer-like mandibles, specialized to kill the host's egg or larva (Michener 2000). Even though the way of life of the cleptoparasitic bees seems somewhat obscure, they represent about 15% of all recently known bee species over the world (Batra 1984). In Europe, as much as about one quarter of all bee species are cleptoparasitic (Schwarz et al. 1996). According to Rozen (2000), cleptoparasitism has evolved independently in 27 bee lineages.

The cuckoo bees are usually strongly bounded to their hosts. Majority of cuckoo bees parasitize in the nests of only few host species (2–5), but approximately one quarter of the European cuckoo bees are specialized to just one host species. Generalists with more than ten host species represent the less numerous groups of cuckoo bees (Bogusch 2003a). Nevertheless, it is important to note that the currently known data on host spectrum of many species are incomplete. With the exception of some North American or Neotropical species with quite well-known ecology (Rozen 1967, 1991; Torchio 1989), the vast majority of knowledge on cuckoo bees host diversity dates back to the dawn of the 20th century (Friese 1923; Blüthgen 1923, 1934; Stöckhert 1933). Nearly all of the following records only cite and repeat these old data. Only during the last 20 years, a few authors (e.g., Vegter 1985, 1993; Westrich 1989; Sick et al. 1994; Bogusch 2003a,b, 2005) have contributed to the knowledge of the host spectrum and general biology of some Central-European cuckoo bees.

In the present paper, we concentrate on host diversity and individual female behavior in two species of cuckoo bees of the genus *Sphecodes*. The general biology of this genus is only poorly known. Females lay eggs mostly into closed brood cells and destroy the egg or young larva. Larvae develop in the nests of the genera *Halictus* Latreille, 1804 and *Lasioglossum* Curtis, 1833; several species parasitize in nests of *Andrena* Fabricius, 1775 and *Colletes* Latreille, 1802. It is interesting to note that some European *Sphecodes* species attack nests of only one host species [e.g., *Sphecodes albilabris* (Fabricius, 1793), *Sphecodes rufiventris* (Panzer, 1798)], but the genus also includes

generalists with 10–15 known hosts (Westrich 1989; Sick et al. 1994; Bogusch 2003a). Many unspecialized bees, e.g., *Sphecodes monilicornis* (Kirby, 1802) or *Sphecodes ephippius* (Linnaeus, 1767), are widely distributed and occupy nearly all localities of their hosts. As far as known, both latter species slightly differ in host spectra: *S. monilicornis* invades only the nests of related genera *Halictus* and *Lasioglossum*, *S. ephippius* also those of some *Andrena* species (Westrich 1989; Bogusch 2003a). How can these parasites with such wide host spectra overcome potentially species-specific defensive mechanisms of their hosts?

The goals of the present paper are (1) to review and revise the hosts spectra of *S. monilicornis* and *S. ephippius* over their ranges, and replenish the list of currently known hosts, (2) to test whether both species are truly generalist even at a local scale, (3) to describe their behavioral strategy of parasitism, and (4) to test the hypothesis of individual specialization, i.e., whether individual female of these generalist cleptoparasites is also generalist, or exploits just one host species.

Methods

The lists of hosts were compiled from our own observations and compared to reliable literary data (Alfken 1912; Stöckhert 1933; Blüthgen 1934; Michener 1978; Westrich 1989; Vegter 1993; Sick et al. 1994). We treated host species where cleptoparasites were reared from the nests as "confirmed". "Likely" hosts include cases where only the behavioral interactions between the cleptoparasite and the host females were observed.

Field work on *Sphecodes* and their hosts was conducted during the years 1999–2004 on several localities in Central and Eastern Europe (the Czech Republic, Slovakia, Hungary, and Bulgaria) from April to August. We had been observing, recording, and analyzing all the types of behavioral interactions between the cleptoparasite and the host. All the interactions observed since April 1999 were divided into seven categories, called "behavioral patterns", which are described in detail in the "Results" section. The list of these categories represents the first attempt to sort the behavioral interactions between the cuckoo bee and its host. We specifically recorded the entries of cuckoo bee females to nests and measured the time they spent inside the host's nest. Consecutively, the brood cells from the parasitized nests were buried out and the offsprings were reared in laboratory and determined.

To test the hypothesis on individual specialization, females of *Sphecodes monilicornis* and *S. ephippius* were observed during their activity time on 26th, 27th, and 28th of April 2004 at the locality Buzice in the south of the Czech Republic. The locality seems to represent the warmest site in the vicinity. It is a path bordered by sunny sides with sandy ground with a lot of nests of nesting bees. Nests were dispersed with the density of about 50 nests per square meter. Nests of several host species were scattered over the same sites. They do not form single-

species clusters within the nest aggregations. Observations of cleptoparasites were conducted during the period, when females of *Andrena*, *Halictus*, and *Lasioglossum* (hosts of *Sphecodes* bees) bees built their nests. Most of the halictid host species are primitively eusocial, but colony formation and enlargement is in motion later in the season, so none or just a few workers were staying in the nests during the time of our work. Only those cases when cleptoparasitic female spent more than 120 s in the host nest were assessed as parasitization, as Sick et al. (1994) demonstrated that *S. monilicornis* female takes 2 min to lay an egg into the host's brood cell. The first two entries longer than 120 s with identifiable host of a particular *Sphecodes* female were recorded. To avoid pseudoreplications, each clepto-parasitic female was caught after two focal entries and marked with a dot of yellow acrylic color on mesonotum.

The owners of nests were collected and determined; their brood cells were digged out in some cases. During the three observational days, there were 52 females of *S. ephippius* and 48 females *S. monilicornis* observed and collected. Records on host identity were put into two matrices, each for a given species of cleptoparasite. A row represents the number of cuckoo bee individuals visiting a nest of particular host species during the first entry recorded; a column represents the number of cleptoparasites visiting given host species during the second entry. Matrix diagonals thus encompass the cases where individual females were faithful to a single host species during both recorded entries. The hypothesis on individual specializa-tion was evaluated using a combinatorial test constructed for this purpose. We designed this test to preserve the distribution of elements among rows, i.e., number of

Table 1 List of hosts of (a) *Sphecodes ephippius* (Linnaeus, 1767) and (b) *S. monilicornis* (Kirby, 1802)

Host species	Host certainty	References
(a) *Sphecodes ephippius*		
Andrena barbilabris (Kirby, 1802)	Likely	Vegter 1993
Andrena flavipes Panzer, 1798	Likely	Present study
Andrena chrysopyga Schenck, 1853	Likely	Alfken 1912; Westrich 1989
Andrena labialis (Kirby, 1802)	Likely	Sowa and Mostowska 1978
Andrena minutula (Kirby, 1802)	Likely	Present study
Andrena wilkella (Kirby, 1802)	Likely	Present study
Halictus maculatus Smith, 1848	Likely	Present study
Halictus rubicundus (Christ, 1791)	Likely	Present study
Halictus tumulorum (Linnaeus, 1758)	Confirmed	Bischoff 1927; Westrich 1989; Vegter 1993
Lasioglossum fratellum (Péréz, 1903)	Likely	Field 1996
Lasioglossum laticeps (Schenck, 1870)	Confirmed	Present study
Lasioglossum lativentre (Schenck, 1853)	Likely	Westrich 1989
Lasioglossum leucozonium (Schrank, 1781)	Confirmed	Stöckhert 1933; Westrich 1989;Vegter 1993; Sick et al. 1994
Lasioglossum malachurum (Kirby, 1802)	Confirmed	Sick et al. 1994
Lasioglossum pauxillum (Schenck, 1853)	Confirmed	Present study
Lasioglossum prasinum (Smith, 1848)	Likely	Vegter 1993
Lasioglossum quadrinotatulum (Schenck, 1861)	Confirmed	Westrich 1989; Vegter 1993
(b) *Sphecodes monilicornis*		
Andrena flavipes Panzer, 1798	Likely	Present study
Halictus maculatus Smith, 1848	Likely	Present study
Halictus rubicundus (Christ, 1791)	Confirmed	Alfken 1912; Blüthgen 1934; Vegter 1993; present study
Halictus tumulorum (Linnaeus, 1758)	Likely	Present study
Lasioglossum albipes (Fabricius, 1781)	Confirmed	Alfken 1912; Stöckhert 1933; Blüthgen 1934; Westrich 1989; Vegter 1993
Lasioglossum calceatum (Scopoli, 1763)	Confirmed	Stöckhert 1933; Blüthgen 1934; Westrich 1989; Vegter 1993; present study
Lasioglossum laticeps (Schenck, 1870)	Likely	Present study
Lasioglossum leucozonium (Kirby, 1802)	Confirmed	Present study
Lasioglossum malachurum (Kirby, 1802)	Likely	Stöckhert 1933; Blüthgen 1934; Westrich 1989; present study
Lasioglossum pauxillum (Schenck, 1853)	Likely	Present study
Lasioglossum prasinum (Smith, 1848)	Likely	Vegter 1993
Lasioglossum quadrinotatulum (Schenck, 1861)	Confirmed	Blüthgen 1934; Vegter 1993
Lasioglossum villosulum (Kirby, 1802)	Likely	Present study
Lasioglossum zonulum (Smith, 1848)	Confirmed	Alfken 1912; Blüthgen 1934; Vegter 1993

females visiting a given host species during the first entry, which was thus taken as an estimation of the representation of each host species in the host spectrum of a cleptoparasite in our locality. First, we computed the number (A) of all matrices with 52, respectively 48 elements (i.e., the number of individual females of each cleptoparasite species), where the number of elements within a single row stays the same as in the original, empirical matrices. Next, we computed the number of matrices (B) with the same number of elements and again with the same number of elements within a single row as in the original matrix, where the number of diagonal elements is the same or higher than in the original matrices. The quotient B/A then represents a probability of obtaining the same or better (from the point of individual specializations) distribution of females among particular host species during the first and the second entry by chance. We compare B/A to the significance level 0.05.

Results

Host spectrum of *S. ephippius* and *S. monilicornis*

Previous authors reported ten host species in *S. ephippius* and seven in *S. monilicornis*. During the current research, seven new hosts of *S. ephippius* and seven of *S. monilicornis* were found. The total amount of recently known host species over the whole cleptoparasite ranges is thus 17 in *S. ephippius* and 14 in *S. monilicornis* (Table 1). Both species parasitize in the nests of both solitary and eusocial bee species; eight (of 14) of the hosts of *S. monilicornis* and nine (of 17) of *S. ephippius* are eusocial.

Behavior of cleptoparasites related to parasitization

Behavior of *Sphecodes* females and their interactions with host females were divided into eight behavioral categories. This ethogram presents the first summarization of *Sphecodes* bees' behavior during parasitization:

1. Search flight is the most frequently observed behavioral pattern of cleptoparasitic females before finding the host nests site. A female flies slowly, low over the ground, she sometimes returns back above the same place after few seconds. *Sphecodes* species somewhat differ from other cleptoparasitic bees (P. Bogusch, personal observation): they apparently use their search flight only to find the nest sites, then they land and find the specific location of the host's nest while walking.
2. Entry into the nest during the absence of host female. *Sphecodes* female does not meet the host female during its visit of the nest.
3. Entry into the nest with the presence of the host female. Host's presence does not prevent the cleptoparasite's entry. In this case, the host returns to the nest during the

Table 2 Behavior observed in (a) *S. ephippius* (Linnaeus, 1767) and (b) *S. monilicornis* (Kirby, 1802) females in the field

Host species	Observed behavioral patterns						
	1	2	3	4	5	6	7
(a) *Sphecodes ephippius*							
Andrena flavipes Panzer, 1798	+	+	+	−	+	+	−
Andrena minutula (Kirby, 1802)	+	+	−	−	−	−	−
Andrena wilkella (Kirby, 1802)	+	+	+	−	+	+	−
Halictus maculatus Smith, 1848	+	+	−	−	−	−	−
Halictus rubicundus (Christ, 1791)	+	+	+	−	+	−	−
Halictus tumulorum (Linnaeus, 1758)	+	+	+	−	−	+	+
Lasioglossum laticeps (Schenck, 1870)	+	+	+	−	+	+	+
Lasioglossum malachurum (Kirby, 1802)	+	−	+	+	−	−	−
Lasioglossum pauxillum (Schenck, 1853)	+	+	+	+	−	+	+
(b) *Sphecodes monilicornis*							
Andrena flavipes Panzer, 1798	+	+	+	−	+	−	−
Halictus maculatus Smith, 1848	+	−	+	−	−	−	+
Halictus rubicundus (Christ, 1791)	+	+	+	+	+	+	−
Halictus tumulorum (Linnaeus, 1758)	+	+	+	−	−	−	−
Lasioglossum calceatum (Scopoli, 1763)	+	−	+	−	−	−	−
Lasioglossum laticeps (Schenck, 1870)	+	+	+	+	−	−	+
Lasioglossum leucozonium (Kirby, 1802)	+	+	−	−	−	−	−
Lasioglossum malachurum (Kirby, 1802)	+	+	+	−	−	−	−
Lasioglossum pauxillum (Schenck, 1853)	+	+	+	+	−	−	−
Lasioglossum villosulum (Kirby, 1802)	+	−	+	−	−	−	−

1 Search flight, *2* entry into the nest during absence of host female, *3* entry into the nest with the presence of the host female, *4* entry into the host's nest *together* with the host female, *5* waiting near a nest for the host female to leave, *6* host defensive behavior at the nest, *7* fighting with stings

cleptoparasite's visit. During the contact, neither of the females fights, nor exhibits any marked conflicts.

4. Entry into the host's nest *together* with the host female. Host and cleptoparasite come together to the nest, and enter the nest side by side without any aggressive encounter. This seemingly weird situation, firstly described by Bogusch (2005) in *Epeoloides coecutiens*, occurs in *Sphecodes* bees in small proportion of all host–parasite interactions.

5. Waiting near a nest for the host female to leave. Cuckoo bee waits next to the occupied nest to the host's departure and then she attacks the nests after the host's left.

6. Host defensive behavior at the nest. Defense such as blocking the nest entrance, chasing the cleptoparasite away or pushing it out of the nest, but without any direct fight.

7. Fighting with stings. Both females fight on the ground. Fights are very fierce and the cleptoparasite's or host female's death is not uncommon.

All observed behavioral patterns concerning each host species are presented in Table 2.

Specialization of individual females

Table 3 presents data on the parasitization of individual *S. monilicornis* and *S. ephippius* female in individual host's nests. Even the first look at the table shows a nonequal distribution of values; the data mainly copy the diagonal representing the cases where cleptoparasitic female consecutively visited two nests of the same host species. The data around the diagonal represent only a small fraction of the observed amount of visits, which proves that each female tends to lay eggs into nests of only one host species. The combinatorial test supports the fact that such results could hardly be obtained by chance. Matrices preserving the number of elements within a single row as in the original matrix, where number of diagonal elements is the same or higher than in the original matrices, are among less than 0.000001 of all matrices with 52, respectively 48 elements, where the number of elements within a single row stays the same as in the original, empirical matrices. As parasitic females usually passed around the nests of several bee species from conspecific host spectra between the first and the second focal visits, the observation of individual specialization cannot be explained by single-species aggregations of nests within the nest sites and successive entries into the two closest nests.

Discussion

The "red queen" hypothesis predicts that under continual evolution of host defense strategies parasites should tend to specialize to a single host species (Timms and Read 1999, but see Stireman 2005). Although our current knowledge of the host spectra diversity in most cuckoo bees is scarce, it is evident that many cleptoparasitic bees are indeed

Table 3 Table of the parasitions of (a) *S. ephippius* (Linnaeus, 1767) and (b) *S. monilicornis* (Kirby, 1802) females in hosts' nests

(a) *Sphecodes ephippius*

Host	Afl	Htum	Hrub	Hmac	Llat	Lpau	Total	N>	N
Afl	6	0	0	0	0	0	6	1	462
Htum	0	8	0	0	0	0	8	1	1287
Hrub	0	0	3	0	0	0	3	1	56
Hmac	0	0	0	1	0	0	1	1	6
Llat	0	1	0	0	6	0	7	6	792
Lpau	0	2	0	0	0	25	27	21	201,376
Total	6	11	3	1	6	25	52	126	3.18634E+16

(b) *Sphecodes monilicornis*

Host	Afl	Htum	Hrub	Lcal	Llat	Lpau	Total	N>	N
Afl	7	1	0	0	0	0	8	6	1287
Htum	0	0	0	0	0	0	0	1	1
Hrub	0	0	19	0	0	0	19	1	42504
Lcal	0	0	0	10	1	0	11	6	4368
Llat	0	0	1	0	6	0	7	6	792
Lpau	0	0	0	0	1	2	3	6	56
Total	7	1	20	10	8	2	48	1296	1.05975E+16

Rows represent the first visit and columns the second visit of each individual female

Afl Andrena flavipes, *Hmac Halictus maculatus*, *Hrub Halictus rubicundus*, *Htum Halictus tumulorum*, *Lcal Lasioglossum calceatum*, *Llat Lasioglossum laticeps*, *Lpau Lasioglossum pauxillum*, *N>* the number of cases with the same number of elements within a single row as in the empirical data, where the number of diagonal elements is the same or higher than in the original row, *N* number of cases where the number of elements within a row stays the same as in the original, empirical data

single-species specialists. Some other species have rather restricted range of hosts, often 2–5 species, which are usually closely related, and thus very similar in appearance, behavior, and ecology (Westrich 1989; Bogusch 2003a). In these species, we can imagine that such host spectra evolved by the recent division of the host of a specialized cleptoparasite into several species. Thanks to the recent host speciation, the cleptoparasite has not kept up to speciate yet. Moreover, it may perceive similar hosts as members of the same species, and due to lag of diversification of specific defense mechanisms, it may still be able to attack them successfully. Alternatively, after closer examination, these species of cleptoparasites may occur to encompass several cryptic species of specialists. Conclusively, we could not strictly consider these cuckoo bees generalists. Nevertheless, some species of cuckoo bees are clearly generalist with wide host spectra encompassing host species from several genera. In the light of the red queen hypothesis, the long-lasting existence of generalist species is rather surprising. Therefore, we started to study the ecology of two species of *Sphecodes* bees, which were previously labeled as generalist (Westrich 1989; Bogusch 2003a).

According to our results, both studied cuckoo bee species have more than ten host species throughout their range. More importantly, we confirmed that both species are generalist even at the local scale, i.e., they have five host species from three genera within the same, single locality (cf. Blüthgen 1923, 1934). Our behavioral observations revealed that the clue to the wide host spectra of two *Sphecodes* bees is the individual specialization of cleptoparasitic females. Although we did not estimate the relative abundance of each host species within our locality (it would be very difficult due to the mass accumulation of the host nests and the necessity of host catching or nest digging for species identification), the distribution of parasitization between *Sphecodes* species at the same place and within the same period shows the nonrandom choice of host nests (Table 3). For example, most *S. ephippius* females chose nests of *Lasioglossum pauxillum*, rarely used by *S. monilicornis*. On the other hand, *S. monilicornis* females preferred nests of *Halictus rubicundus* and *Lasioglossum calceatum*, the latter host species is even missing in the host list of *S. ephippius* (Table 1). The possibility of free choice of host species is further indicated by the diversity and distribution of preferred host nest within a single parasite species. In spite of the wide supply, during their second visit, most females were faithful to the species of the host of the first visit. The repeated choice of the same host species cannot be explained by the choice of the nearest neighboring nest within a nest site (cf. to foraging dynamics of bumblebee, e.g., Chittka et al. (1997). First, nests of several host species are scattered over the same sites, and they do not form single-species clusters. Moreover, during our tests, many cuckoo bees visited two or more nest sites (5–30 m away) to find the second nest of the same host species, even though the nearest nest was accessible no further than 3 cm from the nest they just parasitized.

Using only two consecutive host choices, we cannot unequivocally reject the possibility that cleptoparasitic bees specialize only for a short temporal segment. To test this possibility, it will be necessary to make observations of longer series of choices (due to technical demandingness, we were not able to make longer series during our present research). On the other hand, even the short-term specialization of cleptoparasitic bees (seemingly parallel to well-known and highly studied flower constancy of polylectic bees, where there is a run of choices of one plant species, then a run of choices of another plant species; Chittka et al. (1999) has never been recorded and it would be an interesting phenomenon deserving further study. However, there are reasons to expect the important differences between generalist pollinators and parasites that support the suggestion that the individual specialization of cleptoparasites should be long lasting. Most importantly, parasite's hosts are under strong selection to constantly evolve antiparasitic strategies, and a parasite then has to overcome the always-changing antistrategies of its hosts. As different hosts are likely to evolve different strategies and a parasite is not able to keep up with all of them, during the evolutionary time, it is expected to specialize. And indeed, there is a huge evidence that parasitic way of life often leads to specialization, which is also true in bees—many of cuckoo bee species are truly specialist, see Packer et al. (1995) or Bogusch (2005). In fact, real generalist cuckoo bees are an exception, not a rule. When an individual of generalist parasitic bee goes through the specific antistrategy of one host species, it is likely to overcome defense of other individuals of the same host species, but very likely not the defenses of another host species with different antistrategies. It is quite difficult to imagine, how the short-term specialization could help the cleptoparasite to overcome host defenses—due to potentially species-specific antistrategies, every switch from one host species to another is connected with different way of breaking through the host's defense and should be therefore costly. Furthermore, each host species is under selection to evolve specific antistrategy to prevent the switch of generalist parasite from another host species to itself. Therefore, we suggest that the individuals of a parasitic species be selected to minimize the number of host switches. Conversely, particular plant species with a generalist pollinator are not under selection pressure to evolve species-specific strategies to repel a pollinator; contrariwise, they are selected to attract it. Flower switching should be therefore relatively much cheaper. Moreover, polylectid pollinators can easily switch the flower species according to, e.g., actual nectar supply—they get information on profitability of the flowers immediately during its visit (Chittka et al. 1999). On the other hand, cleptoparasitic bees "acquire" essential information on the given host profitability post hoc, i.e., through the ratio of offsprings from nests of the individual host species surviving to the next generation. We can therefore assume that—due to differences in time lag of information acquisition—the switch between host species is not as flexible as the switch between plant species.

We concluded that the repeated choice of a given host probably reflects the selection pressure on cleptoparasitic female to specialize. The present study is the first documentation of the specialization at an individual level within generalist species of European cuckoo bees. Our behavioral observations were not designed to determine the evolutionary advantages of individual specialization and the potential differences among groups of females attacking single host species, which should be done during future research. We can now only speculate, which traits could serve as the adaptation to a particular host. Our catalogue of types of interactions between hosts and cuckoo bees (Table 2) shows that cleptoparasites can use different behavioral strategies to go through the host defense with minimal costs (e.g., they can visit only empty nests; they can wait by the occupied nest for host leaving; they can be "invisible" for a host, which leads to direct host–parasite interactions without any agonistic interaction...). On the other hand, other interactions lead to host defensive behavior or even aggressive encounters that are usually very costly and dangerous. Why are some parasites recognized by hosts as enemies, while others are tolerated? Do the tolerated and nontolerated parasites differ in a certain adaptation to a particular host species? An example of such an adaptation could be the scent camouflage to a particular host observed in *Nomada* bees, specialists to one single host species, where extremely similar chemical compounds were found in Dufour gland secretion of host females and in the cephalic secretions of male *Nomada* bees in five host–parasite species pairs (Tengö and Bergström 1977). It seems that *Nomada* females could search appropriate males as well as an appropriate host nest using the same scent signal. Moreover, *Nomada* females are presumably perfumed by the secretion of male cephalic gland during copulation, which leads to odor mimetism preventing aggressiveness between parasite and host females during encounters in or outside the nest (Tengö and Bergström 1977). Tengö et al. (1992) studied compounds of the Dufour's gland secretion of several European *Sphecodes* species, but no scent similarities to their hosts were found. Our results show that such analysis in generalist *Sphecodes* species needs to be done at an intraspecific level with the knowledge of the specialization of an individual cleptoparasitic female. The scent differences between cleptoparasite females could potentially explain the outcomes of the contact between cleptoparasite and host females near the nests (Table 2). It would be interesting to explore, whether aggressiveness occurs in cases of host confusion by a female specialized to another host species.

The process of individual host "races" specialization could be accelerated by phenotypic response of a cuckoo bee larva to the host identity. As the brood cell size (and potentially also content of nutrients) differs between variously sized host species (Michener 2000), cuckoo bees emerging from nests of different species could be variously large. This notion is mirrored by the evidence of larger variation in body size in generalist cleptoparasites compared to specialist, the phenomenon first mentioned by Michener (1978). Packer et al. (1995) compared the body size of individuals of two *Coelioxys* species parasitizing two *Megachile* Latreille, 1802 species in North America. Individuals parasitizing *Megachile inermis* Provancher, 1888 were smaller and different in several morphological characters from those using *Megachile relativa* Cresson, 1878, supporting the individual specialization in the North American cuckoo bees, and probable phenotypic differences evoked by the host identity.

The pivotal moment for repeated nonrandom choices of particular host nests is the way cleptoparasites find the nests. *Sphecodes* female presumably finds sites with aggregation of hosts' nest during the search flight, but the choice of component host nest is underway only after landing. *Sphecodes* females have never been recorded shadowing their hosts to nests, which was observed, e.g., in *Biastes emarginatus* (Schenck, 1853), *Epeoloides coecutiens* (Fabricius, 1775), and several species of *Coelioxys* (Bogusch 2003b; Bogusch 2005; Bogusch—personal observation). Shadowing is apparently an effective strategy for finding dispersed nest in species whose hosts use to nest solitarily, while the nest selection during walking could be the best strategy for the determination of an appropriate nest in aggregations.

As *S. ephippius* and *S. monilicornis* parasitize also in eusocial bees, they could potentially arise as social parasites. Social parasites have evolved from social bees and parasitize in their hives, e.g., cuckoo bumblebees. The female of social parasite usually substitutes the eusocial queen. Alternatively, both host's queen and cleptoparasite's female stay in the nest and reproduce there (Michener 2000). *Sphecodes* females usually parasitize in nests of their eusocial hosts in April and May, i.e., before the first host workers emerge and start to guard the nest entrance (Sick et al. 1994). In this case, they can be labeled as cleptoparasites, not social parasites. However, the parazitation of *Sphecodes* in more developed colonies of eusocial bees was also observed. It is thus still open, whether the *Sphecodes* cleptoparasites of eusocial bees have evolved from parasites of the solitary forms and switched from primary solitary host to social *Halictus* and *Lasioglossum* or vice versa (Rozen 2000; Bogusch 2003a). The reconstruction of the origin of parasitization and the genesis of wide host spectra in *Sphecodes* bees will not be possible till the phylogeny of this genus and its relatives is resolved (nonetheless, for caveats of phylogenetic reconstruction of the host ranges see Stireman 2005).

Specialization of individual parasites to a single host can result in a tendency to form ecologically diversified and genetically isolated entities (e.g., in tick *Ixodes uriae* White, 1852 McCoy et al. 2001), respectively, in an evolution of host-specific races (gens) with special inheritance of complex of adaptations to a single host within a single panmictic population as in the case of European common cuckoo. The need of mapping behavioral, morphological, ecological, genetical, and physiological (e.g., scent) adaptation of particular single-host group in cuckoo bees in detail, as well as the success rate estimation of parasitization of an individual cleptoparasite on it vs other

host species, is evident. The following research should also reveal the mechanisms of individual specialization. They might be genetic, by imprinting (e.g., as larvae on host scent), or by flexible learning as adults. To know which of these potential proximate mechanisms is really involved will allow us to better judge the flexibility of generalist cleptoparasites and the evolutionary dynamics of bee communities. We hope that our work will stimulate further research of the fascinating system of cuckoo bees' generalists and their hosts.

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