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Aggressive mimicry among nest cleptoparasites and social parasites (Insecta: Hymenoptera: Apoidea)

Agresivní mimikry u kleptoparazitických blanokřídlých a sociálních parazitů (Insecta: Hymenoptera: Apoidea)

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Na tomto místě bych chtěl poděkovat všem, kteří mi pomohli při mém výzkumu a podíleli se na vzniku publikací a této práce. Především bych rád poděkoval svému školiteli Prof. RNDr. Stanislavu Komárkovi, Dr. za stálou oporu a ochotu pomoci v jakékoliv situaci a ve všech ohledech, od odborných konzultací až po přátelské popovídání. Dále patří můj dík všem kolegům z katedry, v jejichž příjemné společnosti se mi dobře pracovalo, a z nichž zejména Doc. RNDr. Anton Markoš, CSc. a Mgr. Karel Kleisner mi v mnoha ohledech poskytli morální i odbornou pomoc a mají velké zásluhy na úspěšném průběhu mého doktorského studia.

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ÚVOD

Tato doktorská práce se skládá ze dvou částí. První z nich je napsaná v angličtině a je rozdělená do čtyř kapitol. Představuje review shrnující současné publikované informace a další autorovy poznatky pojednávající o významu zbarvení u kukaččích (kleptoparazitických) včel, sociálních parazitů čmeláků a vos, a dalších parazitů a parazitoidů taxonomicky řazených do skupiny blanokřídlého hmyzu (Hymenoptera) označované jako "Aculeata". Do této skupiny jsou řazeny podle současně platného systému tyto nadčeledi: hbitěnky (Bethyloidea), zlatěnky (Chrysidoidea), vosy (Vespoidea) a včely (Apoidea). I když se nejedná o systematickou jednotku, ale pouze o sběrnou skupinu, Aculeata je považována za monofyletickou a hlavním společným znakem všech druhů je přeměna samičího kladélka v žihadlo. V této publikaci nejsou uvedeny podrobně poznatky o predátorech, parazitech a komenzálech mravenců (Formicidae), stejně jako o všech formách mimetismu s mravenci souvisejících. Hlavním důvodem této absence je velké množství informací o těchto skupinách, které by samy o sobě stačily na několik podobných review. Mravenci jsou zde proto používáni jen v některých případech jako srovnávací příklady mimetických interakcí.

První kapitola se zabývá agresivním mimetismem, který je velmi nesourodým typem mimese. Tento typ mimetismu nebyl nikdy řádně definován, je zde proto uvedena nová definice a všechny příklady mimetických komplexů shrnované pod tento typ v minulosti jsou rozděleny do čtyř typů dalších. Tyto nové typy mimetismu jsou zde podrobně popsány a odlišeny a Tabulka 1 může být použita jako "určovací klíč" k jednotlivým typům. U popisu každého nově etablovaného typu mimetismu jsou uvedeny příklady z říše živočichů i rostlin.

Druhá kapitola shrnuje vše známé o kukaččích (kleptoparazitických) včelách, jejich specializaci, chování, interakcích s hostiteli, zbarvení a mimetismu. Většina zde zmiňovaných informací byla poprvé publikována autorem dizertace v podobě některých článků (tvořících druhou část), byly doplněny další dosud nepublikované informace. Podobnosti a zvláštnosti ve zbarvení a vzhledu jsou ilustrovány na fotografiích. Všechny fotografie jsou autorovy originály a zobrazují materiál hmyzu z jeho vlastní sbírky, pouze ve třetí kapitole na obrázku ***Figure 11*** jsou zobrazeny pestřenky se sbírek Národního muzea v Praze (kurátor RNDr. Jan Ježek). Ostatními obrázky jsou grafy srovnávající kleptoparazitické včely a jejich specializaci, zbarvení apod. Většina kvantitativních dat byla vyhodnocena na materiálu evropských druhů včel a v některých případech srovnána se včelami z ostatních částí světa. Kapitola je rozdělena do tří podkapitol, každá z nich se zabývá určitým problémem souvisejícím s mimetismem.

Kapitoly 3 a 4 jsou podobné druhé, zaměřují se na sociální parazity, respektive parazitoidy a ostatní kleptoparazitické blanokřídlé. Jejich struktura je velmi podobná struktuře druhé kapitoly. Třetí kapitola se zabývá parazity čmeláků a vos, tj. pačmeláky a pestřenkami rodu *Volucella*, které parazitují v hnízdech vos a čmeláků (v druhém případě podobně jako pačmeláci), a vykazují mimetické interakce orientované směrem ke svým hostitelům. Čtvrtá kapitola popisuje životní strategie parazitoidů a ostatních kleptoparazitických blanokřídlých v rámci zde studované skupiny, srovnává je s kukaččími včelami a snaží se najít shody a rozdíly ve zbarvení a vzhledu. V této kapitole jsou popsány tři základní Müllerovské mimetické okruhy blanokřídlých včetně jejich Batesovských prvků z řad jiných zástupců hmyzu. Jsou zde uvedeny i další typy zbarvení běžné u žahadlových blanokřídlých. Bohužel, bylo publikováno minimální množství informací o mimetismu a hostitelích těchto živočichů, a tak zde autor srovnal jen zbarvení a nabídl několik hypotéz o jeho funkci při parazitaci v hnízdech hostitelů.

Kromě čtyř zmíněných kapitol obsahuje první část práce ještě krátký závěr ve formě shrnutí (Conclusions). Samostatná diskuse není přiložena, neboť výsledky jsou diskutované již v rámci jednotlivých kapitol. Součástí review je samozřejmě ještě nezbytný seznam použité (nikoliv doporučené) literatury (References) a český Souhrn, který obsahově odpovídá Conclusions.

Druhá část studie je složená ze čtyř článků publikovaných autorem během let 2003 – 2006. Tyto články byly publikovány z výsledků výzkumů provedených během magisterského a doktorského studia.

První z článků (Příloha 1) byl publikován v časopisu *Vesmír* a je napsán v češtině. Jedná se o vůbec první (ale ne první napsaný) článek autora. Shrnuje v té době známé informace o evropských kleptoparazitických včelách, jejich biologii, specializaci a zbarvení. Jeho hodnota spočívá zejména v tom, že obsahuje řadu dosud nepublikovaných informací, a mnoho z nich je podruhé použito právě v textu první části této doktorské práce. Článek také obsahuje první nezávaznou zmínku o pozorování individuální specializace samic generalistů, podrobně zpracované ve čtvrtém článku (Příloha 4).

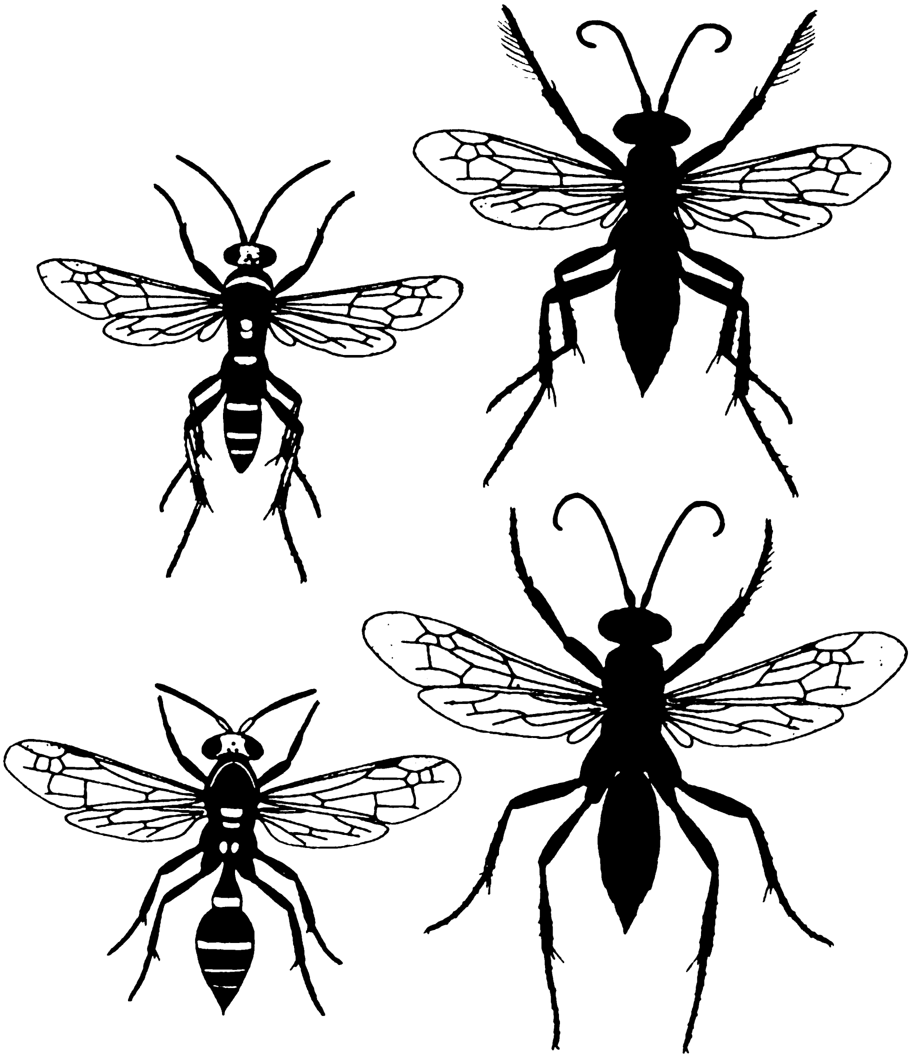
Druhý z článků (Příloha 2) popisuje několik v té době nově zjištěných informací o biologii, hostitelích, fenologii, a rozšíření šesti druhů evropských kukaččích včel. Jedná se o výstup z grantu FRVŠ 1784/2001, publikovaný v *Acta Societatis Zoologiceae Bohemiae*.

Třetí článek (Příloha 3), publikovaný v *Journal of the Kansas Entomological Society*, podrobně popisuje do té doby neznámou biologii (typy lokalit, fenologii, hostitele, navštěvované rostliny, chování) velice zajímavé kleptoparazitické včely *Epeoloides coecutiens*. Tento druh byl dříve považován za nejvzácnější středoevropskou včelu, autor (s pomocí několika dalších evropských odborníků) zjistil, že se jedná o druh se zvláštními nároky na prostředí, a podrobně zmapoval biologii druhu. Studie také srovnává lidské vidění barev se včelím pomocí hexagonálních (nebo lépe řečeno kubických) trichromatických diagramů. Srovnání vidění barev květů bylo vytvořeno za použití metod a naměřených hodnot excitací očních čípků, které vytvořil a poskytl Dr. Lars Chittka, University of London. Publikované údaje ukazují, že nelze srovnávat nároky včel jen na základě lidského vidění barev.

Poslední publikace (Příloha 4) z *Behavioral Ecology and Sociobiology* přináší některé odpovědi na otázky specializace jednotlivých samic generalistů (druhů s více hostiteli) u kukaččích včel a srovnává je s ostatními živočichy s podobnými životními strategiemi a zabývá se evolucí kleptoparazitizmu. Výsledky jasně ukazují, že generalisti existují pouze v případě druhů a ne jedinců, a je pravděpodobné, že kukaččí včely jsou svou specializací na hostitele opravdu hodně podobné kukačkám

– ptákům. Tato publikace byla vytvořena společně s RNDr. Lukášem Kratochvílem a Jakubem Strakou (oba Přírodovědecká fakulta UK, Praha); souhlasy obou autorů s publikováním jejich výsledků jsou uvedeny na začátku práce.

AGGRESSIVE MIMICRY AMONG NEST CLEPTOPARASITES AND SOCIAL PARASITES (INSECTA: HYMENOPTERA: APOIDEA)



Pompilid wasp *Austrochares gastricus*. Male (A) is a Batesian mimic of workers of the social wasp *Polybia parvula* (C); female (B) part of red Müllerian mimetic ring, which includes other pompilid wasp *Dicranoplius satanus*. Adopted from O'Neill (2001).

1. AGGRESSIVE MIMICRY

In general, mimicry is well defined as the resemblance between two or more organisms, which is not caused by their phylogenetical relation or by the convergence[1]. The main cause of the existence of mimetic resemblances is the selection – pressure by predators (Komárek 2003)[2]. Three organisms must take part in every mimetic interaction: the model, which is imitated by a mimic, and the acceptor (receptor) of the signal. For better understanding, we can exemplify this phenomenon using a yellow and black striped hover-fly (mimic), which looks like some species of yellow jackets or wasps (model), and a small songbird (acceptor), which is afraid of it due to its resemblance to the model (wasp). In this case the model is a dangerous animal usually not consumed by small songbirds. Both the mimic and the model form a pair named the mimetic complex. However, classical authors establishing this terminology did not include the acceptor as the third and very important part of the mimetic complex (Wallace 1867; Poulton 1890). In the further text the necessity of knowing the acceptor will be evident; we cannot compare aggressive mimicry with related mimetic types if we do not know the acceptor.

E. B. Poulton established the term "aggressive mimicry" in 1890 as an evolutionary interpretation of the phenotype of newly discovered ant-like spiders of genera *Synageles* and *Synemosyna*. E. G. Peckham published their possible mimetic interactions of *Synageles* to ants in 1889. Consequently, Poulton (1890) named the aggressive mimetic interactions "Peckhamian mimicry". Recently, both terms are understood as synonyms (Wickler 1968; Komárek 2003). Owing to that, aggressive (or Peckhamian) mimicry has never been strictly defined, various authors used to label the majority of mimetic resemblances where the predator plays an important role and/or mimics anything by this term. Even higher level of disorder was caused by the term "Wasmannian mimicry", established according to Wasmann's (1925) studies on myrmecophilous insects and invertebrates, where the author found

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[1] Convergence differs from mimicry usually in geographical or ecological detachment between similar organisms (Tasmanian wolf cannot resemble European wolf because they have never met…).

[2] The term "mimicry" was first used by Kirby & Spence (1817) for the resemblance of insects to plants, further it was generalized to all resemblances between unrelated organisms.

examples of aggressive mimicry, but correctly stated that many of these animals were neither strictly predators nor parasites of ants, at least half of them were only commensals in ant hills. Wickler (1968) and Rettenmeyer (1970) suggested putting this term as a special example of aggressive mimicry. Most of all described mimetic complexes (not only those classified to aggressive mimicry) can be put under optical mimicry where colouration, colour pattern, or body shapes are involved. During last thirty years, more and more examples of chemical (imitation of sex pheromones and semiochemicals used in insect communication) and tactile mimicry (vibratory, mechanical or sound signals) has been discovered and described as mimetic signals. It changes our view especially of aggressive mimetic resemblances, where only a few cases are optical mimicry of general appearance or colouration and most bear with chemical or tactile communication signals.

My aim is to divide all cases of mimetic resemblances usually assigned by the term "aggressive mimicry" to four subcategories. I think it is necessary because these mimetic types have different evolutionary origins and, on the top of that, some of them differ from the others in general. I decided to create new terms according to the role of the mimic in the complex. The anticrypsis is not a mimetic interaction, but some mimetic types can be confused with it, and in some cases it appears together with some mimetic types previously classified as the aggressive mimicry.

Aggressive mimicry has the same meaning as the term **Peckhamian mimicry.** This mimetic type is typical with the fact that the prey (when the predator is the mimic) or the host (when the parasite or parasitoid is the mimic) is identical to the acceptor. The mimetic complex has then only two members – the mimic (predator) and the model, which is of the same species as the acceptor (prey). The predator usually imitates some type of its prey's communication signal or a part of its appearance, and profits from that. Typical example is the bolas spider (see Eberhard 1977; Yeargan 1994): this aranaeid preys on males of several species of moths. The predator sits on a fibre and elicits analogons of sexual pheromones of its prey from glands on the abdomen. Males of moths are allured and spider catches them with its bola – a short fibre with an adhesive ball in the end (see ***Figure 1***). Similar chemical aggressive mimetic signals are used by many species of myrmecophiles (Holldöbler

& Wilson 1995) to prey on ant larvae in their own nests. Another typical example of aggressive mimicry is the imitation of light signals of small American fireflies of the genus *Photinus* by bigger carnivorous fireflies of the genus *Photuris* (Lloyd 1965, 1975, 1990). Vertebrates also use aggressive mimicry; the best known one is the European common cuckoo (*Cuculus canorus*), which parasites in nests of songbirds and imitates the colouration of their eggs (Latter 1903; Harrison 1968). Some other parasitic birds (Viduinae parasitizing in astrilds' nests) use vocal mimicry, which helps them to invade nests of their hosts with less problems (Nicolai 1974; 1975).

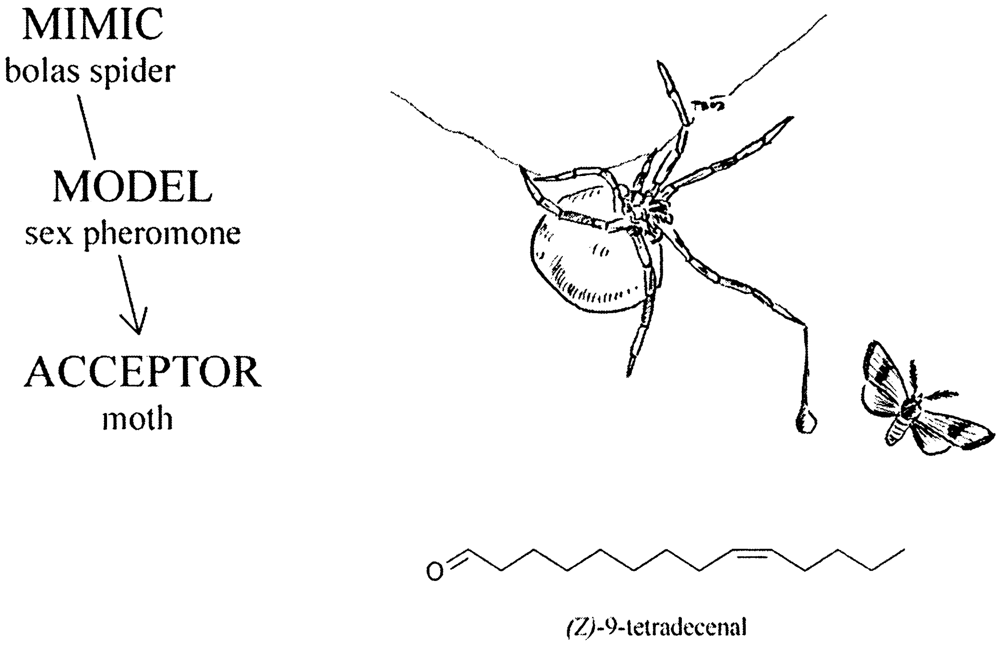

Figure 1: Model of aggressive mimicry shown on the bolas spider. (Orig.).

Inverse (defensive) mimicry represents the other type of mimetic interaction with only two members. This type differs from the aggressive mimicry in the role of the predator (parasite): it does not mimic anything, but is conversely mimicked by its prey or host. For example, several species of long-horned beetles (Cerambycidae)[3] look very similarly to parasitic ichneumonid wasps. We can find them jerky running on the surface of tree branches. This behaviour uses to be interpreted as an imitation of ichneumonids – their parasitoids, which should repel other long-horned beetles from laying their eggs to an "occupied" branch – ichneumonids' larvae feed in tree

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[3] In central Europe species of genus *Necydalis*.

branches (Chemsak & Linsley 1973). Another potential case of this type of mimicry is the similarity of some tephritid flies to jumping spiders (Salticidae), their probable predators (see Eisner 1985). This type of mimicry may look strange, but it could be quite widespread, especially among parasitoids and their hosts. However, chemical signals in these animals are usually not well known, though they probably represent the main part of inverse mimetic interactions.

Aggressive resemblance is in general similar to aggressive mimicry. Here the model is not identical with the prey: the predator is the mimic, and mimics something helpful or incidental for its prey. Marine fish *Aspidontus taeniatus* represents a very good example: this about 10 cm long fish looks very similar to *Labroides dimidiatus*, labroid cleaner of bigger marine fishes. It is not similar only in appearance and colouration, but also mimics typical cleaner's dancing movement, used when coming to a big fish to clean it. When *Aspidontus* comes to the big fish (in the same way as the cleaner model), it does not clean it, but snaps off a part of its fin and swims away. Here we see a typical mimetic complex with three members: *Aspidontus taeniatus* is the mimic and the predator, *Labroides dimidiatus* the model, and the big fish is the acceptor of the signal and prey of *Aspidontus* (for further information see Wickler 1968, or Kuwamura 1983). Another similar types of this mimetic interaction can be found among other fish species, as well as insects and spiders, e.g. a few spider species mimic tactile movements of captured prey in webs of other spiders and capture them (Jackson & Wilcox 1998). This type of mimetic resemblance was at most used as a "typical example of aggressive mimicry", together with the correct type.

Alluring mimicry has similar features to the aggressive resemblance, but there is the main difference in the role of the predator: it allures its prey to something attractive for it, usually to imitations of its prey. The model is usually not as well determined as the previous type (to genus or species) but represents some kind of prey like worm, insect, small fish, flower, etc. The predator does not hide but allures its prey. Typical cases are tropical mantids of genera *Gongylus* and *Idolum* resembling flowers with their front legs and thoraces, and alluring small flies and moths (Sharp 1899; Williams 1904). We can find a very similar example also in plants, orchids of genera *Dactylorhiza* and *Ophrys*: some species resemble smell of flowers attractive for insects, but do not have any nectar. Otherwise, many orchids (majority of *Ophrys* species) use the aggressive mimicry, imitate sexual pheromones of bees and wasps and resemble their females. Both strategies are very useful in pollination; males of bees and wasps are attracted and take pollen to other flowers of the same species (Wickler 1968). Alluring mimicry is well distributed among marine fishes (especially family Antennariidae), snakes (pit vipers), we know also very interesting cases of alluring mimicry in fluke worms (Trematoda) (Wickler 1968) and freshwater bivalves (Haag et al. 1995; 1999).

Table 1: Comparison of the main types of aggressive mimetic interactions.

	anticrypsis	aggressive mimicry	inverse mimicry	aggressive resemblance	alluring mimicry	hiding mimicry
resemblance	no	yes	yes	yes	yes	yes
number of members	-	2	2	3	3	3
mimic	-	predator	prey	predator	predator	predator
well determined model	-	usually yes	yes	usually yes	usually no	yes
predator's behaviour	hiding	several	-	hiding	alluring	hiding

The term **anticrypsis** is used within crypsis in the same way as the aggressive mimicry within all mimetic types: usual definition charges that the predator is according to its cryptic colouration invisible to its prey and can capture it easier. I do not think that this phenomenon can be confused with the aggressive mimicry, but several known aggressive and alluring mimics usually use both. Common European thomisid spider *Misumena vatia* uses the anticrypsis to catch its prey very often; it sits in a flower and changes its colour to the same as the colour of the flower. It was first described already by Dunning (1878). In some cases, this spider was observed to sit on the top of some high, but not flowering plant. The spider resembled a flower and was successful capturing a small moth (Safír 1978). Similar combinations of anticrypsis and aggressive (or alluring) mimicry are common also in mantids (Sharp 1899), and alluring marine fishes (Wickler 1968).

One more interesting behaviour of predators was described among coral fishes, and also in birds of prey. Several species of quite big carnivorous fishes mimic in their juvenile age common coral fishes swimming in huge schools above coral reefs. The predator swims aside from or inside the school. These aggressive mimics hunt their prey in two ways: first, some of them make quick attacks to other fishes swimming around; and second, predator fishes swim in swarms of small fishes searching for food in the ground, these aggressive mimics capture other fishes and invertebrates flushed out of the ground by the models (Ormond 1980). This behaviour stays somewhere between the aggressive resemblance and anticrypsis: it depends on how we explain the school of small fishes. The predator is invisible and uses the anticrypsis (if we explain it as a part of the environment), but it mimics other species of fish and uses the aggressive resemblance (if we explain it as many small fishes of one species in one place and time). We call this interaction a **hiding mimicry**. The same situation briefly disputed by Wickler (1968) and in detail previously described by Willis (1963) was observed in a zone-tailed hawk (*Buteo albonotatus*) in America. It resembles the turkey vulture (*Cathartes aura*) in a colouration, shape, and also in behaviour. The model is not dangerous for small mammals, birds, and lizards (it feeds on carrions), so they are not afraid of the mimic. In some cases the mimic was observed flying in the flock of turkey vultures.

Although this classification of aggressive mimetic resemblances was created with a focus to the behaviour of the mimic, we cannot state that we will not have problems to sort some mimetic interactions in future. The problems are mainly in myrmecomorphic spiders: we cannot decide if they are Batesian or Peckhamian mimics, especially if we do not know their bionomics in detail. We can describe this situation on the first described aggressive mimic, spider *Synageles picata*. Peckham (1889) reported that this spider probably fed on myrmecophilous beetles living aside from the anthills. It resembled ants and captured its prey easier. In that case it used aggressive resemblance. Recently most accepted theory (Holldöbler & Wilson 1995) states that these spiders are Batesian mimics and resemble ants because small birds do not prey on them. In my opinion, the spiders resemble ants, their prey, to come easier near to the anthill and capture several ants. This option is a typical case of aggressive mimicry. Otherwise, in some cases (and probably also in ant-like spiders), two types of mimicry can be combined. ***Table 1*** was compiled according to five main differentiating attributes: presence or absence of mimicry, number of members, character of the mimic (predator or not), model determination, and mimic's behaviour. These attributes should help to recognize all types of aggressive mimetic interactions; they are not similar to attributes of mimicry, as a sympatry of the mimic and the model, higher abundance of the model, etc., for detailed information see Rettenmeyer (1970). Anticrypsis is also included in the table.

2. CUCKOO BEES

Cuckoo bees form within the superfamily Apoidea strictly defined group of organisms. The group is not defined taxonomically (it includes bees of four families that do not form a monophyletic clade) but ecologically (Michener 1978). They represent about 15% of all known species of bees in the world (Batra 1984), in Europe about one quarter (Bogusch et al. 2006). ***Table 2*** presents all known groups of cuckoo bees. Their way of life comes under the term cleptoparasitism and especially European authors call them "cleptoparasitic bees". However, this term is not well chosen, because it has been first stated for prey stealing, known in many groups of animals, best known example represent frigates and jaegers, birds that steal other bird's prey in the air. Recently, term "nest parasites" or "nest cleptoparasites" looks better and more useful (O'Neill 2001). In this study these insects are usually named "cuckoo bees".

I can describe a typical life strategy of cuckoo bees. Mated female does not build its own nest, but seeks for the nest of other (usually solitary) bee species and lays its egg inside. The egg is put into the brood cell and fresh emerged larva feeds on provisions gathered by the owner of the nest (hereinafter called the host). Here is the difference to all Hymenopteran parasitoids like chalcidids (Chalcidoidea), ichneumonids (Ichneumonidae), velvet ants (Mutillidae), and scoliids (Scoliidae), see also Chapter 4. Cuckoo bee larva does not feed on host larvae, but on its provisions (Balthasar 1954; Michener 2000; O'Neill 2001). According to this specialization, cuckoo bee females lay their eggs to fresh or still unclosed brood cells with eggs or very young larvae of their hosts, not to brood cells with mature larvae as do the parasitoids (O'Neill 2001). Parasitizing cuckoo bee must destroy the host's brood. They have evolved two different strategies. First (common in *Sphecodes* bees, some *Stelis*, and *Exaerete*), female destroys host egg and lays its egg into the brood cell, second (common in some Megachilidae and Apidae), the female does not destroy anything and a young larva (usually first instar) has sharp, pincerlike mandibles, and destroys the host egg or larva itself (Michener 2000). Both strategies have advantages and disadvantages. In the first, the brood cell is "cleaned" of host brood; vicelike, the host female can recognize that its egg "disappeared". In the second,

Table 2: List of groups of cuckoo bees. Created according to Michener (2000).

Higher taxa and parasitic taxa	Hosts
Family Colletidae	
Hylaeus* sg. *Neoprosopis	***Hylaeus* sg. *Neoprosopis***
Family Halictidae	
Subfamily Halictinae	
tribe Halictini	
Echthralictus	
Eupetersia	
Halictus sg. *Paraseladonia*	
Lasioglossum* sg. *Dialictus	***Lasioglossum* sg. *Dialictus***
Paradialictus	
Microsphecodes	Halictini
Parathrincostoma	
Ptilocleptis	
Sphecodes	Halictini and others
tribe Augochlorini	
Megalopta sg. *Noctoraptor*	
Megommation sg. *Cleptommation*	
Temnosoma	
Family Megachilidae	
Subfamily Megachilinae	
tribe Osmiini	
Bekilia	
Hoplitis sg. *Bytinskia*	*Hoplitis*
tribe Megachilini	
Coelioxys	Megachilini
Radoszkowskiana	
tribe Anthidiini	
Afrostelis	
Euaspis	*Megachile*
Hoplostelis	Euglossini
Larinostelis	
Stelis	Megachilinae
Dolichostelis	*Megachile*
tribe Dioxyini	Megachilinae
Family Apidae	
Subfamily Nomadinae	many groups
Subfamily Apinae	
tribe Ctenoplectrini	
Ctenoplectrina	
tribe Rhyathymini	*Epicharis*
tribe Ericrocidini	Centridini
tribe Melectini	Anthophorini
tribe Isepeolini	*Colletes*
tribe Protepeolini	*Diadasia*
tribe Osirini	*Macropis*, *Paratetrapedia*
tribe Tetrapediini	
Coelioxoides	
tribe Euglossini	
Exaerete	*Eulaema*, *Eufriesea*
Aglae	*Eulaema*

there is a chance that host brood survives. More than one cuckoo bee egg can be laid into the brood cell and the larvae with pincerlike mandibles must compete and fight. In other words, some species can lay their eggs to nearly closed brood cells or to fresh brood cells with no host's eggs.

2.1. Specialization and phylogenetical relations

Every species of cuckoo bees has one up to several hosts. The hosts are exclusively other species of bees, both solitary and social. Number of hosts does not exceed ten in most cases; most of cuckoo bees are specialized to 1 up to 5 host species. According to Emery's (1909) rule, the parasites of ants are in most cases the nearest relatives of their hosts. This means, as stated by Carpenter et al. (1993) for paper wasps and generally for all Hymenopteran parasites, that both the host and the parasitic species arose from the clade of their ancestor – one line continued in the nonparasitic way of life, and the second became parasitic. We can illustrate it on the example of a hypothetic solitary bee: some females did not continue to build nests, but they began to lay eggs into nests of other females. It seemed to be a good strategy, but the nonparasitic females started to defence. Both nonparasitic and parasitic females had to change and – evolve antistrategies, and under different selection pressures they split into two species (Bogusch et al. 2006). We can find support for this hypothesis within quite widespread intraspecific cleptoparasitism among solitary and also social bees. In this case, we can use the term "cleptoparasitism" without any doubt, usually it looks that some females invade nests of other bees to steal the provisions (in social bees, common also in the honeybee *Apis mellifera*), or to lay their eggs into the brood cells (intraspecific cuckoo bees, in Europe common within the genus *Hoplitis*). Interspecific cleptoparasitism (and to the origin of cuckoo bees) certainly rose from intraspecific cleptoparasitism (Eickwort 1975).

Owing to Emery's rule, every species of cuckoo bees should have only one host species, its nearest relative. The diagram compiled from all known data about the hosts of European cuckoo bees shows that more than half of European cuckoo bees parasitize in nests of bees unrelated to them (related in this case means the species of the same subfamily). Only one quarter invades exclusively the nests of related hosts (***Figure 2***).

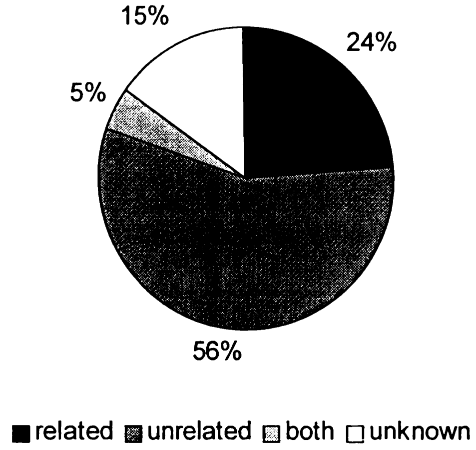

Figure 2: Phylogenetic relation of cuckoo bees to their hosts. N = 167 species.

Another diagram showing percentages of cuckoo bees according to the number of their known hosts seems more "friendly" fitting to Emery's rule (***Figure 3***). More than half of all European cuckoo bees are specialized to 1 to 2 hosts, and only 2% parasitize in the nests of more than 10 species of bees. This result is not surprising: it is much better to be specialized, because the specialist's phenology and bionomics can be tightly bounded with its host. In other words, we must know that majority of them are specialized to parasitation in nests of unrelated taxa (***Figure 2*** together with ***Figure 3***), so their recent hosts cannot be the primary ones.

As shown in the above diagrams, both cuckoo and nonparasitic bees undergo evolutionary processes and change in course of time. Description of the life strategy of cuckoo bees shows that they need to have several up to many (based on every species) adaptations how to find, invade, and lay egg to the host's nest. Every species must response to the changes of the environment, and especially to the host's abundance, which is the main value, on which the cleptoparasite's success (and survival) depends. In some cases, the original hosts could disappear or get extinct, and the cuckoo bees survived only due to finding new host species. This process is called re-orientating (Bogusch 2003; Bogusch et al. 2006) and does not only change host species, but also increases number of hosts. This way of re-orientating and "adopting" of new hosts leads to generalists and also to parasitization in nests of unrelated species, e.g. *Andrena* in *Sphecodes* cuckoo bees (see bellow).

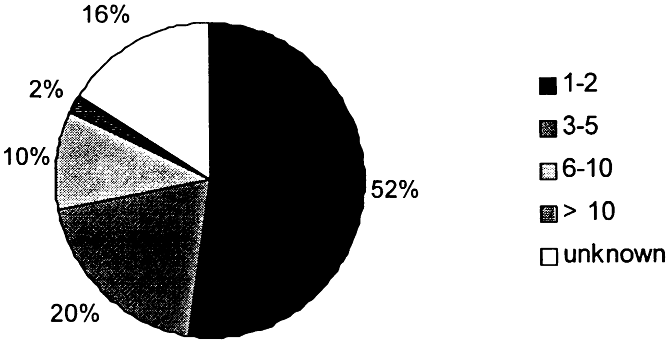

Figure 3: Numbers of hosts of European cuckoo bees. N = 167 species.

We can illustrate the re-orientating process very well on the hosts of European *Sphecodes* species. These cuckoo bees parasitize in nests of their relatives, bees of genera *Halictus* and *Lasioglossum*. Several species parasitize also in nests of other bees, which are not phylogenetically related to them, but quite abundant in the localities. ***Figure 4*** along with the next paragraph graphically illustrate the re-orientating process:

1. We know cuckoo bees with only one host, e.g. *S. rufiventris*.
2. Most of *Sphecodes* species parasitize in 2-5 hosts, and some even in more classified to the phylogenetically related genera (as mentioned above).
3. *S. ephippius*, and also *S. monilicornis*, are the most abundant and common European species of the genus and are generalists parasitizing more than ten hosts. Their hosts are mainly related, but some are unrelated to them, e.g. very common species of the genus *Andrena*.
4. Three species (*S. reticulatus*, *S. rubicundus*, and *S. pellucidus*) parasitize only in the nests of *Andrena* species, they all have 2-5 known hosts of this genus. They probably lost their original hosts, and had to find some new ones. During this way they were probably generalists as *S. ephippius* or *S.*

monilicornis, but after that they specialized. *Andrena* species that are also very similar in nesting habits to *Halictus* and *Lasioglossum* could be the first found hosts.

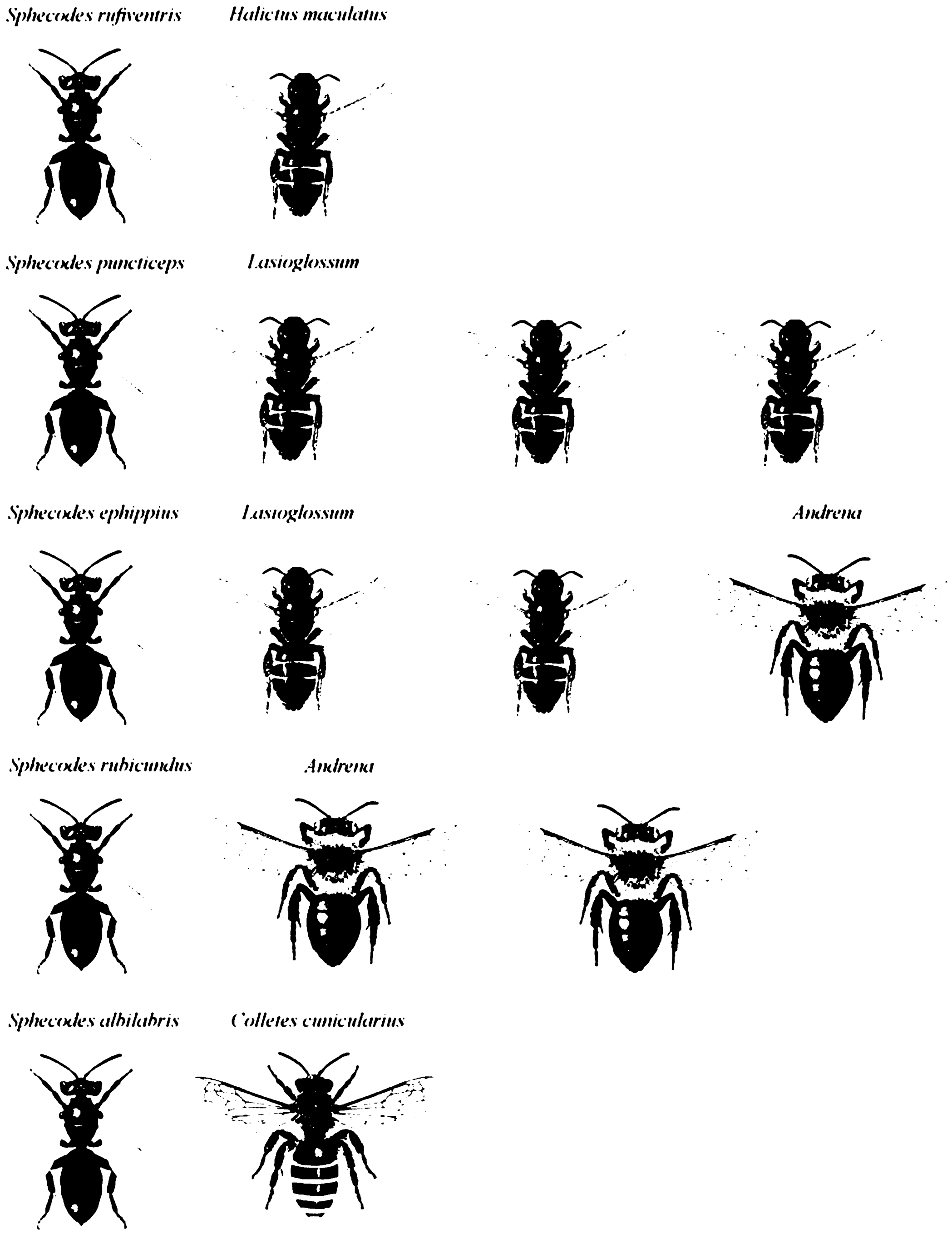

Figure 4: Re-orientating of Sphecodes. (Orig.)

5. European largest species, *S. albilabris*, is strictly bounded to an unrelated species *Colletes cunicularius*, which is very common in sandy localities in

spring. Its cleptoparasite also appears and invades nests early in spring. It is obvious that the coevolution of these species is very close.

Cuckoo bees with many hosts as *Sphecodes ephippius* and *S. monilicornis* are called generalists. Contrariwise to the selection pressures to specialize (it is certainly more profitable to be specialized) and to the Emery's rule, several bees parasitize in nests of more than ten hosts. These species do not look to be unsuccessful; the generalist species belong to the most common cuckoo bees in localities. This problem was partly explained by Bogusch et al. (2006) in above named species, and previously partly solved by Packer et al. (1995) in two North American species of the genus *Coelioxys*. Both studies proved, first by ethological, as well as by genetical and morphological tests, that generalist cuckoo bees choose their hosts in the same way as the cuckoo birds do: the individuals specialize to only one host, which is similar to the gens[4] in European cuckoo. However, the heredity of these strategies is well known in cuckoos (e.g. Marchetti et al. 1998), and very poorly in cuckoo bees. It is interesting that the second possible way that females are unspecialised occurs in birds, too; cowbirds (*Molothrus*) parasitize in nests of other birds, but their females are unspecialised.

Is the specialization necessary? I do not think so, but it could be useful for cuckoo bees at least. It brings a better possibility of coevolution with the host; every species can find the best strategy of invading the host nest or laying its eggs into its brood cell. In other words, specialization to only one species is not advantageous in this case, when the host is disappearing from the locality or a larger part of its distribution area. However, we cannot understand to the host specificity in all cases. From the human's view, there is a problem with hosts of some species as *Sphecodes puncticeps*: it parasites in nests of four related *Lasioglossum* species. All these hosts are very similar in appearance, distribution, and nesting habits. Humans recognize them as four species, but cannot they represent for the cleptoparasite the same bee with the same nesting habits, colouration, and appearance? A contradictory problem emerges with a specialization of the generalists: they can represent more species than

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[4] The gens are groups of genetically similar females within one parasitic species, specialized to parasitize in only one host. If the parasite invades nests of six hosts, its females can be put under six gens (one to each host) but none of them invade nests of more hosts (Marchetti et al. 1998).

one. *Sphecodes monilicornis* seems to be the best example of this case, it occurs within its distributional area in more than 10 morphological forms, that are explained to be geographic (Warncke 1992). But these conclusions were made only with data on morphology and ecology; neither distribution nor molecular analyses were used. Some of the forms were described as subspecies or species (e.g. *S. m. cephalotes*), the others have not been in detail studied and we know only that they preserve and are still not resolved[5]. Molecular analyses should help with the research on cuckoo bees very much, and illuninate some long lasting problems in their taxonomy and biology.

2.2. Behaviour and interactions to the hosts

Coevolution between the cleptoparasite and its host is in some cases very tight. It does not concern the values like in trematode endoparasites and other groups strictly bounded to hosts, but some characters of appearance, communication, and behaviour are remarkable. Cuckoo bees usually use several types of behaviour during their invasion to the host nest. They were put under term "behavioural patterns" and are in general valid for all cuckoo bees (Bogusch 2005; Bogusch et al. 2006). There is no space to explain them in detail in this study, but they are well defined in previously cited works. ***Table 3*** brings only short definitions of the most important of them. All behavioural patterns are forerun by a searching flight, slow flying of the cuckoo bee female low over the ground. It is necessary to find nest sites and after that the nests of hosts. Some cuckoo bees (observed at several species of *Sphecodes*) use the searching flight only to find the nest site, after landing they seek the nest of host "on foot".

Invasion to the nest and a peculiar egg laying much differs within cuckoo bees and corresponds with the type of the nest. We can divide solitary bees into two main groups: those nesting in wood and on the ground. Wood nesting bees have nests without any branches, they have only one tunnel and the brood cells are placed in

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[5] This is quite common that generalist parasites or abundant, well-distributed species of bees are very diverse in colouration and morphology, much more than the specialists or rare species. The answer is perhaps connected with the adaptations to the environment but molecular analyses in last few years found that many cryptic species were sheltered under those taxa.

compartments one after another (see ***Figure 5a***). Each time only one brood cell is opened and cuckoo bees of wood nesting hosts usually sit near to the nest and wait until the brood cell is finished. When the owner of the nest flies away for the last piece of material (usually resin, leaves, or mud) and a small aperture preserves in the brood cell, cuckoo bee comes and lays its egg into the brood cell. This strategy is sometimes used as an explanation to the conically elongated abdomens of some cuckoo bees (in Europe *Coelioxys* or *Dioxys*), and it is typical also in Sapygidae, aculeate Hymenoptera parasiting in the nests of wood nesting bees (see Chapter 4.2.). Ground nests usually consist of one main track and several others on the sides, ended by the brood cells. More brood cells can be opened at the same time, and a complicated network of lacunas makes chance to the cuckoo bee to hide (***Figure 5b***). Cuckoo bees with ground nesting hosts usually use many different behavioural patterns; some of them stay in the nest longer time (hours to days!) and behave like social parasites (Sick et al. 1994).

Table 3: List of behavioural patterns used by cuckoo bees. Created according to Bogusch (2005) and Bogusch et al. (2006).

Behavioural pattern	Description
Search flight	female flies slowly, low over the ground, sometimes returns back above the same place after few seconds
Entry into the nest during the absence of host female	*cuckoo bee* female does not meet the host female during its visit of the nest
Entry into the nest with the presence of the host female	host's presence does not prevent the cleptoparasite´s entry; the host returns to the nest during the cleptoparasite's visit, the females do not fight
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
Waiting near a nest for the host female to leave	cuckoo bee female waits next to the occupied nest to the host's departure and then attacks the nests after the host's left
Host defensive behavior at the nest	blocking the nest entrance, chasing the cleptoparasite away or pushing it out of the nest, but without any direct fight
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
Host female shadowing	flying close after the provisioning host female, shadowing the host female at the locality or at the nest site

Not all of the hosts of cuckoo bees are solitary, e.g. both generalists *Sphecodes ephippius* and *S. monilicornis* invade nests of about 15 known hosts, and about half of them are primitively eusocial (Bogusch et al. 2006). Primitively eusocial bees live in colonies, which are newly established every season (Michener 1974). Bumblebees represent a typical example of primitively eusocial bees: a mated female (called the queen) overwinters, finds a hole, gathers provisions, and brings up few workers in spring, the size of the colony culminates in summer (June-July), males and new queens emerge in August, they mate, and the colony disappears in autumn, when only mated queens survive and overwinter (Pavelka & Smetana 2003). Cuckoo bees of primitively eusocial species usually parasitize in spring (in central Europe usually at the break of April and May), when only the queen or just several workers are present in the nest. Unlike the social parasites as cuckoo bumblebees (*Psithyrus*) that stay in host's nests and live together with host's workers and in some cases also queen(s), they use the same strategies as cuckoo bees of solitary hosts (Goulson 2003).

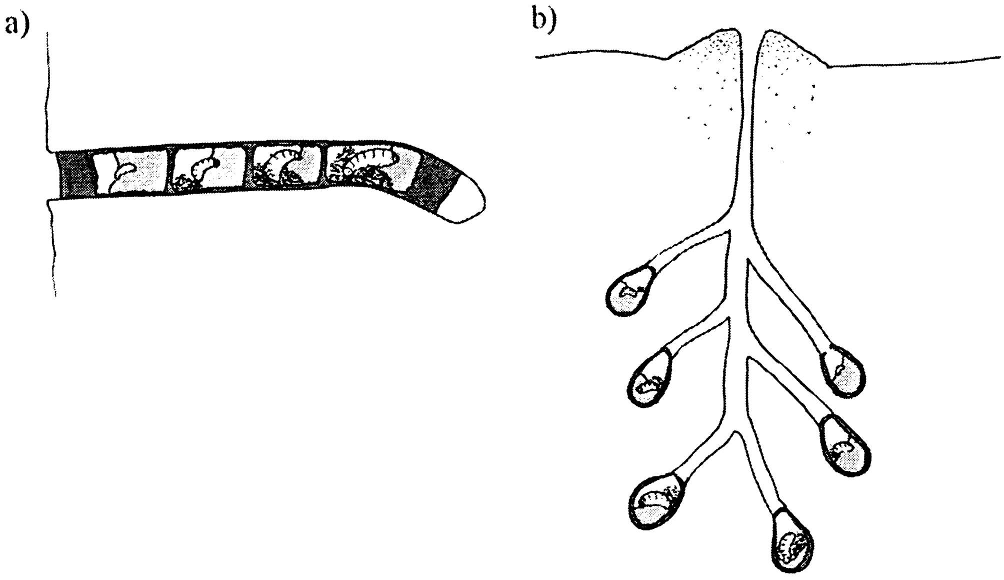

Figure 5: Difference between wood (a) and ground (b) nest of solitary bees. (Orig.)

2.3. Appearance and aggressive mimicry

Most of cuckoo bees are quite clearly distinguishable from their nonparasitic relatives. This stands well especially for females; they do not have any scopa (special tough hair to collect pollen) and are usually less hirsute than bees collecting pollen (Michener 2000). The identification is more complicated in males, but in many cases they are more or less possible to recognize.

In many other groups of animals, the parasites or commensals are similar in appearance to their hosts; remember myrmecophiles and termitophiles studied by Kistner (1969; 1982). Cuckoo bees have also evolved some mimetic interactions to their hosts. It has never been studied in detail in spite of its probably high importance in explaining life strategies of cuckoo bees and parasitic insects.

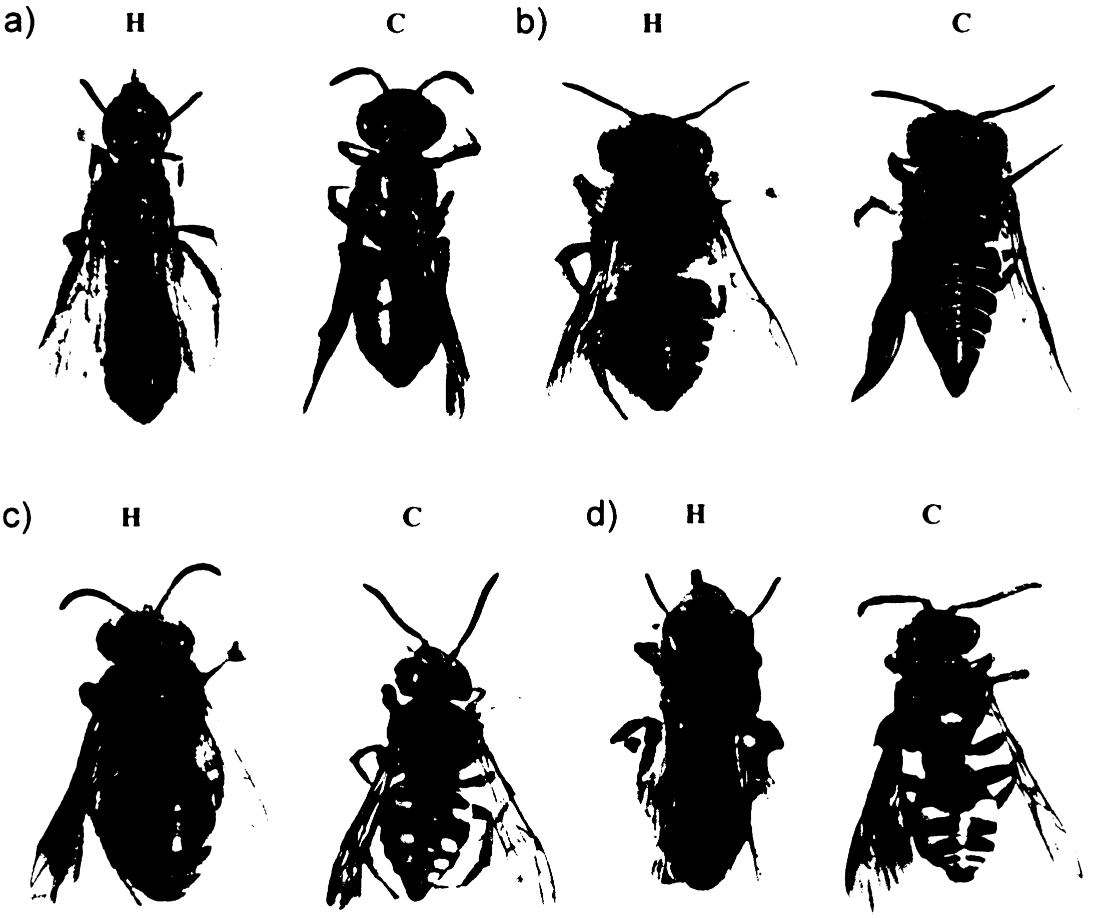

Figure 6: Comparison of appearance in general of cuckoo bees and their hosts in females. (a) *Lasioglossum calceatum* and *Sphecodes gibbus*, (b) *Megachile pilidens* and *Coelioxys afra*, (c) *Colletes similis* and *Epeolus variegatus*, (d) *Andrena flavipes* and *Nomada fucata*. Host species is on the left and marked with "H", cuckoo bee on the right and marked with "C", (a) and (b) represent related taxa and show superficial similarity in appearance, (c) and (d) unrelated taxa with no similarity. All photos © P. Bogusch.

Some groups of cuckoo bees parasitize in the nests of their relatives and are (not very surprisingly) similar to them in appearance, but in attributes typical for the whole group (autapomorphs). Cuckoo bees of the genus *Coelioxys* represent a very good example of this case: they are in general appearance similar to their relatives and hosts of the genus *Megachile*, and differ from them only in the attributes associated with their parasitic life: a conically elongated abdomen and absence of hair and scopa (see ***Figure 6b***). Similar situation preserves in other cleptoparasites of related species, e.g. *Sphecodes* bees differ from their relatives with the absence of hair, scopa, and red coloured parts of the abdomen (***Figure 6a***). We do not need to mention that intrageneric cuckoo bees look nearly the same as their hosts (*Neoprosopis* and *Dialictus*; this applies also for social parasites like cuckoo bumblebees (*Psithyrus*) and their similarity to the bumblebees (*Bombus*), see Chapter 3). A diagram created with the data of appearance similarity of European cuckoo bees brings surprising results: only 5% of cuckoo bees are prominently similar to their hosts, about one quarter only shallow, and more than half of all cuckoo bees look different than their hosts and we cannot think of any case of mimicry in appearance or colouration (***Figure 7***).

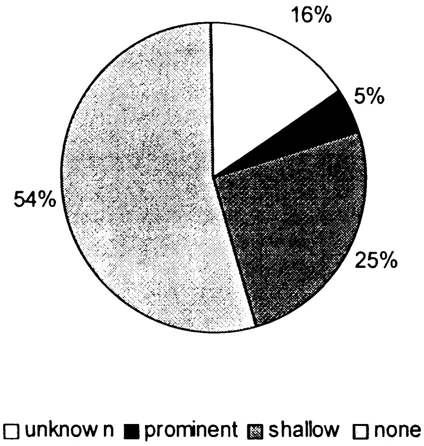

Figure 7: Similarity in general appearance of European cuckoo bees and their hosts. Intrageneric cleptoparasites are excluded. N = 167 species.

Compared to a small percentage of cuckoo bees similar to their hosts, mimetic resemblance to the host in appearance (optical mimicry) presents in the genus *Stelis*. This quite numerous genus is in Europe represented by 10 species. They are taxonomically grouped to Anthidiini, bees without plenty of hairs and often with white or yellow maculae on the body (Michener 2000). Both these attributes are present in some *Stelis* species, but most of them are in general appearance more similar to their hosts than to their relatives. Hosts of these cuckoo bees are other

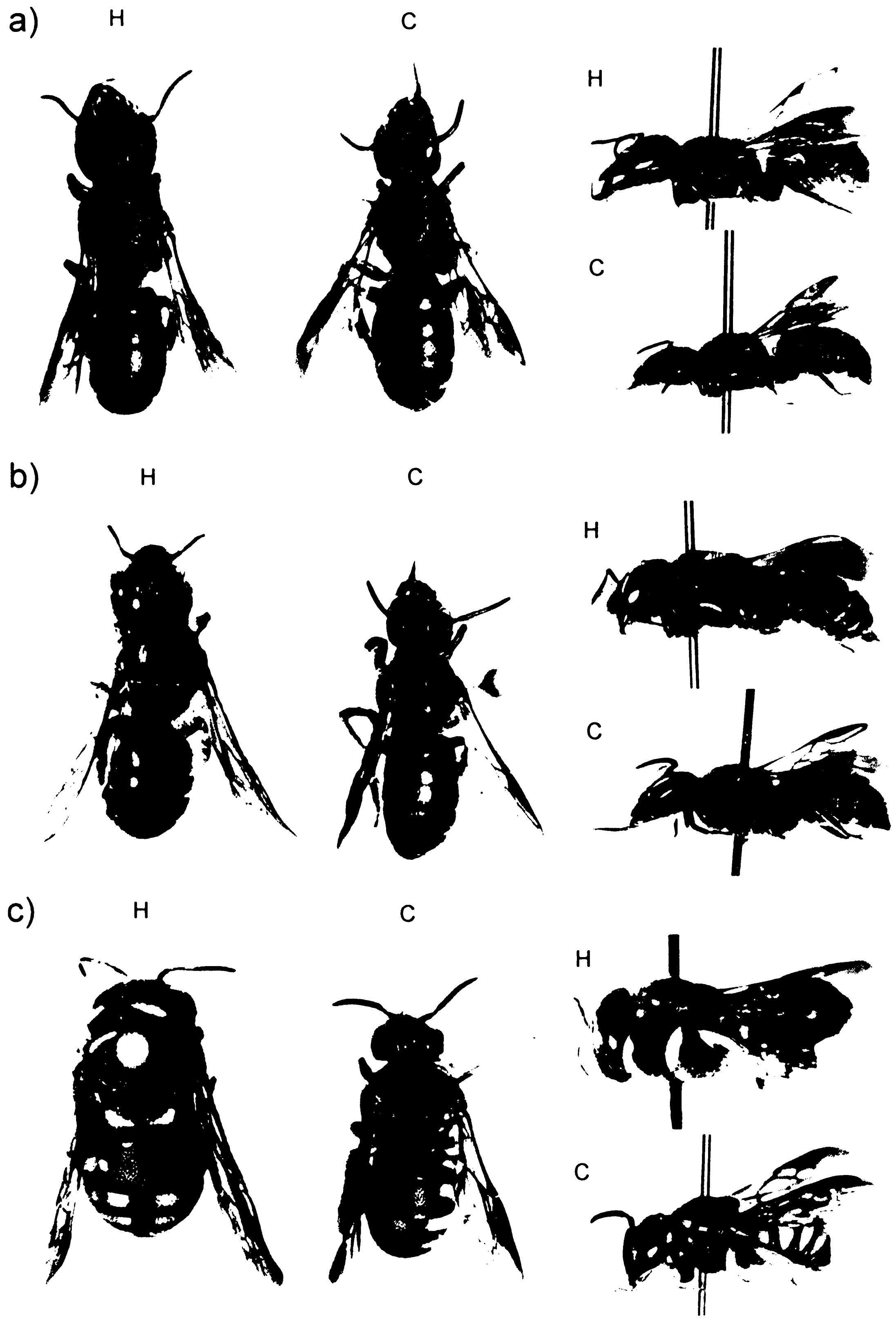

Figure 8: Similarity in general appearance in* Stelis *cuckoo bees and their hosts, dorsal and lateral view. (a) *S. breviuscula* and *Heriades truncorum*, (b) *S. phaeoptera* and *Hoplitis ravouxi*, (c) *S. signata* and *Anthidiellum strigatum*. Host species is on the left and marked with "H", cuckoo bee on the right and marked with "C". All photos © P. Bogusch.

megachilid bees, usually of the genera *Heriades*, *Osmia*, *Hoplitis*, and *Anthocopa*. Some species are specialized to 1 up to 2 related hosts; generalists with 8 up to 12 known hosts are presented in this genus, too. Nearly all species of this genus are much similar in appearance with their hosts. *S. breviuscula* is specialized to wood nests of little bees of the genus *Heriades* and it looks very similar to them in size, bands on the abdomen, and a typical matt appearance, it differs from its hosts only in two remarkable characters: it lost the scopa, and also does not have a special carina on first tergite, typical for *Heriades* (***Figure 8a***). Generalist *Stelis* species usually parasitize in nests of several in appearance similar bees of above mentioned genera and look very similar to them (***Figure 8b***). The main similarity is found in *S. signata*, the parasite of robust *Anthidiellum strigatum* with large yellow spots on the body (***Figure 8c***). The cuckoo bee is coloured with the same black with yellow spots and marks as the host, and the same geographical variances are present: going to south the yellow spots become larger and they cover nearly the whole body on the southern edge of its distributional area[6].

All *Stelis* species can be well distinguished from their hosts by typical attributes of the genus: spines on scutellum or a narrow head, but they in general resemble their hosts. The similarity is in some cases much more higher than in typical kinds of mimetic interactions, like at hover flies and yellow jackets, etc. We can explain their similarity to the hosts in more ways:

1. Aggressive mimicry, cuckoo bee looks like the female of the host's species. This explanation may be true; on the other hand there are no clear advantages for the cuckoo bee's female. Alternatively, they are usually not territorial in the surroundings of the nest, for explanations see Straka (2005); similar appearance can help the cuckoo bee to come nearer. The similarity in appearance can be combined with some other mimetic signal, e.g. chemical or tactile communication.
2. Müllerian mimicry, general appearance of wasps (in *S. signata* and also in other cuckoo bees) or of bees (some of the others). A contrast black-white or black-yellow colouration of many cuckoo bees is probably an example of the

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[6] Bigger size of light maculae on the body of insects connected with the southern localities is well known, but these two species show a very striking similarity.

> Müllerian mimicry. These cuckoo bees form the "vespiform" colour pattern together with scoliid, sphecid, eumenid and social wasps, bees, and also with several ichneumonids, chalcids, sawflies, hover flies, moths or long-horned beetles (see Chapter 4.4.). The same colouration in *Stelis signata* is interesting: why it has evolved only in one species, yet in the only one species with host of the same colour pattern? I think the truth is somewhere between both of these hypotheses.

As in the nest parasites of ants, termites and other social insects, there is very probable that the cuckoo bees have evolved a chemical aggressive mimicry. Although they are parasites, in some cases nearly completely destroy nests and very significantly flout the populations of their hosts, the interactions when the cuckoo bee and its host meet seem to be friendly, usually without any fights. In some cases both cuckoo bee female and host female come together at the host nest, crawl inside, stay there side by side several minutes or hours, and behave like "friends on visit". It seems to be a possible case of an aggressive chemical or tactile mimicry. As many other insects, bees use chemical and tactile communication (but not more than optical) and some ways of this communication are quite simple to mimic (one chemical compound in most cases). However, I have not found any studies on a solitary bee communication or on the communication of cuckoo bees with their hosts. The possibility of chemical aggressive mimicry is likely, because several records on a chemical mimicry in bees have been published: South American bees of the genus *Lestrimelitta* rob in the nests of eusocial stingless bees (mainly in species of genera *Mellipona*, *Trigona*, and *Plebeia*), and the same do African bees of the genus *Cleptotrigona* (Michener 2000). This behaviour was studied on *Lestrimelitta limao* robbing in the nests of small eusocial species *Trigona subterranea*. The robber emits citral, a typical chemical compound used by *Trigona* as an alarming pheromone to invade more easily into the nest of *Trigona* (Blum et al. 1970; Haynes & Yeargan 1999). This species is not a cuckoo bee but there are proved reliable data on chemical compounds identical with their hosts in several species of *Nomada*. Males have in their cephalic gland the same compounds as females of their hosts, which perhaps serve in parasitation. When mating, the male "showers" the female with these chemicals of low volatility, and the female after that finds the nest site of its host, and invades the nests without any aggresses (Tengö & Bergström 1977). Neither similar chemical compounds were proved in other groups of cuckoo bees, nor their emitting by parasiting females, although the behaviour of some parasiting cuckoo bees seems to use them. Chemical compounds of Dufour's glands were studied in *Sphecodes* but not compared with their hosts, only within the genus (Tengö et al. 1992). I hope everything will become much clearer early in the further research. There are also possibilities of a tactile mimicry. When the cuckoo bee and host females meet at the nest, they usually touch on heads or faces with their antennae (observed many times in various species of cuckoo bees), the cuckoo bee probably plays some of the host tactile communicational signals like the myrmecophiles (see Henderson & Akre 1986; Elmes et al. 1991).

Another very interesting thing in the colouration of cuckoo bees is the presence of a red cuticular colour. This colour is well distributed in other groups of aculeate Hymenoptera; some groups (Mutillidae, Pompilidae) contain many red species (typical is red combined with black). Only several species of nonparasitic bees are red (in Europe several species of the genus *Andrena* or megachilid bee *Erythrosmia andrenoides*), and some also have rusty hair on the body surface (Michener 2000). Among the cuckoo bees, many of them are red: about one quarter of European cuckoo bees have a red bigger part of the body, usually at least half of the abdomen, 38% have red coloured smaller parts of the body or the colour is not strictly red but rusty or rust-brownish, and the same percentage is not red coloured (***Figure 9***).

The explanation can be in aposematism, red is very conspicuous for birds and other predators of bees, and so it can serve as an aposematic signal for the predators. But why only cuckoo bees are red? Perhaps cuckoo bees, pompilids and some sphecid wasps stay much more time on the surface of the ground, and the predators have more opportunities to catch them. Cuckoo bees do not have any nests and spend nights usually outside, pompilids usually do not fly over the trees but run on the surface of the ground, similarly as sphecid wasps of genera *Tachysphex*, *Harpactus*, and *Dinetus* (all of them are often red). Interestingly, bees and wasps cannot see the red colour. They have in eyes three types of receptors with maxims of excitation in blue, green, and – ultraviolet[7]. Hosts of cuckoo bees cannot see the signals produced by their cleptoparasites, so the red colour on abdomens of many cuckoo bees must have some different meaning.

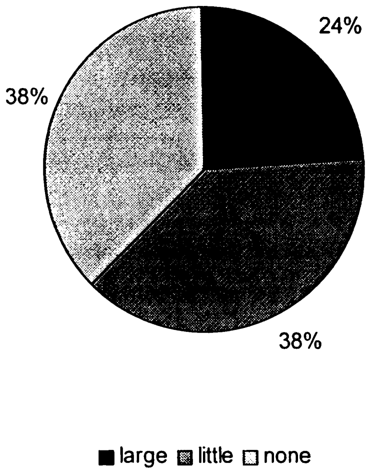

Figure 9: ***Red colour in European cuckoo bees.*** N = 167.

One of the weirdest European cuckoo bees, *Epeoloides coecutiens*, may serve as a proof that the red colour is not signalling for bees but for anybody else. This bee of the family Apidae occurs in wetlands in the whole Palaearctic. *E. coecutiens* is a nest parasite of bees of the genus *Macropis*, which nest in wet localities and collect mainly pollen and floral oils on flowers of *Lysimachia*. *E. coecutiens* female is black with a larger part of the abdomen red and white bands of short hair on last tergites. It looks conspicuously and seems to be almost red when flying. Biology of this species was studied in detail by Bogusch (2005). I observed that *E. coecutiens* female does not need to fight with the host's female during its invasion to the nest. Even - in one case, a very "friendly" behaviour between both females was observed. Both European hosts of *E. coecutiens* have similar white bands on the abdomen like their cleptoparasite, and if we suppose the red colour is invisible (like grey for us) for bees, the cuckoo bee's female is very similar in appearance and colour to its hosts (***see Figure 10***). This cuckoo bee apparently evolved two types of optical signals:

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[7] Humans have a similar trichromatic visual mechanism but with excitation maxims of receptors in blue, green and red. This makes striking differences in human and bee view to flowers of plants (see Straka 2003).

aposematism for birds and other predators, and similarity in appearance to the host. In my opinion, the third case of an aggressive chemical or tactile mimicry certainly occurs in *E. coecutiens* communication with its hosts, too.

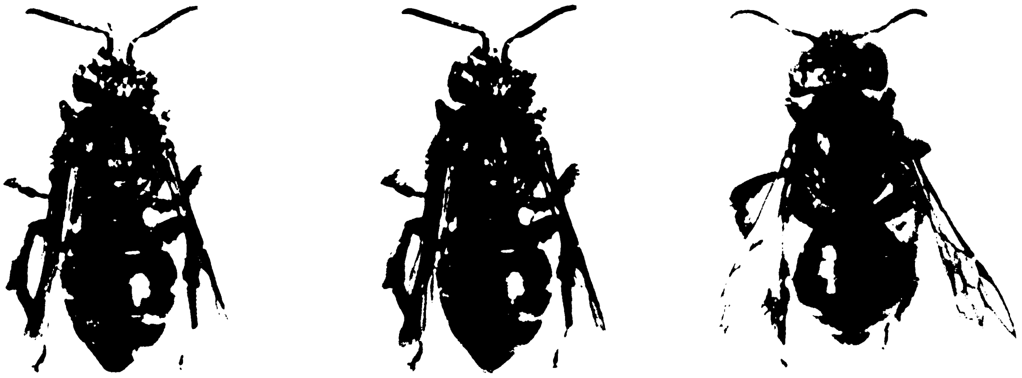

***Figure 10:* Epeoloides coecutiens *and its similarity to its host,* Macropis fulvipes.** Female of *E. coecutiens* (left photo) possesses a red abdomen with bands on last three tergites, host female (right photo) has very similar bands on the abdomen and looks in general appearance very similar to its cuckoo bee. *E. coecutiens* female put into greyscale (centred photo) looks very similar to *Macropis*. All photos © P. Bogusch.

Now we cannot explain the role of red colour in cuckoo bees without any doubt. It seems to be an aposematic signal to the predators and occurs in other above named groups of aculeate Hymenoptera and also in many other poisonous or stinging insects. An ethological research with the hosts and predators can help us. The same situation is with the aggressive mimicry, which is better known in social parasites and myrmecophiles.

3. SOCIAL PARASITES OF BEES AND WASPS

Life strategy of social parasites does not differ considerably from that of cuckoo bees or any other cleptoparasitic insects and animals. Most of them steal provisions in nests, too, and differences are only in two main characters: their hosts are social, and most of social parasite adults spend a long time in host nests (Goulson 2003), even an important part of their whole life or metamorphosis (*Maculinea* blue larval instars and pupae live in ant-hills, cuckoo bumblebees undergo the major part of the metamorphosis in bumblebee nests). This is the main reason why we cannot state that some *Sphecodes* cuckoo bees are social parasites; they invade nests of several species of eusocial bees but parasitize only in the solitary phase (when the queen or even few workers persist in the nest) and do not stay in the nest longer time that is necessary to lay eggs (Bogusch et al. 2006). Cuckoo bumblebees of the genus *Psithyrus*[8], well known social parasites, use the following strategy: the queen invades into the host nest, kills the host queen, and begins to rule over the workers and to lay eggs. Host workers breed her offspring as long as they live (Goulson 2003). In some cases the cuckoo bumblebee queen does not kill the host queen; they both persist in the nest, lay eggs and workers breed offspring both of their queen and the parasite. This behaviour was observed in *P. sylvestris* in the nests of *B. pratorum* (Kupper & Schwammberger 1995).

Social parasites are phylogenetically classified into many groups of invertebrates but their hosts are even the same: ants, termites, social bees and social wasps. In this chapter we study a priori parasites of bees and wasps, which give us good comparative life strategies to the cuckoo bees'. They are also less diverse than the myrmecophiles and termitophiles, usually phylogenetically bounded to their hosts, and have not been studied in detail, even as the other groups. Ant and termite hosts will be used only as groups for comparison, especially in cases when only a little is known about other social parasites, e.g. in the case of aggressive mimicry. Although

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[8] Recently, the phylogenetic relations among bumblebees have been discussed and studied: the opinions of various authors differ from dividing to many genera (Přidal & Tkalců 2001) to put all bumblebees with their cuckoo relatives to one genus *Bombus* (Pekkarinen et al. 1979; Pamilo et al. 1987). Here, we will use the old classification but consider all species as members of one genus *Bombus*.

the term "social parasites" is well established, we must remember that many of these insects are not parasites but commensals or in some cases the relationship with their hosts is mutualistic (Hölldobler & Wilson 1995).

Cuckoo bumblebees of the genus *Psithyrus* represent the only known social parasites classified to superfamily Apoidea (Michener 1974; 2000). They look very similar to the bumblebees but do not have any scopa or glands producing wax. The hosts are their closest relatives, primitively eusocial bumblebees. Main schemes of their life strategy were described in the first paragraph of this chapter. To complete their life circle the queens and males (they do not have any workers) emerge in the host's nest and mate (outside), the queens overwinter and start to seek for nests of bumblebees in the end of spring. They wake up from the hibernation later than bumblebees (they do not need to do it early because they invade a well-developed nest of the host).

There are about 250 species of bumblebees in the world, 45 of them are the cuckoo bumblebees (Goulson 2003). Interestingly, the ratio 45/250 gives a similar percentage as in cuckoo bees, 18% of bumblebees are interspecific parasites. In central Europe, 39 species are known, 9 of them (23%) are the cuckoo bumblebees. There are only little differences within the ratio: the percentage of parasitic bumblebees in the world (18%) is a bit higher than in cuckoo bees (~15%), and in central Europe (23%) a little bit lower than in cuckoo bees (25%). Bumblebees probably represent a distant group from the other bees, unlike the majority of bees they are not specialized for life in warm localities and regions but most of the species are boreomontanneous. The highest diversity of bumblebees is not in tropical, but in temperate regions. Therefore, central Europe represents the region with a high diversity of species in contrary to the cuckoo bees, so the differences in ratios should be lower than in the cuckoo bees.

Most of the cuckoo bumblebees are unspecialised and invade nests of various bumblebee species, in most cases not closely related (various subgenera). Only several of them parasitize in nests of only one species (Goulson 2003; Pavelka & Smetana 2003). In most cases they are similar to their hosts in colouration: 7 of 9 central European species are very similar in colouration to their hosts, only the generalist *P. campestris* is similar in colour to several of its hosts (it parasites in species of two colour types of bumblebees), and *P. norwegicus* looks differently from its host, *B. hypnorum*. Although this similarity can play up to the hypothesis about the aggressive mimicry, most authors (Alford 1975; Prys-Jones & Corbet 1991) adhere to the theory that the colouration similarities belong to Müllerian mimicry and bumblebees with their parasites form mimetic circles defending to the predators with their colouration. The similarity of *Psithyrus vestalis* to its host, *Bombus terrestris* talks against this hypothesis: in major part of Europe both the parasite and the host are black with yellow and white stripes, in southern parts of Europe (Corsica, Greece) they both changed their colouration and are black with yellow or orange stripes. Their colouration similar to the hosts can be interpreted also by the relationship to their hosts: if every cuckoo bumblebee evolved from the nest-usurping individuals (see next paragraph) of its host, it must not change the colouration.

Interspecific parasitism in bumblebees probably arose from the interspecific parasitism, which is in literature often put under the term the "nest usurpation" (Goulson 2003). This behaviour is quite common in many nonparasitic bumblebee species. The queens emerged from the hibernation later than the others often try to invade other nests of the same species, kill the host queen and take the rule over the bumblebee colony (Alford 1975; Goulson 2003). Nest usurpation is common in many bumblebees but it is not present in all species (Goulson 2003), it was also recorded an interspecific nest usurpation within the same subgenus (Milliron & Oliver 1966; Richards 1973). Nest usurpation can bear with the aggressivity of the species, some bumblebees are very calm to other individuals of the same species, nest parasites or predators (in central Europe *B. pratorum* or *B. pascuorum*), but some other species are very aggressive (*B. terrestris*, *B. muscorum* and *B. hypnorum*). These attributes certainly correspond with the ability to usurp nests of other species and to evolve into a social parasite.

Not much is known about the chemical mimicry in cuckoo bumblebees, most of the authors state that much power, a longer sting and a stronger cuticle and mandibles are enough to be successful in parasitation in bumblebee nests (Alford 1975; Goulson 2003). There was also not proved if other bumblebee parasites use the chemical aggressive mimicry, e.g. hover flies of the genus *Volucella*. It probably corresponds with the "chemical vocabulary" of bumblebees; it is quite rich in situation of provisioning but not in cases of nest defending (Goulson 2003). In spite of that there are many parasites of bumblebees among other groups of invertebrates and none of them seem to become extinct, so they probably use chemical or tactile cues or imitations.

Table 4: List of European cuckoo bumblebees and flies mimicking their hosts. Cases with no mimicry are bold emphasized. Created according to Pavelka & Smetana (2003).

Parasite (mimic)	Host (model)
Diptera: Syrphidae	
Arctophilla bombiformis	*Bombus terrestris* group
Arctophilla bombiformis	*Bombus soroensis*
Criorhina berberina	*Bombus hypnorum*
Criorhina berberina	*Bombus pascuorum*
Procota personata	*Bombus terrestris* group
Volucella bombylans f. *bombylans*	*Bombus lapidarius* group
Volucella bombylans f. *haemorrhoidalis*	*Bombus pyrenaeus* group
Volucella bombylans f. *plumata*	*Bombus terrestris* group
Hymenoptera: Apidae	
Psithyrus barbutellus	*Bombus hortorum*
	(***Bombus hypnorum***)
Psithyrus bohemicus	*Bombus lucorum*
Psithyrus campestris	***Bombus pascuorum***
	Bombus subterraneus
	Bombus distinguendus
	Bombus ruderatus
	Bombus pomorum
	(+ other species)
Psithyrus maxillosus	*Bombus ruderatus*
	Bombus subterraneus
Psithyrus norwegicus	***Bombus hypnorum***
Psithyrus quadricolor	*Bombus soroensis*
Psithyrus rupestris	*Bombus lapidarius*
	(***Bombus sylvarum***)
	(***Bombus pascuorum***)
	(*Bombus sicheli*)
Psithyrus sylvestris	*Bombus pratorum*
	(***Bombus jonellus***)
Psithyrus vestalis	*Bombus terrestris*

As stated above, bumblebees have more nest parasites than their closest relatives, moth and butterfly caterpillars, braconids, and various species of flies parasitize in their hives (Goulson 2003). Several species of hover flies (Syrphidae) live in the bumblebee nests; their larvae feed as commensals on waste, as cleptoparasites on provisions, or in some cases they prey on host larvae. Adult flies usually look in their general appearance similar to their hosts (see ***Table 4***). The aim of this study is not a detailed description of all dipteran interactions to bumblebees, the author would like to compare volucellae with cuckoo bumblebees and explain their ways of parasition.

The best-known parasitic flies in bumblebee nests are species of the genus *Volucella.* Five of them are known from Europe, four parasitize in nests of social wasps and one, *V. bombylans*, in bumblebees. *V. bombylans* is quite common in central Europe, it usually occurs in open warmer localities (Roeder 1990). It lives as a parasite or commensal in nests of various species of bumblebees. The females lay eggs at the nest entrances or directly into the nests of various bumblebee species and larvae feed on remains of the provisions, waste, and sometimes also on dead bumblebee larvae. The parasite is in general appearance very similar to bumblebees; in contrary to other syrphids it is robust and has tight hair on the abdomen. Typical for this species is the polymorphism: the main form *bombylans* is black with a red abdomen tip like *Bombus lapidarius*, *plumata* form is black with a yellow thorax and a white apex of abdomen like *B. terrestris*, and *haemorrhoidalis* form looks like *plumata*, but the abdomen is red haired (similar to *B. pyrenaeus*). The photographs of all three forms are in ***Figure 11***. This polymorphism depends on two autozomal genes, which in addition epistatically interact to each other (Gabritschevskyi 1924). Abundances and ratios of these three forms differ with the altitude and locality type, in general *bombylans* form is more abundant than the others; the other two forms become more abundant in higher altitudes (Rupp 1989) nearly to push away the *bombylans* form. Abundance of *haemorrhoidalis* form in the mountains (the Alps) significantly corresponds with a boreomontanneous distribution of its models, and this form is dominant in mountain ranges.

Hosts of this species are various species of bumblebees. Rupp (1989) experimentally proved that all forms parasitize in more than one bumblebee species and do not invade nests solely of hosts of the same colouration, rather contrariwise. This fact rejects questions if they use the aggressive optical mimicry to invade the host nest. *V. bombylans* is probably the Batesian part of Müllerian mimetic rings among bumblebees and cuckoo bumblebees. The reactions of birds and frogs to bumblebees and volucellae support this hypothesis (Rupp 1989). However, there was not studied if volucellae are individually specialized like cuckoos (Marchetti et al. 1998) or cuckoo bees (Packer et al. 1995; Bogusch et al. 2006), but Rupp's (1989) results of experiments suggest that they do not.

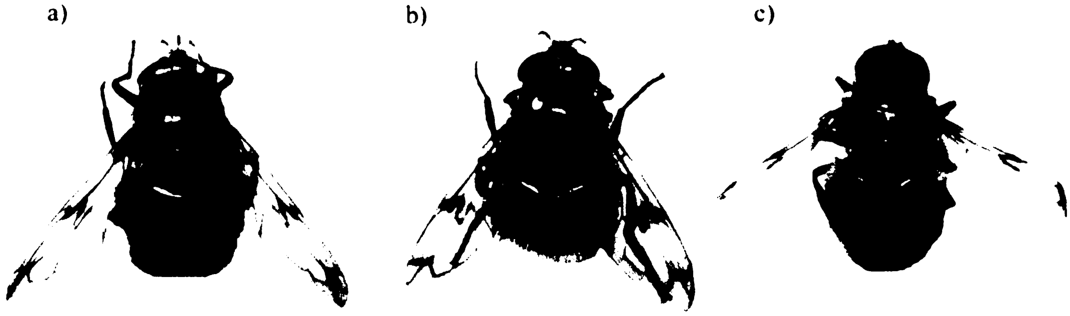

***Figure 11: Three colour forms of* Volucella bombylans.** (a) *Volucella bombylans* f. *bombylans*, (b) *Volucella bombylans* f. *plumata*, (c) *Volucella bombylans* f. *haemorrhoidalis*. All photos © P. Bogusch.

Another published data support the absence of aggressive mimicry in volucellae: the host queens and workers are aggressive to *Volucella* females, and kill them very often. *V. bombylans* females have one good adaptation: they are able to lay eggs after they were killed or stung (Rupp 1989; Goulson 2003), so they can parasitize successfully also if they were found by bumblebee workers. The females seek for the nests in localities at most by visual cues, after finding them they wait for several minutes at the entrance, enter the nest, and lay eggs near the inner surface of the nest wall. This helps them to encounter meeting any bumblebee worker and a potential risk to be killed, but Rupp (1989) comments that they cannot be very successful because bumblebees are aggressive to them. On the contrary to other social insects (i.e. bees or wasps), bumblebees lack alarming pheromones. These chemical compounds serve in most cases as cues of imitation for social parasites using the aggressive mimicry, i.e. staphylinid beetles of *Atemeles* or *Lomechusa* genera or ants

– social parasites of other ants (Hölldobler & Wilson 1995). However, it can be the main reason why the relationship of volucellae and bumblebees is so aggressive and why the flies seem to be unsuccessful in parasitation (Rupp 1989).

Other four species of this genus parasitize in nests of wasps (*Vespula germanica* and *V. vulgaris*) and hornets (*Vespa crabro*). Two of them, *Volucella inanis* and *Volucella zonaria*, are in general appearance similar to their hosts. The first one resembles wasps and the second one the hornet. Both these species parasitize in similar way as *Volucella bombylans* in nests of their hosts. The interactions with them are very similar, too (Rupp 1989). Next two species, common *Volucella pellucens* and rare *Volucella inflata,* parasitize both in wasps and hornets, but they are not similar in appearance to them. Surprisingly, wasps and hornets often attack the first two but not the last two. Rupp (1989) ethologically proved that *V. pellucens* females use aggressive chemical mimicry when invading the host nest. On the other hand, first two species are more parasitoids (their larvae feed on host larvae), contrariwise to the other two commensals living in host nests as cleaners. These different life strategies can be also connected with the interactions to the hosts; *V. pellucens* is harmless or beneficial, so that the wasps do not attack it. Using the chemical aggressive mimicry in wasp parasites is not rare, Žďárek (1997) presents that *Dolichovespula adulterina*, one of several European parasitic wasps that parasitize in nests of other wasps (here the host is *D. saxonica*), probably uses the aggressive chemical mimicry to subjugate the host workers.

4. OTHER PARASITIC ACULEATE HYMENOPTERA

Both cleptoparasitism and social parasitism represent advanced specialized life strategies, originated from predatory behaviour, which is typical for primitive aculeate Hymenoptera. Pollen collecting in bees and massarid wasps can be classified as an advanced life strategy within Hymenoptera, too. However, not the majority of aculeate Hymenoptera are predators like sphecid and eumenid wasps or pompilids (Brothers 1972). About the same deal of species use parasitic ways of behaviour, in most cases parasitoidism. This type of behaviour is typical for various hymenopteran groups (most of Chalcidoidea, Ichneumonoidea, Proctotrupoidea, and e.g. Cynipidae are plant parasites) and several species in other genera, e.g. Phasmatodea, Coleoptera or Diptera. Parasitoids are quite similar to parasites, their brood or adults live to the prejudice of some other species, but they do not kill their host immediately. A typical parasitoid makes the profit of its host during a long part of the host's life, and after that it kills it (as ichneumonids whose larvae eat fat supplies of caterpillars and kill them when reaching the mature age before the pupation). Many groups of solitary wasps classified to Aculeata use the same strategy, or, in more cases, behave as the nest parasitoids, adult females search for brood cells with mature host larvae to paralyse them and lay one up to several eggs on them. Then they serve as living preserve of food for the parasitoid larvae (O'Neill 2001).

Like the cuckoo bees, some groups of Aculeata use the cleptoparasitism as their primary or facultative life strategy. There are two types of this behaviour: some solitary wasps steal a fresh hunted prey, and the nest parasites lay eggs into brood cells or nests of other insects and their larvae feed on host provisions. Unlike the cuckoo bees most cleptoparasitic wasp larvae feed on animal prey; only Sapygidae and several Chrysididae are able to undergo their metamorphosis using a floral diet, i.e. pollen and nectar. These facts are valid for larvae, hence the males of nearly all aculeate groups eat nectar and pollen in flowers (Balthasar 1954), the females are usually carnivorous (O'Neill 2001). Adult female of velvet ant *Pseudophotopsis continnua* preys on adults of a large sphecid wasp *Bembix olivacea* (Mellor 1927), *Mutilla europaea* parasitizes in nests of bumblebees and the adult females kill their workers but not larvae. Many velvet ants prey on various ground nesting Hymenoptera, they bite their prey between the head and prothorax and suck their body liquids (O'Neill 2001). The females of Scoliidae and Tiphiidae feed on nectar in flowers; smaller species frequently suck honeydew from leaves where aphids secrete it.

We must mention that above presented and further in detail described life strategies occur in aculeate Hymenoptera both as obligate and facultative. Several nonparasitic species use the cleptoparasitic, nest parasitic, or parasitoidal ways of life only in occasion, and in most cases intraspecifically, among their own species (Brothers 1972; O'Neill 2001). Thus well known but primarily nonparasitic species as *Ammophila sabulosa*, *Trypoxylon figulus*, and *Crossocerus laticinctus* are classified as the parasites. Their intraspecific parasitic behaviour can be interpreted in a similar way as the intraspecific nest parasitism in bees (well known e.g. in *Hoplitis anthocopoides*, see chapter 2) or the nest usurpation in bumblebees, which probably served as the transition to the obligate cleptoparasitism (Eickwort 1975; Goulson 2003).

4.1. Parasitoids

Most of hymenopteran parasitoid larvae feed inside their hosts, thus they are classified as the endoparasitoids. Among aculeate Hymenoptera the endoparasitoids represent only a fragment of the whole number of parasitic species. They lay eggs inside the host but none of them parasitize in the nests of their hosts and feed in paralysed or living insects. Parasitic aculeate wasps of the family Dryinidae are all endoparasitoids: their hosts are leafhoppers (Auchenorrhyncha). The females lay eggs inside the host body and larvae feed inside producing larval sacs, shelters where they live. Larval sacs are visible on the surface of the leafhopper as darker organs placed usually on thoracic sterna or anywhere on the abdomen. Primitive chrysidid wasps of subfamilies Amiseginae and Loboscelidinae are egg endoparasitoids; their females lay eggs into those of various species of phasmids. Only one egg is placed into one phasmid egg to avoid competition between two or more larvae (O'Neill 2001).

Most of the aculeate parasitoids are ectoparasitic: all members of Bethylidae, Mutillidae, Tiphiidae, Scoliidae, and Ampulicidae, about half of Chrysididae species, and several species of Pompilidae, Crabronidae, and Sphecidae. The females lay eggs and larvae undergo their ontogeny on the body surface of the host, if they feed on body liquids, they usually do not leak into the host body. We can divide these ectoparasitoids to those parasiting outside of nests usually on adults, and to the nest endoparasitoids that invade the host nests and usually feed on mature larvae, praepupae or pupae of their hosts.

Bethylidae are closely related to Dryinidae, but they differ from them in the life history. Most of the bethylids are the ectoparasitoids; their females seek for larvae or pupae of various insects, usually butterflies and moths, beetles or hymenopterans, and lay their eggs on their surface. First instar larvae have pincerlike mandibles adapted to penetrate the host cuticle, get with their head inside and after that exuviate. The same life strategy is typical also for Cleptinae (O'Neill 2001), subfamily of Chrysidididae[9], Tiphiidae, and Scoliidae. Scoliidae are obligate parasitoids of scarabaeid beetles, Tiphiidae parasitize in the same group (Tiphiinae) or in tiger beetles (Methochinae). Among the three families of sphecid wasps, the less numerous one, Ampulicidae, consists of non-nest ectoparasitoids. Unlike the majority of sphecid wasps that are predators, the Ampulicidae prey on cockroaches. Their behaviour represents some transition between nesting predators and parasitoids: when a female finds cockroach, it stings it and carries out to some hole in wood remained after larvae of some wood beetle, puts it into the hole and lays an egg on the cockroach. Larvae feed on these storaged cockroaches, which stay alive and are usually able to move but not very much (Gess 1984). Several other sphecid wasps, e.g. of the genera *Chlorion* (Sphecidae), *Larropsis* and *Larra* (Crabronidae), use similar strategies of nesting, they hunt crickets, respective mole crickets. In all three genera both nesting hunters and parasitoids are present (O'Neill 2001).

Nest parasitoids are also common, all members of families Mutillidae and many species of subfamily Chrysidinae parasitize in nests of other insects. The females

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[9] This group was previously classified as a family related to Bethylidae and Chrysididae.

seek for the nests of their hosts and get to the brood cells. They need brood cells with mature larvae, praepupae, or pupae. If the female finds a brood cell with mature larva, praepupa, or pupa, it lays one egg inside. Larvae feed on the defenseless brood of the host, overwinter and pupate in the brood cell. Some Chrysidinae, e.g. large species *Stilbum cyanurum*, lay eggs into new brood cells with eggs or young larvae of their hosts, in this case the first instar larva of the parasitoid waits until the host's larva reaches maturity, exuviates and starts feeding reaching the second instar (O'Neill 2001). Hosts of Chrysidinae and Mutillidae are usually various species of solitary wasps and bees, some species of the second named group also parasitize in Lepidoptera, Coleoptera and Diptera (Bohart & Kimsey 1982). All these nest parasitoids usually paralyse the host larvae, which then serve as living preserves of food for their larvae (O'Neill 2001). Some Mutillidae parasitize in nests of social insects, both central European *Mutilla* species invade nests of bumblebees where their larvae feed on mature larvae (Baťa et al. 1938).

Interesting parasitizing behaviour was recorded in several Pompilidae, they attack spiders in their webs, paralyse them and lay eggs to or on the paralysed prey. It is somewhere between the ectoparasitoidism and nest parasitoidism, they hunt spiders in their nests, but do not feed on larvae but on adults. Some sphecid wasps, e.g. genera *Sceliphron* and *Isodontia*, hunt spiders in their webs, too, unlike the pompilids they take the caught spider to their own nest and use it in the same way as majority of sphecid wasps – hunters (Blackledge 1998). The pompilid wasp *Pseudopompilus humboldti* hunts spiders in their stocking shaped webs in the same way like the above described pompilids, but it takes the spider to the entrance of the web. It is visible for birds and other predators, but there is lower temperature outside (about 20°C) than inside (50°C), which is not harmful both for the prey and pompilid larvae (Ward & Henschel 1992).

4.2. Cleptoparasites

Since stealing of prey was mentioned in the beginning of the chapter and it is not very important for the study of mimicry, here we give attention to the nest parasitism. It is broadly known among Chrysididae, Pompilidae, Crabronidae, and groups of Apoidea called cuckoo bees (they are in detail described in Chapter 2), but only within the family Sapygidae solely the nest cleptoparasites are known. Life strategies of these groups usually do not differ from those of the cuckoo bees, they invade nests of their hosts (represented only by aculeate Hymenoptera) and lay eggs into the brood cells (O'Neill 2001).

Unlike the cuckoo bees, most of these cleptoparasitic larvae feed on animal prey; only Sapygidae feed on nectar and pollen. There are also differences in the behaviour of females and larvae: the females destroy host eggs only in Pompilidae: *Evagetes,* and Crabronidae: *Stizoides*, but in most cases both the parasitic and host larva compete for the food. In most cases first larval instars of cleptoparasitic Aculeata emerge earlier than the host larva and destroy it (Pompilidae: *Ceropales*, Crabronidae: *Nysson* and *Epinysson*, all Sapygidae, most Chrysidinae), but in some Chrysidinae the larvae do not fight, both the cleptoparasitic and host larva finish their development (O'Neill 2001).

Hosts of the cleptoparasites classified to Chrysidinae are usually sphecid wasps and solitary bees, several species parasitize in Eumeninae. Only several species of Pompilidae are cleptoparasitic, they usually parasitize in their relatives, other pompilids; several species of the genus *Bathozonellus* are facultative intraspecific cleptoparasites within the same species (Tsuneki 1968). The evolution of cleptoparasitic behaviour in Pompilidae went probably in two ways: first genus Evagetes classified to the subfamily Pompilinae, parasitizing in nests of their relatives and destroying the host eggs represent one. Second group, *Ceropales* species classified to the subfamily Ceropalinae, pursue other pompilids that carry prey, fight with them and lay an egg into the respiratory system of the prey (the egg is there invisible). Larvae emerge earlier than the host's brood and kill it. *Evagetes* species have tarsal combs on their forelegs, *Ceropales* lacks them. O'Neill (2001) states that the first group evolved from the nesting prey hunters, the second one from the nest parasitoids. Similar situation occurs in Crabronidae, *Stizoides* parasitize in nests of large sphecids of the genus *Prionyx* and destroy the host eggs (very similar to *Evagetes*), smaller cleptoparasites of genera *Nysson*, *Epinysson*, and

Acanthostethus invade nests of their relatives of genus *Gorytes* s. l.[10], females lay eggs to fresh brood cells just before the host puts its egg inside.

Sapygidae are not much numerous family of Hymenoptera (about 80 species all around the world, 5 in central Europe), of obligate cleptoparasites very similar with their behaviour to cuckoo bees. Most of them invade nests of wood nesting solitary bees of the family Megachilidae; the females usually wait near the nests and lay their eggs stepwise to each of the host brood cells. They hide their little eggs usually somewhere between the leaf layers forming the panel on the sides of the nest (see ***Figure 5***); larvae emerge earlier than the host larvae. Some Sapygidae lay more eggs to one brood cell; in this case the larvae compete and sometimes kill each other. If they do not harm the host egg, host larva finishes its development in spite of the presence of sapygid larvae (O'Neill 2001). Large members of the genus *Polochrum* parasitize in large carpenter bees (*Xylocopa*), also wood nesting species. Only one known sapygid, *Fedtschenkia anthracina*, invades nests of eumenids, but no details on its bionomics are known (Bohart & Schuster 1972).

4.3. Specialization

The specialization in parasitic aculeate Hymenoptera except the cuckoo bees is very poorly known, not many studies were published. From the data published in broader reviews (e.g. Balthasar 1954; Bohart & Menke 1976; O'Neill 2001) we can recognize that both the specialists and generalists are common and their ratio probably corresponds with that of cuckoo bees (***Figure 3***). Bogusch (2006) has presented that the hosts of 29 central European Mutillidae are very poorly known only in the most conspicuous and abundant species, and the biology of majority of them is unknown.

The specialization should correspond to the life strategy (endoparasitoids, ectoparasitoids, nest cleptoparasites); several species seem to be specialized, i.e. egg

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[10] Previously, genera as *Argogorytes*, *Lestiphorus*, *Harpactus* and *Hoplisoides* were put under one genus *Gorytes* (Dolfuss 1991). Recently, *Gorytes* s.l. is used for all these genera together with genus *Gorytes* s. str.

parasitoids Amiseginae and Loboscelidinae. On the other hand, nest ectoparasitoids feeding on mature larvae, such as Mutillidae or Chrysididae, are usually unspecialised (small *Smicromyrme* species). Otherwise, Scoliidae and Tiphiidae usually seem to be specialized; the largest European scoliid *Megascolia maculata* invades larvae of two species of scarabaeid beetles of the genus *Oryctes* (Baťa et al. 1938). The specialization usually corresponds with abundance of species; common species in most cases seem to be the generalists. However, these types of information can be caused just with the abundance and better-known bionomics of common species.

4.4. Colouration and mimicry

The colouration of parasites brings many suggestions; its main advantage is that we can study it also on dried insects in collections. Most of aculeate Hymenoptera are conspicuously coloured. I divided colouration or patterns to six universal types. We can put all aculeate Hymenoptera under them, and the parasites occur in every type (members of all these colour patterns are shown in ***Figure 12***):

1. **Wasp-like black and yellow pattern (*Figure 12a*):** many cleptoparasites and parasitoids, e.g. Scoliidae, Sapygidae part, Sphecidae: *Stizoides*, most *Nysson* species, Megachilidae: *Stelis signata*, *S. nasuta*, Apidae: majority of *Nomada* species. This type of colouration is well distributed within aculeate Hymenoptera and certainly represents the most wide-spread aposematic pattern, all aculeate Hymenoptera with this pattern represent one Müllerian ring, palatable beetles (Cerambycidae: *Plagionotus*, *Clytus*), moths (Sesiidae), and plenty of flies (usually Stratiomyidae and Syrphidae) join this Müllerian ring as Batesian mimics.
2. **Black and red colouration (*Figure 12b*):** some Mutillidae (Myrmosinae), Pompilidae: *Evagetes*, Halictidae: *Sphecodes*, Apidae: *Ammobatoides*, *Pasites, Ammobates*, *Biastes brevicornis*. This colouration is typical for many cuckoo bees (see Chapter 2.3), but also for majority of Pompilidae, and many Sphecidae (*Ammophila*, *Podalonia*, *Sphex*, *Prionyx*) and Crabronidae (genera *Astata*, *Tachysphex*, *Tachytes*, *Alysson*). Probably together with the next one

it represents the second Müllerian ring, followed with many syrphid flies (*Eumerus* and others) as Batesian mimics.

3. **Black and red colouration with whitish spots:** the spots can be cuticular (***Figure 12c***), e.g. in several Sapygidae, Crabronidae: *Nysson dimidiatus*, Apidae: some *Nomada* species, or more frequently hairy (***Figure 12d***): Mutillidae, Apidae: *Epeolus*, *Epeoloides*, *Ammobates punctatus*. Also distributed in nonparasitic insects, this pattern is hardly explained, it probably lays somewhere between the above mentioned, and functionally reaches both of them.
4. **Black (*Figure 12e*):** Tiphiidae, Ampulicidae, and Megachilidae: *Stelis*, *Dioxys tridentata*. Parasites and parasitoids are usually aposematic; this colouration is well distributed among nonparasitic species. In some cases, males of red parasitic species are coloured black: Mutillidae: *Myrmosa*, *Paramyrmosa*, *Mutilla marginata*, *Dasylabris regalis*, *Physetopoda halensis*, Pompilidae: *Evagetes*, Halictidae: *Sphecodes niger*, Apidae: *Biastes brevicornis, B. truncatus*. In *Stelis* cuckoo bees this colouration corresponds with their mimicry to hosts (chapter 2.3.).
5. **Bee-like brown with hair (*Figure 12f*):** this colouration is typical for majority of nonparasitic bees, several cuckoo bees are coloured in this way: Megachilidae: *Coelioxys*, Apidae: *Melecta albifrons*. In both cases, the cuckoo bees parasitize in nests of their relatives, and the colouration is similar with them and shows relationship to their hosts. Males of some cuckoo bees where females are aposematic are bee-like coloured and hirsute (*Ammobatoides abdominalis*, *Epeoloides coecutiens*).
6. **Metallic colouration (*Figure 12g*):** typical for Chrysididae, metallic are also tropical Ampulicidae and some Mutillidae, and several species of cuckoo bees (*Thalestria*)[11]. This colouration occurs mainly in parasitic species, although some bees, usually tropical, are also metallic. Metallic aculeate Hymenoptera form the third, special Müllerian ring. Also blue bands or spots on black bodies of some *Thyreus* cuckoo bees can be put into this group: it

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[11] *Thalestria* is the cleptoparasite of *Oxaea*, non-metallic bee species. Several parasites are metallic, too: species of genera *Exaerete* and *Aglae*, but they probably evolved from their metallic coloured hosts (genera *Eulaema* and *Eufriesea*).

resembles blue metallic bands of their *Anthophora* hosts and they look in flight to be metallic coloured (see ***Figure 13***).

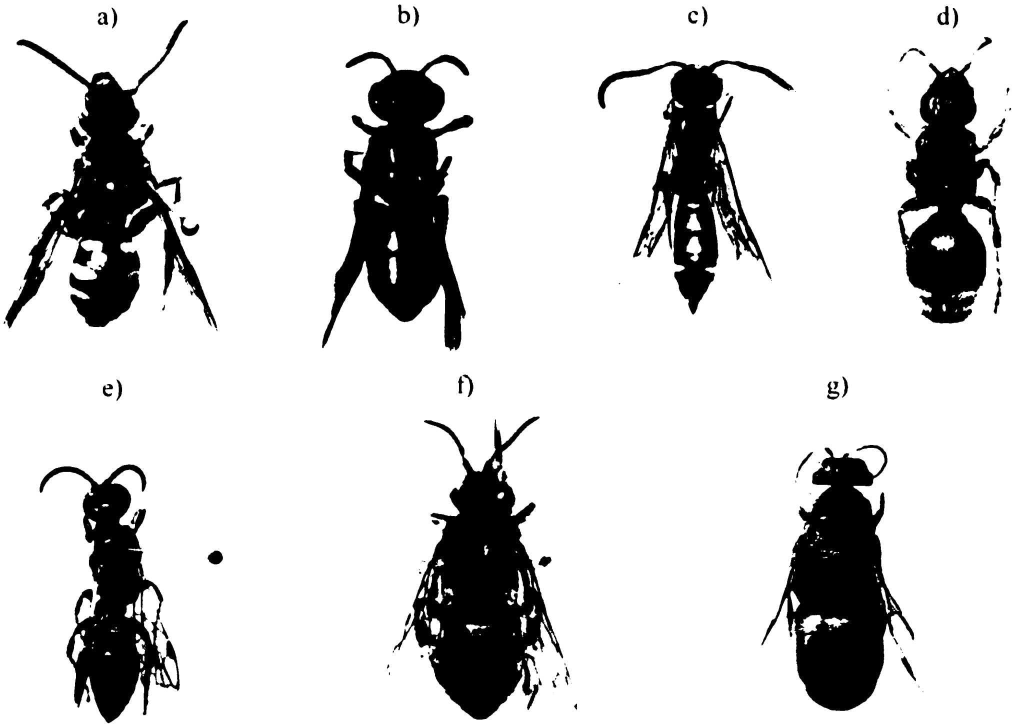

Figure 12: Types of colouration patterns in parasitic Hymenoptera. (a) wasp-like black and yellow cuckoo bee *Nomada sexfasciata*, (b) black and red coloured cuckoo bee *Sphecodes gibbus*, (c) black-red with yellow spots *Sapyga quinquefasciata*, (d) black-red with whitish hair velvet ant *Nemka viduata*, (e) black coloured *Tiphia femorata*, (f) brown haired cuckoo bee *Melecta albifrons*, (g) metallic coloured chrysidid wasp *Hedychrum rutilans*. All photos © P. Bogusch.

We found that three main Müllerian mimetic rings with one transcendental present in aculeate Hymenoptera and several other insects join them. The metallic ring looks most interesting: Suchantke (1965) divided in similar way colouration of tropical butterflies flying in different horizontal parts of tropical forests. He found that the metallic black and blue ones fly usually low over the ground, where the amount of sunshine is the lowest. Metallic coloured nonparasitic bees occur in the same parts of their habitat and probably correspond with Suchantke's (1965) definition. However, we probably cannot explain metallic colouration of parasitic chrysidid wasps and Ampulicidae (and this group occurs usually in higher latitudes of tropical forest) by this way.

The parasitoids usually attack the hosts of unrelated taxa and do not show any similarities to them. Also in cleptoparasites no mimetic resemblances are known, they mainly join Müllerian rings and are coloured aposematicaly. Large sapygid *Polochrum repandum* attacks the nests of black-violet *Xylocopa* bees but it resembles paper wasps (*Polistes*), probably to join wasp's Müllerian mimetic ring. Its colouration was in many cases interpreted as an adaptation to parasitize in paper wasp nests (Baťa et al. 1938), probably it is useful not to disturb nesting hosts (it is better to look like *Polistes* collecting wood than e.g. other *Xylocopa*, presence of the intraspecific parasitism is very likely in European *Xylocopa*). Most of the similarities of parasitic Aculeata to their hosts are in those parasitizing in nests of their relatives (Pompilidae: *Evagetes*, Crabronidae: *Nysson*). If we want to speak about mimicry, there are possibilities of chemical with the same indicia as in cuckoo bees: "friendly" behaviour of some host species during the parasitation, specialization of majority cleptoparasites (those with unrelated hosts too), and individual specialization in generalists, many different types of behavioural patterns used in different cleptoparasites, and broad use of aggressive mimicry both by myrmecophiles and termitophiles (Balthasar 1954; Michener 2000; O'Neill 2001). Balthasar (1954) also presented that some chrysidid wasps use typical stinking substances (probably volatile) to repel their hosts and to get easier into the nest.

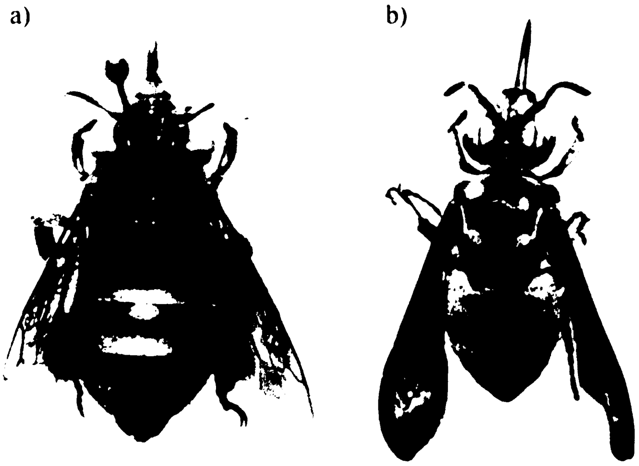

***Figure 13:* *Metallic coloured* Anthophora zonata (a) *and its black-blue parasite* Thyreus nitidulus (b).** All photos © P. Bogusch.

CONCLUSIONS

Since Poulton (1890) defined **aggressive mimicry**, many authors used this term to various mimetic types where the predator plays an important role and usually figures as the mimic or the model. Division of these mimetic types to five categories, all of them newly created and described, is useful, and - in my opinion - necessary. Next important purpose now among all mimetic categories is to change the meaning of the mimetic complex from the "complex of mimic and model" to the "mimic, model, and the acceptor of the signal", because knowing the acceptor in mimetic interactions is necessary for understanding them. The term **aggressive mimicry** should be in future used only for those interactions where the predator is a mimic and mimics its prey. This mimetic complex (in the newly established meaning) has only two members when the prey figures both as the model and the acceptor. As presented in the previous part, this mimetic type does not frequently occur in mimicry of general appearance or coloration, but mainly in patterns of a chemical or tactile communication. **Peckhamian mimicry** is a synonym to the aggressive mimicry, as defined by Poulton (1890); **Wasmannian mimicry** is a problematic term but I recommend to follow Rettenmeyer (1970) and use it as a subset of aggressive mimicry. **Aggressive resemblance, alluring mimicry,** and **hiding mimicry** are similar to the aggressive mimicry but the model is in all these cases different from the aggressive mimicry, and represented by other species than the acceptor.

Though crypsis and mimicry are not strictly divided and both depend on place and time (tiger in a zoological garden is a conspicuous animal, but in Indian grasslands it looks like a part of its environment), we must exclude **anticrypsis** from here-described interactions. The main difference is in the lack of imitation in anticrypsis, and this interaction is here mentioned only because some animals use both the anticrypsis and some type of aggressive mimetic interactions (crab spiders in flowers use the anticrypsis but some of them resemble whole flowers on green sprouts of plants – alluring mimicry). A very interesting mimetic type is **inverse mimicry** occurring usually in parasitoids, this type is self-defined but unlike the aggressive mimicry. Here the roles are inverted, the prey or host is the mimic of its predator or parasite.

Cuckoo bees form together with the family Sapygidae, several Chrysididae, Pompilidae, Sphecidae and Crabronidae, a well-defined ecological group of nest cleptoparasites (see also O'Neill 2001). They invade nests of insects of the same groups and use similar tactics in parasitation, which could be interpreted as behavioural patterns described by Bogusch (2005) and Bogusch et al. (2006). These tactics (from "friendly" to fighting with stings) depend mainly on the type of host nest and also on the parasite's ability to use chemical and/or tactile weapons, including the aggressive mimicry. As nest cleptoparasites apparently evolved from their nesting relatives (better from their hosts), majority of them parasitize in nests of unrelated taxa (see chapter 2.1.) and most of them are more or less specialized. In those unspecialised individual females are specialized and each female parasitizes in the nests of only one host species like cuckoos in bird nests (Packer et al. 1995; Bogusch et al. 2006). It means that in an individual level all hymenopteran cleptoparasites seem to be specialized. Many of them are similar to their hosts in body shape and/or coloration; these similarities are in various species parts of aggressive mimicry, characters of the phylogenetic relationship, or Müllerian mimetic signals to the predators. The evolution of interspecific cleptoparasitism went from intraspecific cleptoparasitism, which is common in several bee and wasp species. Nest usurpation in bumblebees represents another type of intraspecific nest parasitism presenting in social insects. Hosts of cleptoparasites are originally their nearest relatives, many of them had to re-orientate to other species. The process of re-orientation went to the emergence of generalists, and also to origin of secondary use of chemical or tactile weapons, means of aggressive mimicry.

Social parasites use similar strategies of parasition as the cleptoparasites do; they are usually strictly bounded to their hosts. Like the cleptoparasites they use various types of aggressive and gentle behaviour and many of them (best known in myrmecophiles and termitophiles) use chemical and/or tactile aggressive mimicry to get into the host's nest (Hölldobler & Wilson 1995). Wasp and bumblebee parasites probably do the same. Unique social parasites are the hover flies of the genus *Volucella*, which unlike other social parasites use both Müllerian and aggressive mimicry (not all species) and take part in mimetic rings represented by their hosts.

Their behaviour and similarities in appearance to hosts are conspicuous, so they much differ from other social parasites (e.g. myrmecophilous beetles, caterpillars or crickets) but are very similar to the cleptoparasites.

Unlike the cleptoparasites, the **parasitoids** have evolved from prey hunting Hymenoptera and are not strictly bounded to the hosts in coloration and mimicry. Most of them use various strategies how to parasitize in host's nests, owing to their body sclerotization they usually aggressively kill hosts (Mutillidae, Scoliidae). However, many exceptions have been described, as chrysidid egg parasitoids in Phasmatodea and some other chrysidid parasitoids with "friendly" behaviour to their hosts (O'Neill 2001).

Mimetic resemblances in general appearance and coloration are in many cases not aggressive, they are oriented to the hosts and it is better to classify them as Müllerian. They are ranged against the predators, i.e. birds, lizards, or frogs. There are three main types of aposematic coloration in aculeate Hymenoptera forming three distant mimetic rings: (a) black and yellow wasp-like, the most distributed among nearly all groups of Aculeata, and followed by Batesian mimics, i.e. hover flies, long horned beetles, or moths; (b) metallic usually with blue-greenish and gold-reddish coloration, used in majority of Chrysididae, and followed by some flies and beetles (I do not think that metallic coloured carabid beetles are members of the same mimetic rings as chrysidid wasps, but some small chrysomelids or meloids probably are); (c) black and red typical for many cuckoo bees, pompilid and sphecid wasps, and also many hover flies. In some cases the insects are black and red coloured with whitish spots or hairy bands; this pattern forms transition between types (a) and (c). Other coloration types (bee-like brownish with hair, black or dark) are not aposematic and cannot form Müllerian rings. We can also put bumblebees with their social parasites under Müllerian mimicry – cuckoo bumblebees and hover flies of the genus *Volucella*. Three colour forms of *Volucella bombylans* follow three main aposematic colour patterns in bumblebees; the fourth usual pattern is not aposematic (brownish, type species *Bombus pascuorum*).

On the other hand, similarities of *Stelis* bees, cuckoo bumblebees, and some other cleptoparasites and social parasites look neither corresponding with the phylogenetical relations, nor as Müllerian rings. These similarities can be interpreted as an aggressive mimicry in general appearance and coloration but they probably serve to defend in the nest surroundings and not in the nest of the host. Wasp-like coloration of *Nomada* bees or *Polochrum* could represent the case of aggressive resemblance; they look like some not dangerous animal for the host, are overseen and can get nearer to the host nest. Kleisner & Markoš (2004) brought an interesting interpretation of all these similarities with their theory of semes – units of imitation. This theory could be well placed over the mimetic rings among aculeate Hymenoptera, their parasites and mimics.

It is very difficult to make any conclusions on chemical and tactile aggressive mimicry in cleptoparasites and social parasites in aculeate Hymenoptera, because we have only pour information. We can state that they occur both in social parasites and cleptoparasites and they concern not in appearance and coloration but chemical and tactile communication in both groups. Tengö & Bergström (1977) published the only proof, but it does not explain how the parasiting females use the aggressive mimicry (in my opinion all of them surely do not get their scent from the males during the mating process). Presence of aggressive mimicry can be supported by several observed things in cleptoparasites, e.g. "friendly" behaviour of some host species during the parasitation, specialization of majority cleptoparasites (those with unrelated hosts too), and individual specialization in generalists, many different types of behavioural patterns used in different cleptoparasites, and broad use of aggressive mimicry both by myrmecophiles and termitophiles.

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SOUHRN

Poulton (1890) zavedl pojem **„agresivní mimikry“** v roce 1890 na základě objevu pavouků, kteří vypadali jako mravenci. Tento objev publikovala Peckham (1889) a dokonce se pokusila o vysvětlení vzhledu těchto živočichů. Poulton (1890) však pojem striktně nedefinoval, jen uvedl, že pod agresivní mimikry lze řadit ty typy mimetismu, ve kterých hraje predátor podstatnou úlohu v roli mimetika nebo modelu. V následujících letech pak pod tento termín rozliční autoři shrnovali řadu mimetických komplexů, které spolu ale příliš nesouvisí. Agresivní mimikry se staly jakousi sběrnou skupinou pro mimetické typy, které nelze nikam zařadit, a nějak souvisí s predací či parazitizmem.

Hlavním cílem této studie bylo tedy rozdělit dosud známé mimetické komplexy shrnované dříve pod agresivní mimikry do několika jasně rozlišitelných kategorií. Toto rozdělení je dle mého soudu nutné a významně pomůže příštím autorům chápat zmíněné pojmy. Dále jsem pozměnil význam termínu mimetický komplex: dosud byl chápán jako dvojice mimetik – model, v novém pojetí se jedná o trojici mimetik – model – příjemce signálu. Zejména u agresivně mimetických interakcí je nutné znát povahu příjemce signálu právě pro chápání souvislostí a vztahů mezi jednotlivými prvky mimetického komplexu.

Jako **agresivní mimikry** (aggressive mimicry) lze označovat jen ty případy, kdy predátor nebo parazit je mimetikem, a jeho kořist nebo hostitel modelem i příjemcem signálu. Znamená to, že predátor napodobuje něco druhově specifického pro svou kořist (vzhled, komunikační chemickou látku, taktilní signál, zbarvení...). Vystupují zde tedy jen dva organismy, na rozdíl od všech následujících mimetických typů, přičemž model je i příjemcem signálu. **Peckhamovské mimikry** (Peckhamian mimicry) je synonymem jak definoval již Poulton (1890), **Wassmanovské mimikry** (Wasmannian mimicry) je poměrně problematický pojem, neboť zahrnuje rozmanité interakce včetně mutualismu, ale zastávám názor Rettenmeyera (1970) klasifikovat jej jako podmnožinu agresivního mimetismu týkající se myrmekofilů a myrmekoidů. V případě **agresivní nápodoby** (aggressive resemblance), **lákajícího mimetismu** (alluring mimicry) a **ochranného mimetismu** (hiding mimicry) není model totožný s příjemcem signálu; predátor (mimetik) obvykle napodobuje něco nezajímavého nebo naopak atraktivního pro svou kořist.

Antikrypse je opačným případem schovávání se před predátorem, jedná se o predátora schovávajícího se před kořistí. Ta jej nevidí a on může zaútočit (vzpomeňte třeba na kudlanky). I když se nejedná o mimetickou interakci (nikdo nikoho nenapodobuje), některé organismy používají střídavě antikrypsi a některý z agresivně mimetických typů při lovení kořisti. Typickým příkladem je pavouk běžník kopretinový (*Misumena vatia*), který mění barvu a ztratí se v květu (antikrypse), ale občas napodobuje celé květy na vrcholcích prýtů zelených rostlin (lákající mimikry). Dalším trochu odlišným, ale mimetickým typem, jsou **obrácené mimikry** (inverse mimicry), kdy kořist či hostitel napodobuje svého predátora/parazita. Zde vystupují také jen dva organismy, jedná se však o typ mimetismu, který nemá mnoho společného s agresivním mimetismem.

Kleptoparazitické (kukaččí) včely představují společně s drvenkami (Sapygidae), některými zlatěnkami (Chrysididae), hrabalkami (Pompilidae) a kutilkami (Sphecidae et Crabronidae) dobře definovanou ekologickou skupinu označovanou jako hnízdní paraziti nebo hnízdní kleptoparaziti (O'Neill 2001). Samice těchto druhů kladou vajíčka do hnízdních buněk jiných žahadlových blanokřídlých a larvy se živí zásobami, které hostitel nastřádal pro své potomstvo. Při parazitaci používají podobné způsoby oklamání hostitele, které popsali Bogusch (2005) a Bogusch et al. (2006) jako vzorce chování (behavioral patterns). Ty závisí zejména na typu hnízda hostitele a na schopnosti parazita užívat chemické či taktilní prvky agresivního mimetismu, obvykle se projevují na celé škále chování od „přátelských kontaktů" po souboje žihadly.

Hnízdní kleptoparaziti vznikli zřejmě ze svých nejbližších příbuzných, jak tvrdí Emery (1909) a Carpenter et al. (1993). Je proto zvláštní, že většina z nich parazituje v hnízdech fylogeneticky nepříbuzných druhů. Většina druhů je specializovaná na parazitaci v hnízdech menšího množství druhů, u těch, kteří mají více než 10 druhů hostitelů, se předpokládá, že každá samice je specializovaná pouze na jeden druh hostitele. Experimentálně to bylo prokázáno u dvou severoamerických druhů rodu

Coelioxys (Packer et al. 1995) a dvou evropských druhů rodu *Sphecodes* (Bogusch et al. 2006). Znamená to, že generalisti (nespecializované druhy) existují jen na úrovni druhů a způsob specializace kukaččích včel opravdu výrazně připomíná kukačky (Bogusch et al. 2006). Interspecifický (mezidruhový) hnízdní kleptoparazitizmus určitě vznikl z kleptoparazitizmu intraspecifického (vnitrodruhového), který je častý u řady druhů primárně neparazitických včel či vos a „nest usurpation“ u čmeláků představuje asi nejznámější případ. Během času se kleptoparaziti mění a mění se i spektrum jejich hostitelů. Tento proces nazýváme přeorientování (re-orientation) a vede nejen ke vzniku generalistů, ale i k parazitaci v hnízdech fylogeneticky nepříbuzných druhů. Řada druhů hnízdních parazitů je svým hostitelům navíc podobná v tvaru těla nebo zbarvení. Tato podobnost může představovat tři různé adaptace: 1) podobnost příbuzenská, u těch druhů, které parazitují dále u svých příbuzných je samozřejmě dobře rozeznatelná, o intragenerických kleptoparazitech nemluvě; 2) výstražné zbarvení a účast v Müllerovských mimetických okruzích, s tím souvisí červené nebo jinak nápadné zbarvení řady kleptoparazitů; 3) agresivní mimikry, které však lze předpokládat jen v malém množství případů.

Sociální paraziti používají při parazitaci podobné taktiky jako hnízdní kleptoparaziti, jsou však více vázaní na své hostitele. Užití chemických a taktilních zbraní, které jsou často nástrojem agresivního mimetismu, je známé u řady myrmekofilů a termitofilů (viz např. Hölldobler & Wilson 1995; Žďárek 1997), a včelí a vosí paraziti se chovají asi velmi podobně. Unikátními parazity jsou pestřenky rodu *Volucella*, které využívají Batesovské i agresivní mimikry a účastní se coby Batesovské prvky mimetických okruhů okolo jejich hostitelů – vos a čmeláků. Jejich chování a vzhled jsou nápadně podobné jejich hostitelům, čímž se svými mimetickými strategiemi odlišují třeba od myrmekofilů, ale naopak přibližují kleptoparazitům.

Parazitoidi vznikli z hnízdících lovců a nejsou obvykle přímo vázaní na své hostitele, ani nevykazují znaky agresivního mimetismu. Jejich strategie parazitace v hnízdech hostitelů jsou často agresivní, většinou korespondují s mírou sklerotizace jejich těl a řada z nich své hostitele zabíjí, např. kodulky (Mutillidae) a žahalky

(Scoliidae). Na druhou stranu někteří mají hodně odlišné životní strategie, např.zlatěnky parazitující ve vajíčkách strašilek (O'Neill 2001).

Mimikry ve vzhledu a zbarvení ve většině případů nejsou adresovány hostitelům, ale predátorům, tj. ptákům, ještěrkám, žábám apod. Jedná se tedy o mimetismus Müllerovský a autor zde definoval tři hlavní mimetické okruhy, které jsou tvořeny běžnými druhy žahadlových blanokřídlých a jejich nepalatabilními (Müllerovské mimikry) a palatabilními (Batesovské mimikry) mimetiky. Jsou to: 1) černo-žluté vosí zbarvení, velice rozšířené skoro ve všech skupinách žahadlových blanokřídlých s Batesovskými prvky z řad pestřenek (Syrphidae), tesaříků (rody *Plagionotus*, *Clytus*) a nesytek (Sesiidae); 2) kovové většinou s modrou, zelenou a červenou barvou, které se vyskytuje u zlatěnek (Chrysididae), řady dvoukřídlých a brouků; 3) červeno-černé typické právě pro žahadlové blanokřídlé – kukaččí včely, hrabalky a kutilky, a také několik rodů pestřenek. Některé druhy žahadlových blanokřídlých vykazují černo-červené zbarvení s bílou nebo žlutou kresbou, která je v některých případech (kodulky – Mutillidae) suplována skvrnami ze světlých chlupů. Toto zbarvení pravděpodobně představuje přechod mezi typy 1) a 3). Ostatní typická zbarvení nejsou aposematická a netvoří mimetické okruhy. Dílčí mimetické okruhy jsou tvořeny jednotlivými skupinami parazitů a jejich hostitelů, např. tři základní typy zbarvení čmeláků (*Bombus*) a jejich parazitů pačmeláků (*Psithyrus*), následované třemi barevnými formami čmeláčího parazita *Volucella bombylans*. Poslední, hnědo-rezavý typ zbarvení našich čmeláků, představovaný např. druhem *Bombus pascuorum*, netvoří mimetické okruhy, stejně jako neaposematické typy zbarvení včel.

Nápadná podobnost kleptoparazitických včel rodu *Stelis* s hostiteli a podobnost pačmeláků jejich hostitelům však nespadají jen pod příbuzenské podobnosti nebo obranu před predátory. Tyto podobnosti zřejmě slouží k oklamání hostitele v blízkosti jeho hnízda a je možné je tedy klasifikovat jako agresivní mimikry. Jejich využití však není v hnízdě, kde hrají svou roli spíše taktilní a chemické signály, ale v okolí hnízda nebo hnízdiště hostitele. Žluto-černé vosí zbarvení kukaččích včel rodu *Nomada* a drvenek rodu *Polochrum* může být agresivní nápodobou, kdy tyto druhy napodobují nějaké pro predátory nebezpečné, ale pro hostitele nezajímavé druhy.

Chemické a taktilní agresivní mimikry jsou poměrně rozšířené mezi sociálními parazity mravenců, je však velmi obtížné dělat závěry o jejich úloze v komunikaci kukaččích včel se svými hostiteli. Jediný důkaz jejich přítomnosti publikovali Tengö & Bergström (1977), využití komunikační chemikálie při parazitaci však příliš nevysvětlili. Přítomnosti agresivního mimetismu u hnízdních kleptoparazitů také nasvědčují některé jejich behaviorální znaky, jako jsou „přátelské“ kontakty mezi kleptoparazitem a hostitelem u řady druhů, specializace většiny kleptoparazitů, i těch s nepříbuznými hostiteli, a individuální specializace u generalistů, mnoho rozmanitých vzorců chování využívaných při parazitaci, a široké využití agresivního mimetismu u myrmekofilů a termitofilů.

PŘÍLOHA 1

BOGUSCH P. 2003: Včely jako paraziti a hostitelé. *Vesmír* **82** (9): 501-505.

Čmelák rolní (*Bombus pascuorum*), snímek © Václav Laňka

Kukačky včelí říše

Včely jako paraziti a hostitelé

PETR BOGUSCH

Včela medonosná (*Apis mellifera*) představuje svým způsobem života mezi včelami podobný extrém jako člověk mezi savci. Většina ostatních včel (a není jich zrovna málo) žije samotářsky. Každá samice se po vylíhnutí páří, vytvoří hnízdo v zemi nebo ve dřevě, nanosí do něj pyl a nektar z květů a naklade vajíčka. Dále už se o hnízdo nestará – buď má svou práci hotovou, nebo začne stavět další hnízdo. Larvy se živí nastřádanými, převážně pylovými zásobami a v hnízdě se i kuklí. Vylíhlá samička se prohrabe či prokouše ven, vyhledá samce – a koloběh začne nanovo.

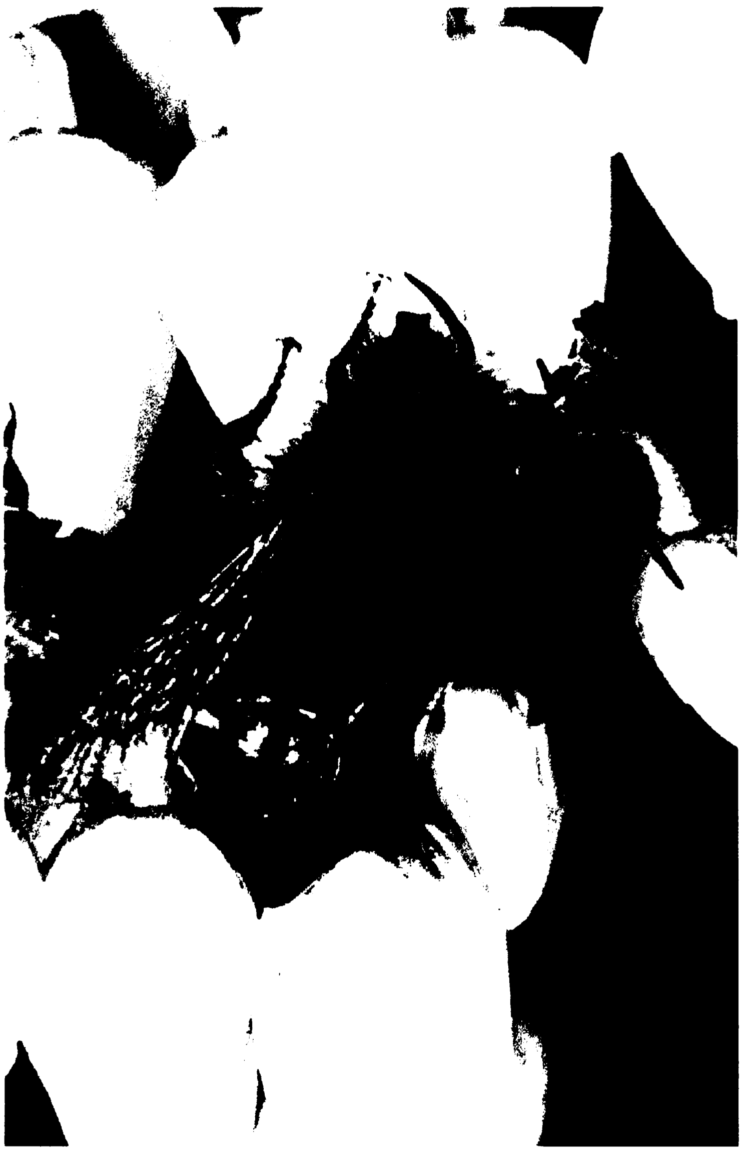
Sociálně žije jen několik málo skupin včel. V jednom hnízdě jich je větší množství a buď se každá stará o něco, nebo se starají všechny o všechno. V každém případě jim jde práce od ruky rychleji než té chudince, která musí dělat všechno sama. Podobně jako jiný společenský hmyz mohou být i sociální včely rozrůzněny na kasty – některé samice jen kladou vajíčka, jiné jen pracují. Na vrcholu vývoje stojí právě včela medonosná, u níž je v jednom hnízdě jedna královna, která klade vajíčka a žije až tři roky, a mnoho dělnic, které žijí asi dva měsíce a vykonávají všechny potřebné práce. Samci, označovaní včelaři jako trubci, pouze oplodňují mladé, čerstvě vylíhlé královny.

U sociálních včel však můžeme najít mnoho různých způsobů soužití (viz rámeček na následující straně). U těch nejprimitivnějších jen více samic používá stejný vchod do hnízda. Čmeláci žijí v koloniích, ale přezimuje jen královna, která každý rok zakládá novou kolonii. Nejkomplexnější jsou společenstva včely medonosné a tropických bezžihadlových včel (Meliponini), neboť nezanikají ani úhynem královny.

Kleptoparazitické včely

Ani do jedné z výše uvedených kategorií nespadají včely kleptoparazitické (z řeckého *klépto* – kradu). Samice těchto včel si nestavějí žádné hnízdo ani nezkoušejí spolupracovat a tvořit společenstva, ale kladou svá vajíčka do hnízd jiných druhů včel, stejně jako kukačky u ptáků. Proto jsou tyto včely označovány i jako „včely-kukačky“. Kladoucí samice nebo vylíhlé larvy zlikvidují vajíčka či larvy hosti-

Mgr. Petr Bogusch (*1980) vystudoval entomologii na katedře zoologie Přírodovědecké fakulty UK v Praze. V současné době se připravuje na doktorské studium teoretické biologie na katedře filozofie a dějin přírodních věd Přírodovědecké fakulty UK v Praze. Zabývá se zbarvením, ekologií a etologií samotářských včel, především kleptoparazitických druhů.



Samec zednice rezavé (*Osmia rufa*). Snímek © Vaclav Laňka

telského druhu. Larva se živí pylem, který do hnízda nanosila samice hostitele.

I když se může zdát, že kleptoparazitických včel asi není mnoho, podle práce S. W. T. Batry z r. 1984 představují asi 15 % všech druhů včel na světě. V České republice by číslo bylo ještě vyšší, asi 25 %. Z nějakých 600 druhů našich včel je jich asi 140 kleptoparazitických. Nepředstavují ovšem žádnou systematickou jednotku. Jde pouze o určité rody z různých čeledí. Vypadají podobně jako příbuzné, normálně žijící včely, liší se jen způsobem života.

Podle čeho takovou včelu poznáme? Znaků je samozřejmě více. Samicím kleptoparazitických včel nejčastěji chybí sběrací aparát na břiše nebo na nohách třetího páru. Samci mají o jeden tykadlový článek více než samice, ale spočítat články tykadel u včely sedící někde na louce na květu skoro není možné. Kleptoparazitické včely také bývají málo ochlupené nebo nápadně zbarvené, takové jsou ale i některé neparazitické včely.

Je lepší podívat se na situaci z jiného úhlu - neptat se, jak kleptoparaziti vypadají, ale co dělají. Musí totiž nějak oklamat svého hostitele a dostat se do jeho hnízda. Každého asi hned napadne, že by mu mohli být podobní. A skutečně! Řada druhů to tak dělá, snaží se svého hostitele napodobit. Některé mají jen stejný tvar těla či hlavy nebo jiné morfologické struktury důležité u včel pro rozpoznání příslušníků vlastního druhu, jiné jsou i stejně zbarvené. Například „kukačka" *Stelis signata* vypadá úplně stejně jako hostitel *Anthidiellum strigatum*, liší se jen tím, že nemá sběrací aparát na břiše. Nejenže je druh *Biastes brevicornis* velmi podobný včelám rodu *Systropha*, v jejichž hnízdech cizopasí, ale také létá na stejné rostliny a nocuje v jejich květech (např. v květech svlačce). Pokud pozorujeme kukaččí včely u hnízd hostitelů, často si můžeme všimnout, že jsou do hnízda vpuštěny bez jakéhokoliv souboje. Výjimkou není ani společný přílet a vstup do hnízda s hostitelskou samicí.

Jiné včely-kukačky jsou naopak zbarveny výstražně. Na jejich těle se často střídá černá s červenou nebo žlutou barvou. Sázejí na překvapení či bázeň, napodobují vosy a jiné nebezpečné tvory nebo prostě jen varují, že jsou nebezpečné. Při setkání se samicí hostitele často používají žihadlo. Někdy dokonce samice kleptoparazita u vchodu do hnízda cíleně zabíjejí hostitele.

Posledním typem, vlastně kombinací obou předchozích, jsou včely-kukačky, které sledují hostitele v terénu nebo vyčkávají nedaleko jeho hnízda. Některé kleptoparazitické včely doslova „stojí" ve vzduchu (podobně jako některé parazitické mouchy) několik centimetrů za samicí hostitele, která na rostlině sbírá pyl či nektar. Snadno ji pak mohou sledovat až k hnízdu. Takový příživník jen vyčká, až hostitel odletí, a má zelenou.

Proč některé druhy vyhledávají hostitele, kteří jsou jim příbuzní?

Výše uvedené údaje naznačují, že není jedno, do jakého hnízda samice kukaččí včely nakla-

SOCIALITA U VČEL

SAMOTÁŘSKÉ (SOLITÉRNÍ) CHOVÁNÍ: Každá samice si staví svoje vlastní hnízdo, nosí do něj pyl a nektar, klade svoje vlastní vajíčka.

SPOLEČENSKÉ (SOCIÁLNÍ) CHOVÁNÍ: Skupinové soužití nebo spolupráce několika samic jednoho druhu, často rozlišeni dominantní a submisivní (podřízení) jedinci.

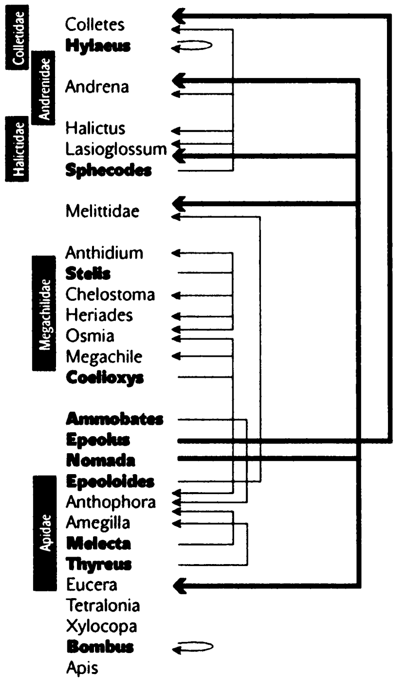
– Komunální chování: **U druhů s velkými agregacemi hnízd či se společným vchodem do více hnízd samice spolupracují při hlídání.**

– Subsociální chování: **Samice včel se starají o potomstvo, krmí je.**

– Semisociální chování: **Jedné plodné samici pomáhá při obraně hnízda několik jiných, nekladoucích samic, podobné chování se vyskytuje u ptáků (tzv. helper-jedinci).**

– Eusociální chování: **Rozdělení jedinců ve společenstvu na plodné samice (královny), které žijí často až několik let a zajišťují rozmnožování, a dělnice, které žijí několik týdnů, jsou neplodné a vykonávají všechny potřebné práce. Sem patří např. včela medonosná (*Apis mellifera*) a čmeláci (*Bombus*).**

Podle C. D. Michenera (1974) a W. T. Wcisla & B. N. Danfortha (1997)



Některé rody našich včel seřazené podle fylogenetické příbuznosti. Jednotlivé skupiny rodů představují jednotlivé čeledi včel. Kleptoparaziti (tučným písmem) jsou propojeni se svými hostiteli, spojnice je u hostitele zakončena šipkou. Každá šipka tedy vychází od kleptoparazita a směřuje k hostiteli nebo k hostitelům. Z obrázku je patrné, že někteří kleptoparaziti mají více rodů hostitelů, jiní parazitují jen u příbuzných taxonů a ještě jiní téměř výhradně u taxonů nepříbuzných. U nepříbuzných parazitují zejména včely rodu *Epeolus* a *Nomada*, u nichž jsou spojnice vyznačeny tlustými čarami. Některé druhy rodu *Hylaeus* a někteří čmeláci parazitují na jiných zástupcích téhož rodu, což vyznačuje šipka otáčející se zpět ke stejnému rodu

de svoje vajíčka. Každý druh má jednoho nebo několik svých hostitelů. Entomology vždy zajímalo, jestli v tomto výběru existují nějaké zákonitosti.

V roce 1909 uvedl profesor C. Emery ve své práci o mravencích parazitujících u jiných mravenců, že *parazit bývá nejbližším příbuzným svého hostitelského druhu.* Tuto větu, v dnešní době označovanou jako *Emeryho pravidlo*, aplikoval E. O. Wilson v druhé polovině dvacátého století i na ostatní žahadlové blanokřídlé (Aculeata) včetně včel. Podle J. M. Carpentera se pravděpodobný společný předek obou druhů rozdělil do dvou linií, parazitické a hostitelské. Zjednodušeně řečeno, někteří jedinci kdysi vynalezli snadnější životní strategii. Už nemuseli stavět hnízda a nosit do nich zásoby pylu, a pokud se ubránili případnému zavržení ostatními členy druhu, mohli poměrně snadno se svou novou strategií přežít. Nově vzniklí parazitičtí jedinci se možná ani nemuseli bát žádných útoků, protože si prostě zachovali některé důležité prostředky hmatové a chemické komunikace stejné jako jejich hostitel.

Emeryho pravidlo však zřejmě neplatí neomezeně. Už na první pohled každého zarazí, že řada kleptoparazitických druhů klade svá vajíčka do hnízd včel, které zaujímají ve fylogenetickém stromě hodně vzdálená místa (schéma na této straně). Některé druhy rodu *Sphecodes* se specializují na parazitaci v hnízdech blízce příbuzných zástupců rodů *Halictus* a *Lasioglossum*, ale zaměřují se i na nepříbuzné druhy rodu *Andrena* nebo *Colletes*. Existují totiž ještě jiná kritéria, jak si kleptoparaziti vybírají svého hostitele. Malý příklad - ve střední Evropě žije necelých třicet druhů rodu *Sphecodes*, z nichž čtyři - na rozdíl od ostatních - parazitují téměř výhradně u nepříbuzných včel. Zřejmě se během svého vývoje přeorientovaly na příživnictví u nových hostitelů. Proč? Inu třeba je to méně práce, třeba se tito hostitelé tolik nebrání nebo jich je prostě na lokalitě víc.

Kleptoparazitické druhy se tedy během svého fylogenetického vývoje nemusí striktně držet svých hostitelů, naopak se předpokládá, že přibírají nové. Příkladem mohou být právě okruhy hostitelů některých druhů rodu *Sphecodes*, ze kterých si můžeme poskládat krásnou řadu…

Nahoře: samec včely druhu *Anthidium manicatum*. Dole: Samice čalounice (*Megachile nigriventris*) odkusuje části listu, jimiž vystýlá hnízdní buňky. Snímek © Václav Laňka

	Halictidae	Megachilidae	Apidae
druhy specializované na jediný druh	4	4	2
specializované druhy (2-5 druhů)	7	6	11
nespecializované druhy (více druhů jedné skupiny)	4	8	1
generalisté (i více rodů)	1	1	0
přeorientované druhy (na jiné skupiny)	3	1	0
přeorientovaní specialisté (na 1 nepříbuzný druh)	1	0	0
hostitelé neznámí	7	4	2

Tab. I. Počty specializovaných a nespecializovaných druhů kleptoparazitických včel rozložené do šesti kategorií podle specializace kleptoparazitických druhů. Jako přeorientované byly brány v úvahu pouze některé druhy početnějších rodů *Sphecodes* a *Coelioxys*, u nichž je takové vysvětlení nejpravděpodobnější. Čeleď Halictidae zahrnuje zástupce jediného rodu *Sphecodes*, čeleď Megachilidae rod *Coelioxys* s 13 druhy, *Stelis* s 9 druhy a dva malé rody, čeleď Apidae zástupce 8 rodů s 1–5 zástupci. Nejčastěji specializovaní jsou zástupci čeledi Apidae, u rodu *Sphecodes* najdeme nejvíce přeorientovaných zástupců, což však souvisí spíše s početností rodu. Do tabulky nebyly zaznamenány údaje o nejpočetnějším rodu *Nomada* a řadě vzácných druhů, u nichž vůbec neznáme hostitele.

JAK SE MŮŽE KLEPTOPARAZIT PODOBAT SVÉMU HOSTITELI? (VNÍMÁNO Z LIDSKÉHO POHLEDU)

- **Kleptoparazit s hostitelem si mohou být podobni k nerozeznání. Jen při detailním pozorování lze rozeznat jednoho od druhého. Často musíme jedince usmrtit a zkoumat pod lupou. Takto se hostitelům podobají např. zástupci rodu *Stelis* a samozřejmě druhy, jejichž hostiteli jsou úplně nejbližší příbuzní, čili jiní zástupci téhož rodu (některé druhy rodu *Hylaeus* a pačmeláci rodu *Psithyrus*).**
- **Někteří kleptoparaziti jsou podobní svým hostitelům barevně, morfologická podobnost už tak výstižná není. Z našich zástupců jde o druhy rodu *Coelioxys*, parazitující na příbuzných druzích rodu *Megachile* a *Osmia*.**
- **Nejčastěji jsou kleptoparazitické druhy svým hostitelům podobné tvarem těla a velikostí, ale barevně se liší. Zbarvení jejich těl je často aposematické nebo obsahuje červenou. Tak vypadají např. všechny druhy rodů *Biastes* a *Sphecodes*, druh *Epeoloides coecutiens* nebo zástupci rodů *Thyreus* a *Melecta*.**
- **A nakonec nemusí být kleptoparaziti svým hostitelům podobní vůbec. Připomeňme jen nomády a jejich hostitele rodu *Andrena* nebo kleptoparazity rodu *Epeolus*, kteří jsou úplně odlišní od svých hostitelů rodu *Colletes*.**

- Druh *Sphecodes rufiventris* má jediného známého hostitele, který je mu blízce příbuzný. Nikdy nebyla pozorována parazitace jiného druhu, tento kleptoparazit je tedy specializován jen na jediného hostitele a je mu věrný.
- Jiný druh má čtyři nebo pět hostitelů a všichni jsou mu příbuzní.
- Další druh parazituje nejméně na deseti druzích náležejících do příbuzných rodů.
- Ještě jiný druh parazituje na velkém množství (zatím známe asi dvacet druhů) příbuzných včel, ale i na několika druzích nepříbuzného rodu *Andrena*. Tady vstupuje do hry nový prvek, a sice nepříbuzný hostitelský druh.
- Tři druhy rodu *Sphecodes* parazitují u některých zástupců nepříbuzných druhů rodu *Andrena*. Všechny tyto kleptoparazitické druhy žijí na teplých písčitých lokalitách, kde jsou některé druhy rodu *Andrena* velmi početné, na rozdíl od zástupců rodů příbuzných parazitovi.
- Zvláštním článkem tohoto řetězce by mohl být druh *Sphecodes albilabris*. Má jediného hostitele, nepříbuzný druh *Colletes cunicularius*, který létá pouze od března do května a je v době svého výskytu na písčitých lokalitách nejhojnější včelou. Parazit má jen jednu generaci do roka (naprostá většina ostatních zástupců rodu má generace dvě), přičemž samice létají od července do května příštího roku, před zimou se páří a na jaře kladou svá vajíčka do hnízd hostitele. Parazit přizpůsobil svůj životní cyklus životnímu cyklu hostitele.

Zadní křídlo včely medonosné (*Apis mellifera*). Na přední hraně křídla (v horní části snímku) jsou patrné háčky, které za letu spojují obě křídelní plochy v jednu. Snímek © František Weyda

Co jsou generalisté, specialisté a přeorientované druhy?

Nebude na škodu uvedené postřehy rozškatulkovat. Je patrné, že každý druh má jiný počet hostitelů.

- *Specialista* je specializován; v našem případě parazituje u jednoho či několika málo hostitelů.
- *Generalista* specializován není a hostitelů má více, ba dokonce mnoho.
- *Přeorientovaný druh* je kleptoparazit, který si našel nové nepříbuzné hostitele.

Přeorientování všech kleptoparazitů však nelze bezpečně určit, jelikož neznáme detailně fylogenetický vývoj včel a u některých málo početných parazitických rodů cizopasí všechny druhy u nepříbuzných hostitelů. U početných rodů však platí, že několik málo zástupců má hostitele z jiné skupiny než všichni ostatní. Kromě druhů rodu *Sphecodes* je tomu tak kupříkladu u rodu *Coelioxys* (ve střední Evropě žije necelých 20 druhů), kde jeden zástupce parazituje výhradně na nepříbuzných včelách a několik dalších druhů má ve svém okruhu hostitelů alespoň jeden sobě nepříbuzný druh. Zástupci nejpočetnějšího rodu *Nomada* kladou svá vajíčka do hnízd rozmanitých druhů rodu *Andrena* (které jsou kleptoparazitovi nepříbuzné), několik málo kleptoparazitů tohoto rodu má hostitele z dalších čtyř rodů včel. Nejvíce specialistů najdeme u čeledi Apidae (viz tabulku I).

Jak si rozdělují práci samice jednoho druhu kleptoparazita?

Jak to chodí, pokud má kleptoparazit více hostitelů? Dejme tomu, že na lokalitě létá větší množství samic jednoho „kukaččího" druhu a samice pěti hostitelských druhů si budují hnízda, nosí do nich zásoby a kladou vajíčka. Soustředí se všechny samice kleptoparazita na jeden nejběžnější druh hostitele? Nebo jen na jeho největší hnízdiště? Anebo si rozdělí úlohy a postupně ovládnou hnízda všech hostitelů?

Na tyto otázky dlouho neexistovala odpověď. Proto jsem na jaře 2001 sledoval parazitické samice a jejich pohyb na jedné jihočeské lokalitě. Výzkum jsem zaměřil na dva parazitické druhy. Oba mají nejméně patnáct hostitelů. Pozorované samice obou parazitických druhů létaly pomalu při zemi a pátraly po hnízdech hostitelů. Ani v jednom případě se „nespletly“ - vždy navštívily hnízda jen jediného hostitelského druhu, i když se často pohybovaly po rozsáhlém území. Nejčastěji se však zdržovaly na malých plochách, kde bylo soustředěno více hostitelských hnízd, odkud občas odlétly a zase se na toto hnízdiště vrátily. Samice kleptoparazitů tedy mají na lokalitách rozdělené úlohy a napadají různé druhy hostitelů, zejména však dávají přednost druhům, které svá hnízda soustřeďují na určitých místech.

Uvedené výsledky podporuje i fenomén větších rozdílů ve velikosti mezi jedinci generalistických druhů. U obou druhů, které jsem sledoval v terénu, existují různě velcí jedinci, často jsou některé samice i dvakrát větší než jiné. U specializovaných druhů nejsou rozdíly tak nápadné, což podporuje hypotézu, že větší samice generalistů parazitují u větších druhů hostitelů a naopak. Zajímavé výsledky by určitě přineslo statistické vyhodnocení tohoto fenoménu.

Co z toho vyplývá aneb jak si správně vybrat

Hostitelem kleptoparazitické včely nemusí být nejpříbuznější druh, protože při výběru hostitelů hrají roli i mnohé jiné důvody. Možná že Emeryho pravidlo je jen výsledkem toho, že blízce příbuzný kleptoparazit má totožné nebo podobné morfologické a chemické komunikační prostředky s hostitelem, a proto hostitele snadno přelstí. „Napálení“ hostitele může také usnadňovat podobnost kleptoparazita s hostitelem ve tvaru a zbarvení těla. Nemusí být příliš důležitá, nicméně u řady druhů je až zarážející (viz rámeček na protější straně). Jak jinak vysvětlit, že často vstoupí do hnízda společně samice kleptoparazita se samicí hostitele, aniž se hostitelská samice pokusí příživnici zahnat.

Někteří kleptoparaziti se přeorientovali na nepříbuzné hostitele, kteří byli na lokalitě početnější než hostitelé původní nebo jejichž hnízda mohla skýtat lepší útočiště pro larvy. Faktory se také mohou „sčítat“ - ideální hostitel je početný na lokalitě, nebrání se parazitaci (což je typické zejména u příbuzných druhů) a staví hnízda nejlépe ve větších shlucích. Pokud třeba pískomilné druhy rodu *Andrena* splňovaly tato kritéria, byla parazitace jejich hnízd velmi dobrou životní šancí pro větší pískomilné druhy rodu *Sphecodes*. Nalezení nového, lepšího hostitelského druhu asi nebylo tak jednoduché, jak se zdá. Kleptoparazit musel určitě vyzkoušet mnoho jiných včelích druhů, než našel toho správného, hojného a „mírumilovného“ hostitele. Někteří kleptoparaziti takového hostitele třeba nenašli, a proto to mají stále „rozjeté na více frontách“. Opravdu, generalisté mohou stále hledat svého vytouženého hostitele, který bude po všech stránkách vhodnější než těch dvacet hostitelů současných. Až ho najdou, mohou se specializovat a opustit tak alespoň některé současné hostitelské druhy.

Může to být ale úplně jinak. Aby kukaččí včely přežily, musí umět parazitovat u více druhů hostitelů, zvláště v případě, když jejich dosavadní hostitel na lokalitě vyhyne nebo se stane méně početným. Čím lépe se umí kleptoparazit přizpůsobovat, tím větší má šanci na úspěch. Taková přizpůsobivost se ale týká druhu jako celku. Každá konkrétní samice kleptoparazita přitom může být zaměřena na jediný druh hostitele. Má jistotu, že se nesplete a nevleze do nežádoucího hnízda, kde ji někdo zabije nebo vyžene. Podle této hypotézy vlastně žádní generalisté neexistují. Jsou jen kleptoparazitické druhy, jejichž samice jsou všechny specializovány jen na jednoho hostitele, a druhy, jejichž samice tvoří „čety“ zaměřené na jednotlivé hostitele. Emeryho pravidlo tedy u včel může platit, jelikož přeorientování souvisí s přežitím druhu.

Nebo mají generalisté více hostitelů jen proto, aby získali co nejvíce hnízd pro své larvy. Proti tomu však hovoří velký počet úspěšných specializovaných druhů.

Včely jsou málo známí živočichové, a tak zná málokdo i jejich česká jména. Ona také nejsou moc potřeba, vždyť o jednotlivých druzích samotářských včel mezi sebou hovoří jen odborníci, a ti sáhnou spíš po latině. Přesto se r. 1952 při vytváření českých názvů na včely nezapomnělo (ostatně jako na žádnou skupinu živočichů).

1) ***Sphecodes*** **- rděnka (je červená, ale jen na zadečku)**
2) ***Halictus, Lasioglossum*** **- ploskočelka**
3) ***Andrena*** **- pískorypka (hrabe hnízda v zemi, písku)**
4) ***Colletes*** **- hedvábnice**
5) ***Hylaeus*** **- pravčela (je primitivní)**
6) ***Psithyrus*** **- pačmelák (podobný čmeláku, ale parazitický)**
7) ***Megachile*** **- čalounice (vystýlá hnízda listy)**
8) ***Osmia*** **- zednice (staví si hnízda či zátky na hnízda z „malty“)**
9) ***Nomada*** **- nomáda (kočovník, parazit...)**
10) ***Dasypoda*** **- chluponožka (opravdu má dlouhé sběrací chlupy na nohách 3. páru)**
11) ***Anthophora*** **- pelonoska (nosí velké množství pylu)**
12) ***Eucera*** **- stepnice (žije na teplých stepních lokalitách)**
13) ***Xylocopa*** **- drvodělka (staví si hnízda ve dřevě)**

Podle J. Kratochvíla & E. Bartoše, 1952.

K dalšímu čtení

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Včela medonosná (*Apis mellifera*). Snímek © František Weyda

PŘÍLOHA 2

BOGUSCH P. 2003: Hosts, foraging behaviour and distribution of six species of cleptoparasitic bees of the family Apidae (Hymenoptera: Apoidea). *Acta Societatis Zoologiceae Bohemiae* **67**: 65-70.

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Hosts, foraging behaviour and distribution of six species of cleptoparasitic bees of the subfamily Anthophorinae (Hymenoptera: Apidae)

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Abstract. Records of new hosts, cleptoparasitic accounts, their behaviour near host's nests and plants visited by the following cleptoparasitic species of bees of the subfamily Anthophorinae (Hymenoptera: Apidae): *Ammobates punctatus* (Fabricius, 1804), *Biastes emarginatus* Schenck, 1853, *Epeoloides coecutiens* (Fabricius, 1775), *Epeolus schummeli* Schilling, 1849, *E. variegatus* (Linnaeus, 1758) and *Nomada lathburiana* (Kirby, 1802) are presented. A new host species, *Macropis fulvipes* (Fabricius, 1804) for the cleptoparasite *Epeoloides coecutiens* (Fabricius, 1775) is recorded.

Behaviour, cleptoparasitism, host, nest, host plants, distribution, Hymenoptera, Apidae, Anthophorinae, Central Europe

INTRODUCTION

Cleptoparasitic bees form a specialized ecological group within the family Apidae. Representatives of sixteen genera occur in central Europe (Kocourek 1989, Celary 1989, Celary 1990, Celary 1991). They parasitize the nests of other species of bees, nesting in wood or in the ground (Batra 1984).

The interesting group of cleptoparasitic bees of the subfamily Anthophorinae in central Europe consists of numerous species of the genus *Nomada* Scopoli, 1770 and a group of small genera, sometimes called "the cuckoo bees", with one to five species. The cuckoo bees are rare,which probably accounts for our poor knowledge of them (Celary 1990). The species *Epeoloides coecutiens* (Fabricius, 1775) was even mentioned as "the rarest bee species in the Central Europe" (Smiedenknecht 1930).

The published records of the hosts and behaviour of cleptoparasitic bees near and inside the nests of their hosts are rare. There are data on the bionomics of host species, but rarely of the cleptoparasites (Blair 1920, Stoeckhert 1922, Torka 1935, Kocourek 1966, Celary 1990, Westrich 1990).

Ammobates punctatus (Fabricius, 1804) is a specific parasite of *Anthophora bimaculata* (Panzer, 1798), occurring in warm and sandy localities (Celary 1990, Westrich 1990). Westrich (1990) states that the cleptoparasite is not rare at most of localities where *Anthophora bimaculata* is common. *Ammobates punctatus* is supposed to be more thermopilous than its host.

Biastes emarginatus (Schenck, 1853) is one of the three central European species of this genus. Hosts are species of the genus *Rophites* Spinola, 1808; two of which *Rophites algirus* Pérez, 1902 and *Rophites quinquespinosus* Spinola, 1808, are cited by Celary (1990) and Westrich (1990). However, *Biastes emarginatus* was not collected in localities where the host species, *Rophites quinquespinosus*, is abundant (Přidal 1999). Celary (1990) also cites two species of the genus *Systropha* Illiger, 1806 as hosts of *Biastes emarginatus*.

Epeoloides coecutiens (Fabricius, 1775) is the only species of this genus in central Europe (Celary 1990, Westrich 1990). This species is very rare. The only known host is *Macropis europaea* Warncke, 1973, a species living in wet localities (Stoeckhert 1933, Westrich 1990). Another member of the genus *Macropis* Panzer, 1809, *Macropis fulvipes* (Fabricius, 1804), living in the same localities as *Macropis europaea*, is recorded as an alternative host (Westrich 1990).

Epeolus schummeli Schilling, 1849 is a very rare species and for a long time was not recorded from the Czech Republic (Přidal 2001). It is a parasite in nests of *Colletes nasutus* Smith, 1853 (Celary 1990, Westrich 1990).

The hosts of *Epeolus variegatus* (Linnaeus, 1758) are *Colletes daviessanus* Smith, 1846 and *Colletes fodiens* (Geoffroy in Fourcroy, 1785), not rare, as sometimes large numbers of specimens can be collected at one locality (Celary 1990, Westrich 1990). Some other species of the genus *Colletes* Latreille, 1802 are mentioned as alternative hosts (Westrich 1990).

Nomada lathburiana (Kirby, 1802), which prefers warmer localities, is not a rare species. Its host is the commonly observed *Andrena vaga* Panzer, 1799 (Alfken 1912, Kocourek 1966, Westrich 1990), and a rare species *Andrena cineraria* (Linnaeus, 1758) (Westrich 1990). Kocourek (1966) mentioned that Andrena hosts do not defend their nests against the cleptoparasite.

This paper presents the results of studies on six species of cleptoparasitic bees of the subfamily Anthophorinae, namely *Ammobates punctatus*, *Biastes emarginatus*, *Epeoloides coecutiens*, *Epeolus schummeli*, *E. variegatus* and *Nomada lathburiana*. The results include data on interactions between the host and the cleptoparasite in the entrance of a host's nest, host plants of cleptoparasites and information on new host species.

MATERIAL AND METHODS

The material was collected using standard entomological methods and equipment, with catching individuals at nest sites and on plants as the preferred method. A few individuals were caught in Moericke traps; these specimens were used only as the comparative material during determinations. The material of *Colletes daviessanus* and *Epeolus variegatus* was partly got from laboratory rearing of larvae collected in the field. Most of the material is deponated in author's collection.

Material studied

The nomenclature used is that of Schwarz et al. (1996). Scheuchel's (2000) key was used to determine the material. Numbers of squares are in brackets.

Ammobates punctatus: Moravia, Bzenec env. (7069), military training area, 18.viii.2001, 1f, P. Bogusch lgt., det. and coll.;

Andrena vaga: Bohemia, Praha, Prokopské údolí (5952), 10.iv.2001, 3m and 1f, P. Bogusch lgt., det. and coll;

Anthophora bimaculata: Bohemia, Hradec Králové env., Na Plachtě (5761), 6.–9.viii.2001, 3m, 1f, P. Bogusch lgt., det. and coll.; Moravia, Bzenec env. (7069), military training area, 18.viii.2001, 1f, 19.viii.2001, 1m, 1f, P. Bogusch lgt., det. and coll.;

Biastes emarginatus: Bohemia, Buzice (6549), 5.viii.2000, 1f, P. Bogusch lgt. and coll., A. Přidal det.;

Colletes daviessanus: Bohemia, Buzice (6549), 24.vi.1998, 1f, 5.vii.1998, 1f, 7.vii.1998, 2f, 23.viii.1999, 3f, 7.iv.2000, 1m, 1f, 13.vii.2000, 1m, 16.vii.2000, 1m, 1.iv.2001, 1m and 1f ex larvae, 7.iv.2001 1m ex larvae, 11.iv.2001 2f ex larvae, 17.iv.2001 2m and 1f ex larvae, 24.iv.2001 1f ex larvae, P. Bogusch lgt., J. Straka and A. Přidal det., P. Bogusch and J. Straka coll.;

Colletes fodiens: Moravia, Bzenec env., Váté písky (7061), 18.viii.2001, 1f, P. Bogusch lgt. and coll., A. Přidal det.;

Colletes graeffei: Slovakia, Turňa nad Bodvou (7390), 2.viii.1999, 2m and 2f, P. Bogusch lgt. and coll., A. Přidal det.;

Colletes similis: Bohemia, Buzice (6549), 25.vii.1999, 2f, P. Bogusch lgt. and coll., A. Přidal det.; Moravia, Bzenec env., Váté písky (7061), 18.viii. 2001, 3f, P. Bogusch lgt. and coll., A. Přidal det.;

Epeoloides coecutiens: Bohemia, Praha, Javornická street (5853), July 1998, 2f, J. Straka lgt., det. and coll.; Bohemia, Buzice (6549), August 1997, 1f, P. Bogusch lgt., J. Straka det. and coll.; Bohemia, Hradec Králové env., Na Plachtě (5761), 17.vii.1999, 4m, J. Straka lgt., det. and coll., 6.viii.2001, 1f, P. Bogusch lgt., det. and coll.;

Bohemia, Běstvina env. (6159), 21.vii.2001, 1m, P. Bogusch lgt., det. and coll.; Moravia, Jedovnice env. (6666), August 1990, 1f, D. Všianský lgt. and coll., A. Přidal and B. Tkalců det.;

Epeolus schummeli: Slovakia, Turňa nad Bodvou (7390), 2.viii.1999, 1m, P. Bogusch lgt., det. and coll.;

Epeolus variegatus: Bohemia, Buzice (6549), 22.vi.1998, 1f, 20.viii.1998, 1m, 1f, 20.vii.1999, 1f, 25.vii.1999, 1f, 23.viii.1999, 2f, 16.vi.2000, 1m, 13.vii.2000, 1f, 24.iv.2001, 1f ex larvae, P. Bogusch lgt. and coll., P. Bogusch and A. Přidal det.; Moravia, Bzenec env., Váté písky (7069), 18.viii.2001, 1m, 4f, P. Bogusch lgt., det. and coll.;

Moravia, Bzenec env. (7069), military training area, 18.viii.2001, 2m, 2f, 19.viii.2001, 1f, P. Bogusch lgt., det. and coll.;

Macropis fulvipes: Bohemia, Praha, Javornická street (5853), August 1998, 2f, J. Straka lgt., det. and coll.; Bohemia, Buzice (6549), 26.vii.1998, 2m, P. Bogusch lgt., det. and coll.; Bohemia, Hradec Králové env., Na Plachtě (5761), 6.viii.2001, 1f, P. Bogusch lgt., det. and coll.; Moravia, Jedovnice env. (6666), August 1990, 1f, D. Všianský lgt. and coll., A. Přidal det.;

Macropis europaea: Bohemia, Hradec Králové env., Na Plachtě (5761), 6.viii.2001, 4m and 2f, P. Bogusch lgt., det. and coll.;

Nomada lathburiana: Bohemia, Praha, Prokopské údolí (5952), 10.iv.2001, 1m and 1f, P. Bogusch lgt., det. and coll.;

Rophites quinquespinosus: Bohemia, Buzice (6549), 5.viii.2000, 1f, P. Bogusch lgt. and coll., A. Přidal det.;

Sphecodes gibbus: Moravia, Bzenec env. (7069), military training area, 18.viii.2001, 1m, 1f, P. Bogusch lgt., det. and coll.;

Sphecodes monilicornis: Moravia, Bzenec env. (7069), military training area, 18.viii.2001, 1m, 2f, P. Bogusch lgt., det. and coll.

RESULTS

Ammobates punctatus (Fabricius, 1804)

Female of *Ammobates punctatus* was observed crawling out of a ground nest of *Anthophora bimaculata* at sandy site on the military training area at Bzenec in August. A host female emerged about two minutes after the parasitic female flew away. Three other cleptoparasitic species were common at this locality: *Sphecodes gibbus* (Linnaeus, 1758), *Sphecodes monilicornis* (Kirby, 1802) and *Epeolus variegatus* (Linnaeus, 1758), but none of them was observed near nests of this host. Recently, the host species was collected at the locality Na Plachtě in the area of Hradec Králové; but *Ammobates punctatus* was not observed or known from there.

Biastes emarginatus (Schenck, 1853)

One female of *Rophites quinquespinosus* Spinola, 1808 was observed on a flower of *Balota nigra* L. (Lamiaceae), probably the flower it most commonly visits. This female was "shadowed" by a female of *Biastes emarginatus*, which stayed in the air and copied every movement of the host female. Similar behaviour was observed in *Epeoloides coecutiens* (Fabricius, 1775).

Epeoloides coecutiens (Fabricius, 1775)

Epeoloides coecutiens is not rare at the locality Na Plachtě in Hradec Králové, where both host species of the genus *Macropis* Klug, 1809 occur. One female of *Macropis fulvipes* visiting a flower of *Lythrum hyssopifolia* L. (Lythraceae) was observed in August. The female of *Epeoloides coecutiens* flew close to the host female near its ground nest in sand not far from the plant. The interactions at the nest entrance were quiet, they did not result in a fight, and both females crept into the nest. The host female followed by the cleptoparasitic female emerged after four minutes. Similarly no interaction was observed between *Epeoloides coecutiens* and *Macropis europaea*.

Other data on the occurrence of *Epeoloides coecutiens* and *Macropis fulvipes* at several localities, see material and methods, strengthens the hypothesis that *Epeoloides coecutiens* is a parasite of *Macropis fulvipes*. The species *Macropis europaea* was never collected at these localities.

Three new plants visited by the species *Epeoloides coecutiens* were recorded: *Campanula rotundifolia* L. (Campanulaceae), male, Běstvina, July 2001; *Thymus serpyllum* L. (Lamiaceae), males, Na Plachtě, July 1999; *Lythrum hyssopifolia* L. (Lythraceae), female, Na Plachtě, August 2001.

Epeolus schummeli Schilling, 1849

A male of *Epeolus schummeli* was caught in August 1999 at Turňa nad Bodvou. The known host species, *Colletes nasutus*, was not found, however another species of the genus *Colletes* Latreille, 1802, *Colletes graeffei* Alfken, 1900, was abundant.

Epeolus variegatus (Linnaeus, 1758)

The interactions between *Epeolus variegatus* and *Colletes daviessanus* were observed in detail during the period 1998 to 2001 at Buzice, where is a large colony of about one thousand nests of the host species. Cells containing immature stages were collected from nests in the winters 1999/2000 and 2000/2001 and kept under laboratory conditions. One female of *Epeolus variegatus* emerged in April 2001. This brood cell did not differ from other cells, containing host larvae. Fights were observed at the nest entrance of another host species, *Colletes similis* Schenck, 1853 at Buzice in July 1999. A *Colletes similis* female successfully forced a female of *Epeolus variegatus*, which was trying to get into the nest, to leave. The same was observed in August 2001 at Váté písky, Bzenec. In this locality, *Colletes fodiens* and *Colletes similis* are similarly abundant, but *Epeolus variegatus* females only attacked nests of *Colletes similis*.

Nomada lathburiana (Kirby, 1802)

Two specimens of *Nomada lathburiana*, one of them still incompletely sclerotized, were collected at a place where there was *Andrena vaga* host colony. The colony was at Prokopské údolí, and mass hatching of *Andrena vaga* was observed in April. No interactions between the host and parasite were observed. The number of nesting bees was too large that no other bee species except the cleptoparasite lived there.

CONCLUSIONS

The only known host species of *Ammobates punctatus* is *Anthophora bimaculata* (Celary 1990, Westrich 1990). Females of both species were observed at a nest of *Anthophora bimaculata*, but no interactions or fights between females were observed. *Ammobates punctatus* is a rare, thermopilous species, occurring only in few localities together with *A.bimaculata*.

Rophites quinquespinosus is the only host, observed in association with *Biastes emarginatus*. A female of this cleptoparasite, observed at Buzice, closely followed a host female visiting flowers. *Epeoloides coecutiens* females show similar behaviour. There are no publications where these parts of behaviour of cleptoparasitic bees were expressed. This behaviour is very similar to that of some comensals and inquilines of solitary bees, particularly representatives of the families Phoridae a Conopidae (Diptera), in which the females follow host females at the nest entrance (Blair 1920).

Tab. 1. List of the host species of the cleptoparasites studied

Cleptoparasite	host	author
Ammobates punctatus Fabricius, 1804	*Anthophora bimaculata* (Panzer, 1798)	Celary 1990, Westrich 1990
Biastes emarginatus Schenck, 1853	*Rophites quinquespinosus* Spinola, 1808	Celary 1990, Westrich 1990
	Rophites algirus Pérez, 1902	Westrich 1990
	Systropha curvicornis (Scopoli, 1770)	Celary 1990
	Systropha planidens Giraud, 1861	Celary 1990
Epeoloides coecutiens (Fabricius, 1775)	*Macropis europaea* Warncke, 1973	Celary 1990, Westrich 1990
	Macropis fulvipes (Fabricius, 1804)	Westrich 1990
Epeolus schummeli Schilling, 1849	*Colletes nasutus* Smith, 1853	Celary 1990, Westrich 1990
	Colletes graeffei Alfken, 1900	
Epeolus variegatus (Linnaeus, 1758)	*Colletes fodiens* Geoffroy, 1785	Celary 1990, Westrich 1990
	Colletes similis Schenck, 1853	Celary 1990, Westrich 1990
	Colletes daviessanus Smith, 1846	Westrich 1990
Nomada lathburiana (Kirby, 1802)	*Andrena vaga* Panzer, 1799	Westrich 1990
	Andrena cineraria (Linnaeus, 1758)	Westrich 1990

Other potential host species, e. g. *Rophites algirus* Pérez, 1902, *Systropha curvicornis* (Scopoli, 1770) or *Systropha planidens* Giraud, 1861 (Celary 1990) were not observed in association with *Biastes emarginatus* .

The species *Macropis europaea* is recorded as a host of *Epeoloides coecutiens* (Celary 1990, Westrich 1990). No contacts between *Macropis europaea* and *Epeoloides coecutiens* were observed, but that *Macropis fulvipes* is a host, previously mentioned by Westrich (1990), was confirmed. A female of *Epeoloides coecutiens* was observed following a *Macropis fulvipes* female from a plant to its nest. Other data on the co-occurrence of *Epeoloides coecutiens* and *Macropis fulvipes* at several localities strengthen the hypothesis that *Epeoloides coecutiens* is a parasite of *Macropis fulvipes*. The main host, *Macropis europaea*, was never collected at the localities mentioned above.

New plants visited by *Epeoloides coecutiens* were recorded: *Campanula rotundifolia*, *Thymus serpyllum* and *Lythrum hyssopifolia*. However, *Epeoloides coecutiens* was never observed visiting *Lythrum saliciaria* L., the most important plant for this species cited by Westrich (1990). *Epeoloides coecutiens* was observed on flowers of two other plants, as previously recorded by Westrich (1990): *Calunna vulgaris* L. (Karas, unpublished data) and *Knautia arvensis* L. (present paper). All these host plants belong to different higher taxa, but all have pink or purple coloured flowers. Cleptoparasite, does not visit exactly the same plants as *Macropis fulvipes*, as was supposed (Westrich 1990). Collecting *Epeoloides coecutiens* caught in Moericke traps at different localities, might define the relationship between this bee and various plants.

One male of *Epeolus schummeli* was caught at Turňa nad Bodvou, where the host species, *Colletes nasutus* does not occur. However, a similar species, *Colletes graeffei*, was abundant at this locality. *Epeolus schummeli* probably has other hosts, for example *Colletes graeffei.*

The only cleptoparasitic species reared in the laboratory is *Epeolus variegatus*. A female emerged from a brood cell of *Colletes daviessanus*, one of two main hosts of this cleptoparasite (Celary 1990, Westrich 1990). The other host is *Colletes fodiens* (Celary 1990, Westrich 1990). No interactions between *Epeolus variegatus* and *Colletes fodiens* were observed even though they occurred at the same locality (Bzenec). Fights between females of *Epeolus variegatus* and its hosts *Colletes daviessanus* and *Colletes similis* were observed at nests of the hosts (Buzice, Bzenec). The second host species was previously reported as a potential host of *Epeolus variegatus* (Westrich 1990).

Occurrence of freshly emerged specimens of *Nomada lathburiana* in colonies of *Andrena vaga* is indirect evidence that *Nomada lathburiana* is a parasite of *A. vaga.*

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Biology of the Cleptoparasitic Bee *Epeoloides coecutiens* (Hymenoptera: Apidae: Osirini)

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ABSTRACT: This study presents comprehensive data about the biology of the rare cleptoparasitic European bee species *Epeoloides coecutiens* (Fabricius, 1775). The phenology and behavioral patterns observed at several localities are described; new information about floral resources (22 species) of *E. coecutiens* is presented. A new host bee, *Macropis fulvipes* Fabricius, 1804, is confirmed for *E. coecutiens*. The differences in color vision of humans and bees affect the interpretation of *E. coecutiens* floral preferences.

KEY WORDS: *Epeoloides coecutiens*, cuckoo bees, Europe, Czech Republic, phenology, behavioral patterns, hosts, *Macropis*, color vision

According to the current classification, the species *Epeoloides coecutiens* (Fabricius, 1775) is the only Palearctic species of the tribe Osirini, family Apidae (Michener, 2000). Roig-Alsina (1989) considered *Epeoloides* Giraud, 1863 to be morphologically similar to the otherwise American species of this tribe. Larvae of species of Osirini feed on provisions stored by their hosts, including floral oils and pollen, and Rozen (2001) commented on the identical structure of the ovaries and ovarioles of Osirini. Nevertheless, the classification of the two species of *Epeoloides* — *E. coecutiens* and the North American *E. pilosula* Cresson, 1878—is uncertain, because morphological and behavioral similarities to members of the otherwise neotropical tribe Osirini have been explained as convergence (Roig-Alsina and Michener, 1993).

The last find of *E. pilosula* in North America dates back to 1942 and the species may be extinct (Michener, 2000; Rozen, unpubl. data). *Epeoloides coecutiens*, however, is known from isolated localities in the whole Palearctic region; it is not obviously most abundant in the warmer regions, such as the Mediterranean or southern parts of Europe (Westrich, 1990). It is rarely collected and the finds are mostly accidental; Schmiedenknecht (1930) considered *E. coecutiens* to be the rarest central European bee. The distribution of this species has been described in detail for the German province Baden-Würtemberg (Westrich, 1990), Poland (Celary, 1990) and Scandinavia with a focus on Denmark and Finland (Pekkarinen *et al.*, 2003). Other publications present data about several localities for *E. coecutiens* in the Czech Republic and Slovakia (Zavadil, 1951; Bat'a, 1952) or describe other localities in Poland (Celary and Wisniowski, 2001) and Germany (Friese, 1923; Stöckhert, 1954; Dötterl and Hartmann, 2003).

The bionomics of this species has not been described in detail. Extensive studies on bees (Friese, 1895, 1923; Stöckhert, 1954) or all Hymenoptera (Schmiedenknecht, 1930) present at most information about localities in Germany or the Czech Republic. Some references, mostly floral records, were summarized by Westrich (1990) and new data were presented in faunistic studies by Celary (1990) and Celary and Wisniowski (2001). Brief mentions of *E. coecutiens* are included in publications about biology of *Macropis* Panzer, 1809 species (Petit, 1990; Pekkarinen *et al.*, 2003); however, the presented data are mainly records adopted from older studies.

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Macropis europaea Warncke, 1973, is known as the host of the cleptoparasite *E. coecutiens* Stöckhert (1933, 1954). Westrich (1990) suggested that the related species, *Macropis fulvipes* (Fabricius, 1804), was another likely host; this species was considered as the confirmed host by Celary and Wisniowski (2001), but without explanation as to how the parasitism was confirmed.

The first floral records were presented by Friese (1923), who stated that *Lythrum salicaria* L. (Lythraceae) is the nectar-producing plant for *E. coecutiens*. Stöckhert (1954) listed five further floral records, and a more detailed list of such plants was published by Westrich (1990). Two works described the phenology of *E. coecutiens*: Banaszak (1989) stated that *E. coecutiens* is active in July; Westrich (1990) reports its occurrence in July and August.

Material and Methods

Interactions between the cleptoparasite and host females were observed at nest sites of the host species, *Macropis europaea* and *M. fulvipes*, at nine localities in the Czech Republic during the years 1997–2002. Brood cells from *Macropis* nests visited by *E. coecutiens* females were buried and transferred to the laboratory. The offspring were overwintered and kept in the laboratory until the emergence of adults. The behavior of *E. coecutiens* and *M. fulvipes* individuals was observed in the field, and behavioral patterns of the former were divided into seven categories:

- *Searching flight*–female's slow flight low over the ground near the host's nest site, which was necessary for finding nests. This is a typical behavior of cleptoparasitic aculeate Hymenoptera.
- *Feeding at flowers*–nectar sucking or pollen collecting on flowers, not flying about the plant.
- *Sitting on plants*–flying toward or sitting on the host plant, not gathering provisions.
- *Host female shadowing*–flying close after the provisioning host female, shadowing the host female at the locality or at the nest site.
- *Entering the host nest*
- *Sitting in the undergrowth*–the main activity for bees with no nests (all cleptoparasites) during cold and wet weather and at night, or for freshly emerged individuals.
- *Unknown activity*–activity of captured individuals is not known.

The phenology was determined from specimens of *E. coecutiens* in the collections of German, Czech, and Polish apidologists and some European museums, together with published data from the literature (Westrich, 1990; Bogusch, 2003). Data were obtained from 188 *E. coecutiens* specimens from seven European countries (Czech Republic, France, Germany, Poland, Austria, Slovakia, and Switzerland), slightly dominated by females (57% of all individuals). The sources were the following collections: German Institute of Entomology, Eberswalde, Germany (Prof. H. H. Dathe); South Bohemian Museum, České Budějovice, Czech Republic (Dr. Z. Kletečka); Moravian Museum, Brno, Czech Republic (Dr. V. Kubáň); National Museum, Praha, Czech Republic (Dr. J. Macek); M. Blösch, Erlangen, Germany (data gathered from Mr. H. Dörfler); P. Bogusch, Charles University, Praha, Czech Republic; Dr. W. Celary, University Krakow, Poland; Z. Karas, Zliv, Czech Republic; M. Mikát, Hradec Králové, Czech Republic; Dr. A. Přidal, Mendel's University, Brno, Czech Republic; R. Prosi, Crailsheim, Germany; E. Scheuchl, Velden, Germany; Dr. M. Schindler, University of Bonn, Germany; Ch. Schmid-Egger, Herrsching–Breitbrunn, Germany; and J. Straka, Praha, Czech Republic.

Data about the host plants were obtained from observations made by the author and several other apidologists, and from the literature. Colors of each host plant flower, as seen by bee vision, were determined by Dr. Lars Chittka, University of London. The "bee vision colors" were calculated using the spectral sensitivities of the ultraviolet, blue, and green receptors of the honey bee eye (*Apis mellifera*) (Chittka, 1992; Briscoe and Chittka, 2001), using excitation maxims synthesis, wherein a hexagon divided into six color parts is used to simulate the trichromatic color vision of bees (Chittka, 1992). Data obtained from honeybee vision is likely indicative of vision in other bees because the vision of the majority of bee species is virtually identical (Briscoe and Chittka, 2001). Counts of each host plant color were statistically tested twice, once using the color perceived by human vision and once by bee vision. Host plant preferences by the sex of examined bee species were also tested. The null hypothesis "*Macropis* and *E. coecutiens* do not prefer some colors more than others" was tested with the probability level 5%. The color spectrum of the rainbow (excluding orange) was used as the "human spectrum"; the "bee spectrum" consisted of blue, green, ultraviolet and all three intermediate colors—blue-green, UV-blue and UV-green. Pure ultraviolet color, which appears in flowers of only 0.05% plant species (Richards, 1997), was removed and not analyzed. Information about *E. coecutiens* host plants was compared with information about host plants of both species of the genus *Macropis*.

The only used statistic method is the χ^2 test. The analysis was made in Microsoft Excel using calculations and values of parameters presented in Zvára's (1997) publication.

Data about pollen, nectar, and floral oils in flowers of host plants were adopted from Richards (1997); scientific names of plants were unified according to Kubát *et al.* (2002).

Results

Characteristics of the Localities

Characteristics of nine *E. coecutiens* localities in the Czech Republic were compared. The most important factors for *E. coecutiens* occurrence in the locality were the presence of hosts (*Macropis*), of preferred host plants, and a warm microhabitat, for example a south-facing sandy site. *Macropis* bees usually nest in wet localities, in sandy banks of ponds, puddles and streams. *Epeoloides coecutiens* females only attack nests in warm sandy sites with the undergrowth of *Thymus*, *Lotus*, and *Knautia*, among others (all nine localities). Most of the localities monitored are anthropogenous (5 of 9 localities); these are: the surroundings of a granite quarry, a sand pile, a former military exercising ground, a sand quarry, and a sandy flood barrier.

Phenology

Comparison of the "Czech" bees (56 specimens) with the "German" (99 specimens) showed no difference between *E. coecutiens* phenologies in these countries; data from all central European localities were therefore treated together.

Epeoloides coecutiens was collected in May, June, July, and August. The earliest exemplar is a male from Zliv, Czech Republic (26.5.1985, Z. Karas coll.); the latest is from Kuppenheim, Germany (31.8.1987, P. Westrich coll.). Figure 1 shows the number of individuals collected in ten-day (or eleven-day) periods. Figure 2 shows the sex ratios for the same time periods, demonstrating that *E. coecutiens* abundance culminates in the

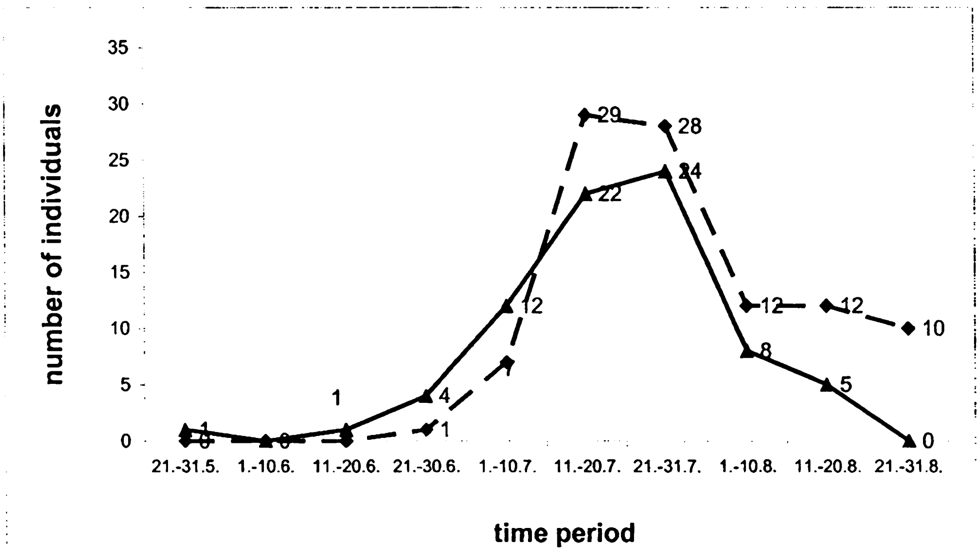

Fig. 1. Abundance of *Epeoloides coecutiens* males and females through time based on collection records from diverse sources (see text). The dark line with triangles represents the number of males; the dashed line with diamonds represents the number of females. The x-axis (Time Period) shows ten- or eleven-day periods of time for the months of May (5) through August (8).

second half (second and third ten-day periods) of July; males emerge earlier and their occurrence finishes earlier, mostly in the first half of August.

Behavior of *E. coecutiens* Individuals in the Field

The behavioral patterns of 43 *E. coecutiens* individuals observed at localities in the Czech Republic are presented in Table 1. The most frequently observed behavioral patterns are feeding at flowers (both sexes) and searching flight (only females). Most females were observed during searching flights; feeding at flowers is the most common behavioral pattern for males.

Behavior in cold and wet weather was also observed. A female caught in Bĕstvina, Czech Republic (2.8.1996, J. Straka coll., P. Bogusch lgt.), was found sitting 20 cm above ground in the grass undergrowth on a dry sandy side of a site with *Macropis* nests. This female had not bitten into the stalk with its mandibles, unlike as was described by Westrich *et al.* (1992). It was about 2 P.M., with cool weather after rain (temperature about 18°C) and the undergrowth was still wet. Two males at the same locality on 17 July 2001 were climbing upwards on the dry shanks of undetermined plants. The weather was quite warm (about 22°C) but cloudy, the sun was beginning to shine and other solitary bees were beginning to fly and visit flowers.

Hosts

Macropis europaea Warncke, 1973

Shadowing of a *M. europaea* female by an *E. coecutiens* female was observed only once; parasitism was not recorded.

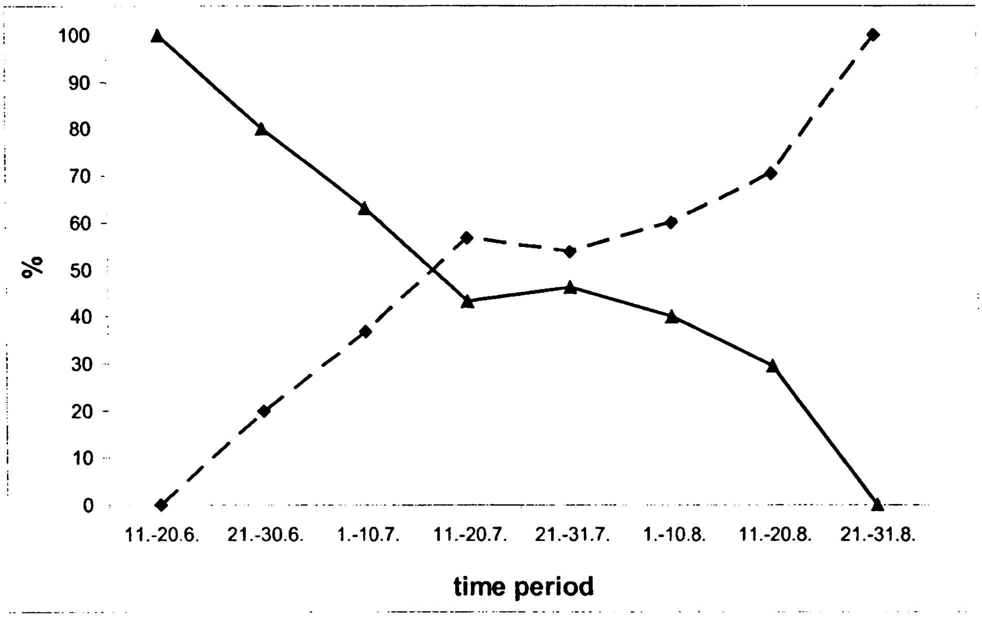

Fig. 2. Gender ratio of *Epeoloides coecutiens* males and females through time based on same collections used for Fig. 1. The dark line with triangles represents the number of males; the dashed line with diamonds represents the number of females. The x-axis (Time Period) shows ten- or eleven- day periods of time for the months of May (5) through August (8).

Macropis fulvipes (Fabricius, 1804)

Host female shadowing was described by Bogusch (2003). An *E. coecutiens* female emerged from a brood cell of *M. fulvipes* nest collected on 6 August 2001 in the protected area Na Plachtě. The brood cell from which the cleptoparasitic female emerged was not noticeably different from other brood cells of the host. The strongest layer outside the cell was made of soil and coated inside with a glossy secretion approximately from the Dufour's gland. The cocoon of *E. coecutiens* was made of silk and was as large as the inside space of the brood cell. Brood cells were 7.6–8.8 mm long and 4.8–5.2 mm wide (5 measurements); the brood cell from which *E. coecutiens* emerged was 8.8 mm long and 5.0 mm wide.

Table 1. Behavioral patterns observed for individuals of *Epeoloides coecutiens*.

Activity	Males	Females	Together
Searching flight	0	10	10
Feeding at flowers	11	6	17
Sitting on plants	2	2	4
Host female shadowing	0	2	2
Entering the host's nest	0	3	3
Sitting in the undergrowth	3	1	4
Unknown activity	1	2	3
Total	17	26	43

Table 2. Food plants of *Epeoloides coecutiens* and colors of their flowers. Legend: St—Stöckhert 1954, W—Westrich 1990, C—Celary 1990, B—P. Bogusch, own observation, DEI—data from Deutsches Entomologisches Institut, Eberswalde, Germany, S—J. Straka, own observation, K—Z. Karas, own observation. Colors: B:blue, B–G—blue-green, G—green, U–B—UV-blue, U–G—UV-green, V—violet, W—white, Y—yellow, ?—unknown.

	Published/Observed							Sex		Colour	
Plant species	St	W	C	B	DEI	S	K	M	F	Human	Bee
Achillea millefolium		*							*	W	B-G
Anchusa officinalis					*			*	*	B	U-B
Arctium minus	*							*		V	?
Calluna vulgaris		*					*	*	*	V	B
Campanula rotundifolia				*				*		B	U-B
Chamaerion angustifolium		*	*					?	?	V	B
Cirsium palustre	*								*	V	B
Hieracium pilosella		*						?	?	Y	U-G
Hypericum perforatum	*							?	?	Y	U-G
Jasione montana		*		*				*	*	B	B
Knautia arvensis	*	*		*				*	*	V	B-G
Lotus comiculatus						*		*		Y	G
Lythrum hyssopifolia				*					*	V	U-B
Lythrum salicaria	*	*	*						*	V	U-B
Melilotus album				*					*	W	B-G
Rubus fruticosus	*	*							*	W	B-G
Satureja montana					*				*	W	?
Thymus serpyllum			*	*				*	*	V	B
Trifolium arvense		*						?	?	V	G
Trifolium repens		*							*	W	B-G
Veronica officinalis	*								*	V	B
Vicia cracca	*							?	?	V	B

Floral Resources

Epeoloides coecutiens was observed visiting flowers of the following plants: *Jasione montana* L. (Campanulaceae)—1 male sucking nectar; *Knautia arvensis* (L.) (Dipsacaceae)—males and females feeding; *Lythrum hyssopifolia* L. (Lythraceae)—1 female shadowing *Macropis fulvipes* female collecting pollen on flowers of this plant; several *E. coecutiens* males sucking nectar; *Thymus serpyllum* L. (Lamiaceae)—many individuals (the most visited plant); *Calluna vulgaris* (L.) (Ericaceae)—4 males and 2 females feeding, observed and collected by Z. Karas; *Lotus corniculatus* L. (Fabaceae)—1 male, observed and collected by J. Straka (this plant is dominant at the locality and *E. coecutiens* was sucking nectar (Straka, unpubl. data)); *Campanula rotundifolia* L. (Campanulaceae)—1 male caught on flowers; and *Meliotus albus* Med. (Fabaceae)—1 female feeding.

Macropis fulvipes and *M. europaea* were observed on flowers of the plants listed in Table 3. Presumably the bees were taking pollen from *Lysimachia*, nectar from the others. Neither feeding nor collecting nectar on *Lythrum salicaria*, the presented main host plant, was observed. The 22 flower species on which *E. coecutiens* has been observed or collected are recorded in Table 2. Tables 2 and 3 also show the sexes of the bees and colors of flowers by human and bee vision.

Flowers visited by *E. coecutiens* and both *Macropis* species were sorted by the color of their flowers by human and bee vision. Results of the statistical analysis (chi-squared test)

Table 3. Food plants of *Macropis europaea* and *Macropis fulvipes* and colors of their flowers. Legend: St—Stöckhert 1954, W—Westrich 1990, Sch—Scheuchl 2000, P—Petit 1990, B—P. Bogusch, own observation, Pr—A. Přidal, own observation, S—J. Straka, own observation. Colors: B—blue, B-G—blue-green, G—green, U-B—UV-blue, U-G—UV-green, V—violet, W—white, Y—yellow, ?—unknown.

	Published/Observed							Sex		Colour	
Plant species	St	W	Sch	P	B	Pr	S	M	F	Human	Bee
Alisma plantago-aquatica				*	*			*		W	?
Angelica sylvestris				*					*	W	B-G
Bidens tripartita				*					*	Y	?
Chamaerion angustifolium				*	*				*	V	B
Cirsium arvense				*				*	*	V	B-G
Cirsium palustre		*			*				*	V	B
Crepis capillaris				*				*		Y	G
Epilobium parviflorum				*	*				*	V	B
Eupatorium cannabinum				*					*	V	B-G
Fallopia dumetorum				*					*	V	?
Fragaria hortensis						*			*	W	B-G
Frangula alnus				*				*	*	G	?
Galeopsis speciosa					*				*	Y	?
Geranium palustre		*			*				*	V	U-B
Geranium pratense						*			*	B	U-B
Geranium sylvaticum		*								V	U-B
Hieracium laevigatum				*					*	Y	U-G
Leontodon autumnalis				*					*	Y	G
Lycopus europaeus				*	*				*	W	?
Lysimachia nummularia		*							*	Y	G
Lysimachia punctata		*	*	*	*			*	*	Y	G
Lysimachia vulgaris	*	*	*	*	*			*	*	Y	G
Lythrum hyssopifolia					*				*	V	U-B
Lythrum salicaria	*	*	*	*				*		V	U-B
Mentha aquatica				*					*	V	B-G
Myosoton aquaticum				*					*	W	B-G
Persicaria lapathifolia				*					*	V	?
Peucedanum palustre				*					*	W	B-G
Rubus fruticosus agg.		*			*		*	*	*	W	B-G
Solidago gigantea				*				*		Y	G
Solidago virgaurea				*				*		Y	U-G
Stachys sylvatica		*			*			*		V	U-B

are presented in Table 4; greater details of the analysis are presented in Tables 5 and 6. When both sexes are analyzed together, *E. coecutiens* preferred flowers that are violet (56% of all host plant species) by human vision and blue (33%) by bee vision. *Macropis* species preferred violet (44%) and yellow (29%) flowers by human vision, but no color was preferred by bee vision (three colors above 20%, the highest number is 25% for blue-green plants). Analyzed with human vision, the null hypothesis "*Macropis* bees and *E. coecutiens* are not specialized to prefer some colors over others" is rejected; however the null hypothesis is accepted based on bee vision (Table 4).

Statistical analysis of host plant preference by the sex of *Macropis* species and *E. coecutiens* produced less distinct results; no preference is larger than 50%. *Epeoloides coecutiens* females preferred violet (43%) and white (36%) in human vision, i.e., blue-green (39%) and blue (39%) flowers in bee vision; males preferred violet (50%) and blue

Table 4. Color preferences for *Epeoloides coecutiens*, *Macropis europaea* and *Macropis fulvipes*; χ^2 values for all analyzed data. Null hypothesis: "*Macropis* bees and *E. coecutiens* do not prefer some colors over others". Critical value of χ^2 for bee vision is $\chi^2 = 9.4884$ with $k = 4$; for human vision $\chi^2 = 11.071$ with $k = 5$. The large difference between bee and human vision facilitates distinguishing between the two results within the statistic analysis. H_0—null hypothesis.

	BEE vision	Result	HUMAN vision	Result
E. coecutiens – males	3.71	Accept H_0	11.50	Reject H_0
E. coecutiens – females	9.69	Reject H_0	16.00	Reject H_0
E. coecutiens – both sexes	4.42	Accept H_0	29.96	Reject H_0
Macropis – males	4.89	Accept H_0	10.40	Accept H_0
Macropis – females	7.05	Accept H_0	22.00	Reject H_0
Macropis – both sexes	4.80	Accept H_0	32.35	Reject H_0

(38%) in human vision and only ultraviolet-blue flowers (43%) in bee vision. *Macropis* females preferred violet (42%) flowers in human vision, i.e., blue-green (42%) in bee vision. Yellow flowers made up only 27% of flowers utilized by *Macropis* females, even though the most important flowers with oils and pollen, *Lysimachia vulgaris* and *L. punctata*, have yellow flowers. However, males preferred yellow flowers (50%) in human vision, i.e., green flowers (44%) in bee vision. Neither *E. coecutiens* nor *Macropis* individuals were observed on red or ultraviolet flowers.

Table 5. Counts of food plants of each color for *Epeoloides coecutiens*, *Macropis europaea* and *Macropis fulvipes*. Table A is for human vision, Table B for bee vision. Legend: Nj—recorded values, %j—percentage values, npj—probability values, X—partial χ^2, H_0—null hypothesis. Bold number is the total χ^2 value for each file.

TABLE A

	Epeoloides				*Macropis*			
Color	Nj	%j	npj	X	Nj	%j	npj	X
Violet	13	56.52	3.83	21.92	15	44.12	5.67	15.37
Blue	3	13.04	3.83	0.18	1	2.94	5.67	3.84
Green	0	0.00	3.83	3.83	1	2.94	5.67	3.84
Yellow	3	13.04	3.83	0.18	10	29.41	5.67	3.31
Red	0	0.00	3.83	3.83	0	0.00	5.67	5.67
White	4	17.39	3.83	0.01	7	20.59	5.67	0.31
X^2	23	100.00	23.00	**29.96**	34	100.00	34.00	**32.35**
								Rejected H_0

TABLE B

	Epeoloides				*Macropis*			
Color	Nj	%j	npj	X	Nj	%j	npj	X
UV-Blue	4	19.05	3.80	0.01	6	18.75	5.00	0.20
Blue	7	33.33	3.80	2.69	3	9.38	5.00	0.80
Blue-Green	4	19.05	3.80	0.01	8	25.00	5.00	1.80
Green	2	9.52	3.80	0.85	6	18.75	5.00	0.20
UV-Green	2	9.52	3.80	0.85	2	6.25	5.00	1.80
Unknown	2	9.52			7	21.88		
X^2	21	100.00	19.00	**4.42**	32	100.00	25.00	**4.80**
								Accept H_0

Table 6. Counts of food plants of each color for *Epeoloides coecutiens*, *Macropis europaea* and *Macropis fulvipes* differentiated by sex. Table A is for *E. coecutiens*, Table B for *Macropis* species. Legend: Nj—recorded values, %j—percentage values, npj—probability values, X—partial χ^2, H_0—null hypothesis. Bold number is the total χ^2 value for each file.

TABLE A

	Epeoloides – males				*Epeoloides* – females			
Color	Nj	%j	Npj	X	Nj	%j	Npj	X
Violet	4	50.00	1.33	5.33	6	42.86	2.33	5.76
Blue	3	37.50	1.33	2.08	3	21.43	2.33	0.19
Green	0	0.00	1.33	1.33	0	0.00	2.33	2.33
Yellow	1	12.50	1.33	0.08	0	0.00	2.33	2.33
Red	0	0.00	1.33	1.33	0	0.00	2.33	2.33
White	0	0.00	1.33	1.33	5	35.71	2.33	3.05
Total	8	100.00	1.33	**11.50**	14	100.00	2.33	**16.00**
UV-Blue	3	42.86	1.40	1.83	3	23.08	2.60	0.06
Blue	2	28.57	1.40	0.26	5	38.46	2.60	2.22
Blue-Green	1	14.29	1.40	0.11	5	38.46	2.60	2.22
Green	1	14.29	1.40	0.11	0	0.00	2.60	2.60
UV-Green	0	0.00	1.40	1.40	0	0.00	2.60	2.60
Total	7	100.00	1.40	**3.71**	13	100.00	2.60	**9.69**

TABLE B

	Macropis – males				*Macropis* – females			
Color	Nj	%j	Npj	X	Nj	%j	Npj	X
Violet	2	20.00	1.67	0.07	11	42.31	4.33	10.26
Blue	0	0.00	1.67	1.67	1	3.85	4.33	2.56
Green	1	10.00	1.67	0.27	1	3.85	4.33	2.56
Yellow	5	50.00	1.67	6.67	7	26.92	4.33	1.64
Red	0	0.00	1.67	1.67	0	0.00	4.33	4.33
White	2	20.00	1.67	0.07	6	23.08	4.33	0.64
Total	10	100.00	1.67	**10.40**	26	100.00	4.33	**22.00**
UV-Blue	2	22.22	1.80	0.02	3	15.79	3.80	0.17
Blue	0	0.00	1.80	1.80	3	15.79	3.80	0.17
Blue-Green	2	22.22	1.80	0.02	8	42.11	3.80	4.64
Green	4	44.44	1.80	2.69	4	21.05	3.80	0.01
UV-Green	1	11.11	1.80	0.36	1	5.26	3.80	2.06
Total	9	100.00	1.80	**4.89**	19	100.00	3.80	**7.05**

Conclusions and Discussion

The cleptoparasitic bee species *E. coecutiens* is not the rarest bee living in central Europe, as Schmiedenknecht (1930) stated, yet it requires very specific abiotic and biotic conditions. Only a few types of localities meet these demands, since two of them, namely the xerothermic, requirement and the presence of their wetland host-bees, clash with each other. The hosts of the genus *Macropis* prefer wet localities and build their nests usually in sandy pond or stream banks. When the nest site is south directed and sunny, with plants of the genera *Thymus*, *Lotus*, *Knautia* etc., then the thermophilous *E. coecutiens* is able to lay its eggs in the nests of its host.

The univoltine nature of *E. coecutiens*, recorded by Westrich (1990), is here confirmed. *Epeoloides coecutiens* flys in July and August, the period corresponding to the nesting period of its hosts.

Due to their searching behavior, *E. coecutiens* females are frequently more notable than males. Shadowing of host females, also recorded for other cleptoparasitic bees, was observed in two cases. Males are most often observed while sucking nectar on flowers.

The host species *Macropis fulvipes*, previously recorded in literature as a probable host, was confirmed herein. *Epeoloides coecutiens* has two known hosts; the other is the related species *Macropis europaea*, which has long been considered as a confirmed host (Stöckhert, 1933; Westrich, 1990). However, supporting evidence to back up this confirmation is missing in these publications. Likewise, although *M. fulvipes* was recorded as a confirmed host of *E. coecutiens* by Celary (1990) and Celary and Wisniowski (2001), these data are not reliable; both studies made use of the same literary source (i.e., Westrich, 1990). This also applies to Celary's (1991) article about hosts of European *Sphecodes* Latreille, 1805; lists of "confirmed" hosts consist of many bee species recorded only as probable hosts in the older publications (e.g., Blüthgen, 1934; Stöckhert, 1954). The entering of a *M. fulvipes* nest by *E. coecutiens* is not sufficient evidence to confirm that it is a cleptoparasite of *M. fulvipes* (Celary, unpubl. data). More convincing evidence is that there are four localities recorded in the Czech Republic where *E. coecutiens* occurs together with *M. fulvipes*, but where *M. europaea* has never been recorded. No fights, conflicts or aggressive behavior were observed; host females did not seem to mind the cleptoparasite. Parasitized and non-parasitized brood cells had the same structure, corresponding with data about *Macropis* nests published by Rozen and McGinley (1974) and Rozen and Jacobson (1980).

Most of the host plants visited by *E. coecutiens* have violet flowers (13 species, 56%); the others are blue, white and yellow. The most frequently recorded plants are *Lythrum salicaria* and *Knautia arvensis*, the former of which is the main nectar source utilized by *Macropis* (Westrich, 1990). However, neither *E. coecutiens* nor *Macropis* individuals were observed on flowers of this plant during my study. *Lysimachia vulgaris* and the introduced *Lysimachia punctata* are the main sources of pollen and floral oils for the *Macropis* species; they also serve as the meeting points for the sexes. Most of the other host plants are used only as sources of nectar; *Macropis* species were often observed sucking nectar from flowers of *Lythrum*, *Geranium* and *Cirsium*. The largest number of flower records was previously recorded by Petit (1990) for *M. europaea*. *Macropis* species are highly specialized and oligolectic for pollen and oil sources, but unspecialized in nectar sources.

Characteristics of host plant flowers are important orientation guides for pollen and nectar collecting and interactions of *E. coecutiens*, *M. europaea*, and *M. fulvipes* (and probably all bee species). However, flower color preferences of the cleptoparasite and its host species do not reject the null hypothesis "*Macropis* bees and *E. coecutiens* are not specialized to prefer some colors over others," so color is likely not a key flower characteristic utilized by these bees. Other potential key characteristics might be the amount of nectar or pollen produced by the plant, the presence of attractive odors, or the presence of uncommon floral oils; the interaction of the total flora of a locality might also have an effect. Humans see colors of flowers differently from bees and therefore bee color preference should not be determined by human color preception, as shown by the statistical analyses presented herein. The χ^2 parameters for human vision (29.96 for *E. coecutiens* and 32.35 for *Macropis* species; critical value with $P = 5$ is $k = 11.071$) and bee vision (4.42 and 4.80; $P = 4$; critical value $k = 9.4884$) differ by an order of magnitude.

Statistical analysis of the gender-specific preferences of host plants yields incongruent results, which can further be interpreted as evidence for the weak correlation between flower color and host plant preference for these species.

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ORIGINAL ARTICLE

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

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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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Keywords Cleptoparasite · Cuckoo bees · Generalist · *Sphecodes*

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 cleptoparasitic 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 specialization 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 (Pérez, 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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