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COMPARATIVE DEVELOPMENT AND COMPETITIVE ABILITY OF *DIBRACHYS PELOS* (HYMENOPTERA: PTEROMALIDAE) ON VARIOUS POTENTIAL HOSTS

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ABSTRACT

Dibrachys pelos (Grissell) is an occasional gregarious ectoparasitoid of *Sceliphron caementarium* (Drury). We report the second record of this host association, collected in western Nebraska, and present results of laboratory experiments on host suitability and utilization. When *D. pelos* was reared alone on prepupae of 6 possible hosts, 4 proved entirely suitable: the mud dauber wasps *Sceliphron caementarium* and *Trypoxylon politum* Say, and two of their parasitoids, a velvet ant, *Sphaeropthalma pensylvanica* (Lepeletier) and a bee fly, *Anthrax* sp. On these hosts *D. pelos* completed development in 2-4 weeks, with average clutch sizes of 33-57, of which 24.7% were males. The other two hosts tested, the flesh fly *Neobellieria bullata* (Parker) and the leaf-cutter bee *Megachile rotundata* (Say), proved marginal, with very few adult progeny produced. When reared on these same 6 hosts with the addition of a competing parasitoid, *Melittobia digitata* Dahms, *D. pelos* fared poorly, being the sole offspring producer in at most 30% of the trials (on *Anthrax* hosts) and failing to prevail at all on *T. politum* hosts. Comparative data on host conversion efficiency indicated that *M. digitata* was more efficient than *D. pelos* on every host except *Anthrax*.

Key Words: host conversion efficiency, interspecific competition, *Melittobia digitata*

RESUMEN

Dibrachys pelos (Grissell) es un ectoparasitoide gregario ocasional de *Sceliphron caementarium* (Drury). Reportamos el segundo registro de este parasitoide asociado al mencionado hospedador, colectados en el oeste de Nebraska. Se presentan los resultados de experimentos de laboratorio acerca de la utilización y conveniencia de hospedadores por *D. pelos*. Al criarlo sobre prepupas de seis posibles hospedadores, cuatro resultaron altamente convenientes: las avispas de nidos de barro *Sceliphron caementarium* y *Trypoxylon politum* Say, así como sus parasitoides, la hormiga de terciopelo *Sphaeropthalma pensylvanica* (Lepeletier) y la moscaabeja *Anthrax* sp. *D. pelos* completó su desarrollo sobre estos hospedadores en 2-4 semanas, con una descendencia promedio entre 33-57 individuos, de los cuales el 24.7% fueron machos. Los otros dos hospedadores utilizados, la mosca *Neobellieria bullata* (Parker) y la abeja *Megachile rotundata* (Say), fueron marginales en eficiencia, produciendo una progenie reducida. Al agregar *Melittobia digitata* Dahms como competidor, en crías sobre estos mismos hospedadores, *D. pelos* lo hizo pobremente, ganando, como máximo, solo en 30% de los ensayos (sobre *Anthrax*) y fallando totalmente sobre *T. politum*. Datos comparatives sobre la eficiencia de conversión del hospedador como único productor de progenie mostró que *M. digitata* fue más eficiente que *D. pelos* sobre cada hospedador excepto sobre *Anthrax* sp.

Translation provided by the authors.

Mud dauber wasps (Hymenoptera: Sphecidae) of the widely distributed genera *Trypoxylon* and *Sceliphron* share a complex ecological web of inquilines that either parasitize them or use their nests (Matthews 1997). Habits, prey, and inquilines are particularly well known for the organ pipe mud dauber, *Trypoxylon politum* Say (Barber & Matthews 1979; Brockmann & Grafen 1989; Cross et al. 1975; Molumby 1995; Volkova et al. 1999) and the yellow-and-black mud dauber, *Sceliphron caementarium* (Drury) (Shafer 1949; Hunt 1993).

In addition to heavy parasitism by *Melittobia* (Hymenoptera: Eulophidae) wasps and sarcophagid and bombylid flies, both mud dauber species also have other parasitoids that are less commonly encountered (Matthews 1997a). One of the latter is *Dibrachys pelos* Grissell (Hymenoptera: Pteromalidae) (Fig. 1a), an ectoparasitoid apparently distributed across North America (Grissell 1974) but infrequently collected. The only published record of *D. pelos* as a member of the mud dauber "community" is that of Grissell (1974). Despite an extensive survey of trap-nesting wasps and bees and their inquilines (mainly from the eastern United States), Krombein (1967) found no associated *Dibrachys* species. In our own wide-ranging collections of mud dauber nests east of

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the Mississippi River and particularly in the southeastern US over the last 20 years, we have never before found *D. pelos*.

Grissell (1974) reared this species on prepupae of *S. caementarium* and other hosts, but little is known of its natural host preferences or possible competition with other parasitoids. Elsewhere, other *Dibrachys* species have been reported to parasitize various families of Hymenoptera and Diptera (Floate et al. 1999; Smith & Rutz 1991; Urban & Eardley 1995; Whiteman & Landwer 2000), suggesting that *D. pelos* may be an opportunistic polyphagous parasitoid capable of attacking a variety of host species.

Field collection of a *Sceliphron caementarium* nest that was parasitized by *D. pelos* enabled us to investigate the latter species' ability to parasitize other potential hosts. In order to better understand its apparent rarity as a parasitoid of mud dauber wasps, we also staged interspecific competition studies with *Melittobia digitata* Dahms, one of the most common parasitoids of mud dauber wasps.

Materials and Methods

Three cells of a S*celiphron caementarium* nest collected by RWM at Lake McConaughy, Keith Co., Nebraska on June 21, 2003 contained pupae and recently emerged adults of *Dibrachys pelos*. These were brought to our laboratory at the University of Georgia, Athens, GA and reared for one generation on *S. caementarium* prepupae.

To investigate relative suitability of additional common potential hosts, individual 2-day-old mated female progeny from this *D. pelos* culture were placed on prepupae of 5 species known to be acceptable hosts for *M. digitata*: *T. politum* Say, the leaf-cutter bee, *Megachile rotundata* Say (Hymenoptera: Megachilidae), the flesh fly *Neobellieria bullata* Parker (Diptera: Sarcophagidae), the velvet ant *Sphaeropthalma pensylvanica* (Lepeletier) (Hymenoptera: Mutillidae), and a bee fly *Anthrax* sp. (Diptera: Bombyliidae). The first 3 species have been routinely used as hosts in other studies on *M. digitata* (González & Matthews 2002; Silva-Torres & Matthews 2003) and are available readily; the last 2 species are themselves parasitoids of *T. politum* (Cross et al. 1975; Matthews 1997a, b). Concurrently, parallel cultures of *D. pelos* were maintained on *S. caementarium*. Ten replicates of each host species were used in all experiments except for *Sph. pensylvanica*, for which only 3 prepupae were available. All cultures were maintained at 25°C, 65% RH. Development time, progeny production, sex ratio, and host use (suitability) were recorded.

To investigate potential interspecific competitive interactions, an additional 10 replicates were concurrently established on each host (except *Sph. pennsylvanica* due to limited availability). For these we simultaneously placed one mated 2-day-old female each of *D. pelos* and *M. digitata* on the host, and maintained these under the same conditions as the other cultures. Outcomes of these competition experiments were scored as won (only *D. pelos* adults emerged), lost (only *M. digitata* adults emerged), or coexistence (adults of both parasitoids emerged). Number of adult progeny emerging and their sex ratio, were also recorded. We did not conduct a parallel series of intraspecific competition experiments (2 females of *D. pelos* on each host).

As one indicator of the relative suitability of the various hosts, host conversion efficiency values (analogous to feed conversion efficiencies for poultry or pork) were calculated for both *D. pelos* and *M. digitata*. To do this, samples of 10 males and 10 females of each parasitoid species were individually weighed on a Mettler® balance and the average weight of a single female and male of each species was determined. Ten individuals of each of the various hosts were also weighed to obtain an average host weight. The average number of males and females reared from each host when each of the parasitoids were alone was multiplied by the individual wasp's average weight, this being apportioned according to the average sex ratio obtained when reared alone on the respective hosts. This value was then divided by the average host weight and the result multiplied by 100 to give a percent, the host conversion efficiency.

Results and Discussion

Host Suitability and Development Time

Grissell (1974) reported that *D. pelos* laid eggs on prepupae of *Sceliphron*, as well as *Ancistrocerus* and *Euodynerus* (Hymenoptera: Vespidae, Eumeninae), and *Megachile pacifica*, but completed development only in the first 2 hosts. In our experiments, *D. pelos* oviposited also on at least some of all hosts offered (Table 1).

The most successful development occurred with 4 taxonomically diverse but ecologically related species—the mud daubers *S. caementarium* and *T. politum*, and their parasitoids, the velvet ant *Sph. pensylvanica* and the bee fly, *Anthrax* sp. (Fig. 1c); all individuals (100%) of these host species were parasitized successfully, as defined by emergence of *D. pelos* adult progeny. Development times on these 4 preferred hosts were quite similar, requiring 1-3 days for eggs, 7-14 days for larvae, and 7-12 days for pupae, with the total development time ranging from 16-27 days. These ranges for each developmental stage are consistent with data for *D. pelos* on *S. caementarium* reported by Grissell (1974).

Although some eggs were laid on *Megachile rotundata* and *N. bullata* hosts, most immature *D. pelos* perished, so that on average fewer than

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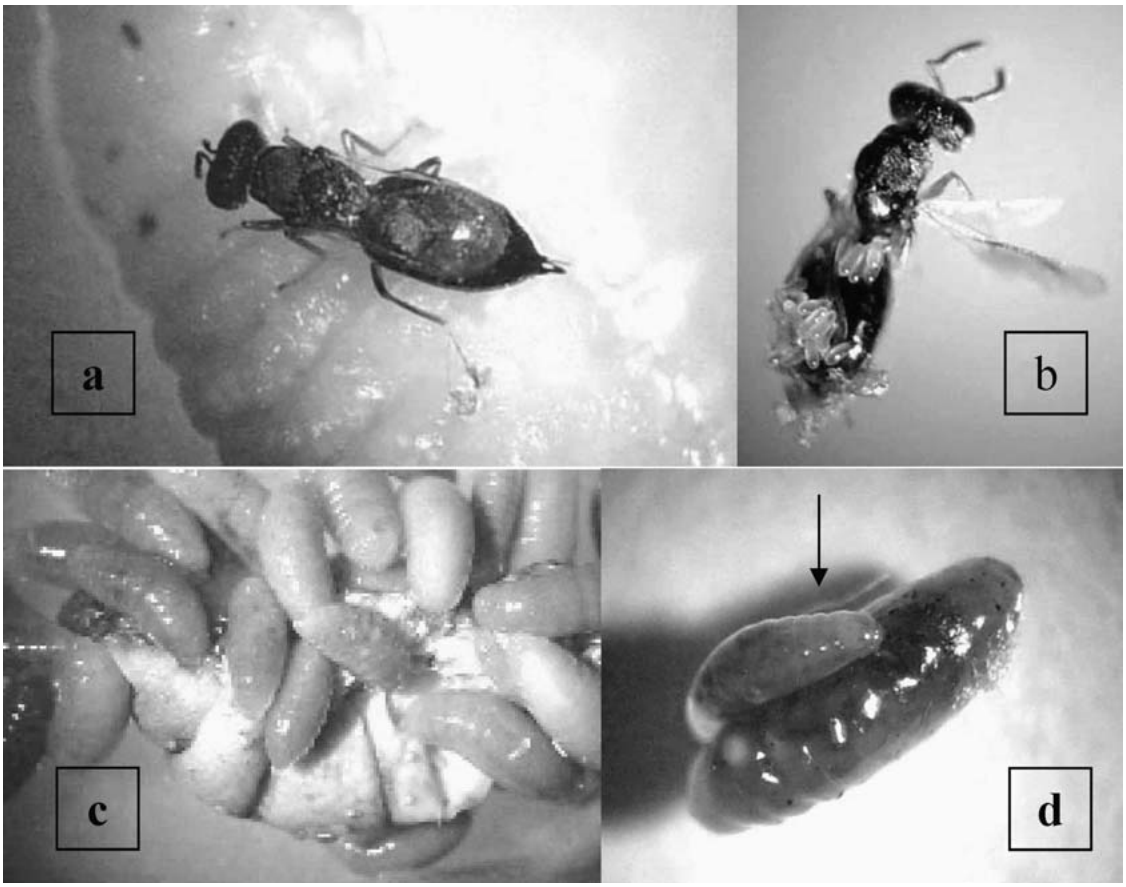


Fig. 1. (a) *Dibrachys pelos* female on prepupa of *S. caementarium*; body length of adult female *D. pelos* = 3 mm; (b) Eggs of *M. digitata* on abdomen of newly eclosed adult *D. pelos*; (c) Gregarious larvae of *D. pelos* feeding on *Anthrax* sp. (Diptera: Bombyliidae); (d) Larva of *M. digitata* (arrow) feeding on larva of *D. pelos*.

4 adults eclosed from these 2 hosts (Table 1). Furthermore, the life cycle took significantly longer to complete on these "marginal" hosts. For example, whereas *D. pelos* started laying eggs on most hosts within 24 hours, oviposition was delayed for up to 4 days on *N. bullata*. Development was also strikingly slower on *N. bullata* at every stage with the result that adults emerged only after 24 to 36 days, compared to 16-27 days on the 4 preferred hosts. Development was also somewhat slower on *Megachile*, requiring from 19-31 days. Grissell (1974) attempted to rear *D. pelos* on *Megachile pacifica*, and obtained progeny on 19 of 71 hosts. However, 75% of the eggs laid on *M. pacifica* prepupae failed to complete development to adults. Similarly, we noted significant larval mortality on *M. rotundata* hosts and the few adult progeny obtained were on only 3 of the 10 host replicates.

Comparable data for the progeny of *M. digitata* on the same suite of hosts (except *Sphaeropthalma*, unpubl. data) showed that all hosts were acceptable with adults of both sexes reared from 100% of the replicates (n = 10 for each host).

Sex Ratios

Grissell (1974) reported male-biased sex ratios for *D. pelos* on *Sceliphron* and *Ancistrocerus*. In contrast, we obtained female-biased sex ratios in nearly every trial on every host (Table 1). These ratios appeared to vary with the host species. On the 4 most successful host species, *D. pelos* produced an average of 24.7% males; on the two "marginal" hosts, 43% were male. Overall, the smallest host species (*M. rotundata*) yielded the highest proportion of males (48%). The 13% on *Neobellieria bullata* is probably not representative, as it was based on very few individuals.

Interspecific Competition

In our staged competition experiments with one female each of *D. pelos* and *M. digitata* on a

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TABLE 1. OFFSPRING PRODUCTION (MEAN ± SD) AT 25°C, 65% RH BY *D. PELOS* ON VARIOUS HOSTS, ALONE, AND FOR THE THREE POSSIBLE COMPETITIVE OUTCOMES WITH *M. DIGITATA* (*N* = 10).

Host species	Experiment	No. of hosts parasitized	No. of adult progeny produced (Mean ± SD)		Sex ratio (% males)
			Males	Females	
		Successful hosts			
Sceliphron caementarium	Alone	10/10	14.5 ± 6.5	31.3 ± 12.1	32
	Competition "winner"	1/10	26	25	51
	Competition "loser"	7/10	0	0	0
	Coexistence	2/10	5.5 ± 6.4	12 ± 8.5	31.4
Trypoxylon politum	Alone	10/10	12.9 ± 7.6	44.3 ± 15.8	23
	Competition "winner"	0/10	0	0	—
	Competition "loser"	9/10	0	0	0
	Coexistence	1/10	1	3	25
Sphaeropthalma pensylvanica	Alone**	3/3	6.3 ± 1.2	26.7 ± 10.0	19
Anthrax sp.	Alone	10/10	13.6 ± 2.7	39.9 ± 4.2	25
	Competition "winner"	3/10	16.3 ± 10.2	20.3 ± 7.0	45
	Competition "loser"	4/10	0	0	0
	Coexistence	3/10	7.3 ± 3.8	13 ± 6.0	36
		Marginal hosts*			
Megachile rotundata	Alone	3/10	3 ± 2.6	3.3 ± 3.5	48
	Competition "winner"	1/10	2	1	67
	Competition "loser"	3/10	0	0	0
	Coexistence	0/10***	0	0	0
Neobellieria bullata	Alone	5/10	0.4 ± 0.5	2.6 ± 0.5	13
	Competition "winner"	0	0	0	—
	Competition "loser"	9/10	0	0	0
	Coexistence	0/10***	0	0	0

*Marginal hosts are those on which *D. pelos* managed to produce a few adult progeny in fewer than half of the 10 competition replicates.

**Limited number of available hosts did not allow use in competition trials.

***In 6 replicates with *Meg. rotundata* hosts and 1 replicate with *N. bullata* hosts, no adult progeny of either competitor were produced.

host, the 2 females seldom coexisted successfully. Only in 2 replicates with *Sceliphron*, 1 replicate with *Trypoxylon*, and 3 replicates with *Anthrax* were hosts successfully shared, as defined by the subsequent appearance of adult offspring of both sexes of both species (Table 1, coexistence). Overall, *D. pelos* was the loser in the competition experiments, producing no adult progeny in 20 of the 30 trials with the three hosts preferred by females alone (Table 1).

These outcomes were not simply related to host size. Despite being the smallest of the 3 preferred hosts, *Anthrax* was the most likely to be shared (3 replicates), but *D. pelos* also was the outright competition winner in 3 replicates and the loser in 4 replicates. However, on *Sceliphron* sharing occurred in 2 of 10 trials; in 7 trials, *Melittobia* were the sole progeny to emerge as adults, and in 1 trial, only *Dibrachys* adults emerged. On *Trypoxylon*, the largest hosts, 9 of the replicates resulted in only *Melittobia*, and in only 1 trial did adults of both species emerge.

When *D. pelos* won the competition on *Anthrax* hosts the number of males emerging was not different than when alone (no competitor), but the number of females emerging was fewer than when alone (Student's *t*-test, males $P = 0.69$, females $P = 0.04$). When both *D. pelos* and *M. digitata* adults emerged after competition for an *Anthrax* host, the number of *D. pelos* females was again fewer than when *D. pelos* was alone (Student's *t*-test, $P = 0.005$), but not when compared to when it won outright (Student's *t*-test, $P = 0.24$). Reduced numbers of progeny in competitive situations is not surprising since the host resource is not unlimited and, when shared, both host quality and quantity decline due to host feeding by each of the female parasitoids.

One straightforward reason why *D. pelos* suffers most from this competitive interaction was immediately apparent when larvae of *M. digitata* were observed feeding upon *D. pelos* larvae (Fig. 1d). Subsequently, emerged *M. digitata* were observed laying eggs directly upon pupae and even

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TABLE 2. CONVERSION EFFICIENCY* OF *DIBRACHYS PELOS* AND *MELITTOBIA DIGITATA* REARED ON DIFFERENT HOSTS; BASED ON MEANS FOR $N = 10$.

Host species	Weight (g) (Mean ± SD)	Conversion Efficiency Index (%)	
		D. pelos	*M. digitata*
Suitable hosts for *D. pelos*			
S. caementarium	0.14 ± 0.003	22.5	25.5
T. politum	0.30 ± 0.006	13.7	21.2
Anthrax sp	0.25 ± 0.005	15.3	13.3
Marginal hosts for *D. pelos*			
M. rotundata	0.03 ± 0	13.1	17.3
N. bullata	0.1 ± 0.01	2.3	13.6; 15.9**; 15.3***

*Conversion efficiency = (total number of adult offspring x individual body weight)/ host weight × 100; average weights of individuals were for *D. pelos* (males = 0.42 mg, females 0.80 mg) and for *M. digitata* (males 0.16 mg, females 0.12 mg). Further explanation in text.

**Data from Silva-Torres and Matthews (2003), $n = 4$, host weight = 0.11 g

***Data from Randall and Guinan (unpubl.), $n = 23$, host weight = 0.12 g.

on newly emerged adults (Fig. 1b); in the former case the larvae developed into adult wasps, but larvae perished in the latter case. Depending on the host, *M. digitata* complete development to adults in 14-24 days (González & Matthews 2002), somewhat more rapid than *D. pelos* development in this study.

Differences in fecundity on these hosts may provide equally or more important explanations for this disparity. A single *M. digitata* female on a *Trypoxylon* host produces an average of 458 females and 13 males (unpubl. data), whereas a single *D. pelos* female produces the same number of males but about 10 times fewer females (Table 1). Similar disparities exist for the other hosts, although *M. digitata* is more broadly polyphagous (Dahms 1984) and successfully reproduces large clutches of progeny on both of the hosts that proved only marginally suitable for *D. pelos*.

In the 5 experiments (total from all hosts) where *D. pelos* "won" in competition against *M. digitata*, the proportion of *D. pelos* males increased substantially from that obtained for a female ovipositing in the absence of competition (Table 1). In the 6 replicates (total from all hosts) where adults of both parasitoids emerged, *D. pelos*' sex ratios remained similar to those obtained for *D. pelos* females alone on hosts, although the proportion of males was elevated for *Anthrax* hosts. However, small sample sizes and low numbers of progeny in the competition treatments make it difficult to draw definitive conclusions.

So why does *D. pelos* appear to be relatively rare in field collections of mud dauber nests? In addition to its poor success in our staged competitions for hosts, it may be physiologically less efficient in converting host biomass to parasitoid progeny. To gain a perspective on this possibility, we compared the host conversion efficiency of *D. pelos* and *M. digitata* on each of the hosts used in these experiments (Table 2). *Melittobia digitata* were more efficient on every host tested but *Anthrax*. This suggests that perhaps the hosts we tested were less suitable for *D. pelos* development. Perhaps *D. pelos* is better adapted to twig-nesting wasps or some other unknown host, and its occurrence on *S. caementarium* was strictly opportunistic and facultative at sites not concurrently colonized by *Melittobia*. (In our extensive field collections of *S. caementarium* and *T. politum* nests over several years in eastern N. America, *Melittobia* is by far the commonest parasitoid found [unpubl. data].). In support of this it is notable that in the extensive sample of mud dauber nests taken from the same bridge in Nebraska where *D. pelos* was originally collected failed to turn up any *Melittobia*.

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