

Parasitism Rates in Relation to Nest Site in Bees and Wasps (Hymenoptera: Apoidea)

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To account for differences in occurrence of social behavior in different lineages of bees, Michener (1985) hypothesized that ground nests are more easily located by parasites than are twig nests. In the former case parasites search in two dimensions, while in the latter they search in three-dimensional space. One prediction derived from this hypothesis is that ground nests will have higher rates of parasitism than twig nests. A survey of published reports on rates of cell parasitism for 92 species of nesting bees and wasps (Apoidea) shows no significant differences in mean parasitism rates between these two classes of nests. The analyses were repeated at the generic level (N = 44), yielding the same pattern. These data may be biased due to phylogenetic effects. Paired comparisons (n = 11 pairs) of related taxa that differ in nest site show that ground-nesting taxa more often have higher rates of parasitism than twig-nesters. The use of artificial "trap-nests" to study twig-nesters significantly enhances the success rate of parasites. This bias, as well as several other limitations, suggests that experimental studies of the host-searching capabilities of parasites and predators may be more efficacious than such comparative tests.

KEY WORDS: Apoidea; bee; sphecid wasp; parasitism; search behavior; habitat.

INTRODUCTION

If group-living is advantageous due to mutualistic benefits associated with nest defense (e.g., Lin and Michener, 1972), then such benefits might be greater in hostile environments, relative to enemy-free ones (Wcislo, 1996). Social behavior apparently has evolved much more frequently among ground-nesting halic-

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tine bees, relative to twig-nesting ceratinine bees (Michener, 1985). In an attempt to account for this difference, Michener (1985, 1990) hypothesized that nests in the ground (i.e., those distributed in two-dimensional space) would be easier for enemies to locate than those in the ends of twigs (i.e., those distributed in three dimensions). Others (e.g., Matthews, 1991) have suggested the hypothesis applies to social evolution in groups like spheciform wasps. Michener's hypothesis incorporates considerations from foraging theory and search behavior (e.g., Bell, 1991; Bernays and Weislo, 1994) but has been neither modeled nor empirically tested. Michener's hypothesis has a straightforward prediction: on average, twig-nesting forms should have lower rates of parasitism than those nesting in the ground or on flat surfaces. I compiled data from available literature on Apoidea as an indirect test of this hypothesis. Bees (Apiformes) constitute a monophyletic group, and bees plus some spheciform wasp lineages together constitute a monophyletic Apoidea (Alexander, 1992). As emphasized in the Discussion, this effort is preliminary since there are numerous confounding factors associated with this kind of comparative survey.

METHODOLOGY

Information on parasitism rates initially was gathered from a survey of papers in the *Journal of the Kansas Entomological Society* (1965 through 1974), as well as select published reports. The initial survey was not intended to be comprehensive, and numerous papers could have been included but were not.

I included all studies that quantified parasitism rates or that specifically reported no observed parasitism. Those which did not mention parasites were excluded, since it was unclear whether an absence of data reflected natural history or the authors' disinterest (cf. Hawkins, 1994). All included species were solitary, or populations of exclusively solitary individuals (e.g., *Halictus rubicundus*). I included mortality from obligate cleptoparasites (*sensu* Weislo, 1987) but omitted intraspecific parasitism, so in all cases rates of parasitism are conservative estimates. I also included several mud-nesters, as indicated in footnotes. I excluded solitary species in which males potentially guard nests (e.g., *Trypargilum*). I combined reports with different parasites, sample sizes, study durations, and host densities.

Species were classified as "ground-nesting" or "twig-nesting." Even this simple classification is somewhat arbitrary. For example, a twig-nesting colletid bee nested only in twigs of a shrub which had fallen to the ground; a halictine nesting in dead logs on the ground was classified as ground-nesting.

For twig-nesting forms, nests were also scored as "natural" (i.e., found in undisturbed sites), "artificial" [i.e., obtained through the use of trap-nests (see Krombein, 1967)], or "manipulated natural nests" (i.e., natural substrates that were artificially clustered). Although information on nest density was usu-

ally not given, trap-nests are typically put out in bundles of several to many nests, so they may be at higher densities than natural nests.

Statistical tests [Kruskal-Wallis one-way analysis of variance (ANOVA) and one-way ANOVA after arcsine transformation of the data] were performed using SYSTAT (Wilkinson, 1989) on a personal computer. Analyses were done for all species pooled together, as well as separately for Apiformes (bees) and Spheciformes (wasps). I also repeated the analyses at the generic level. Since species and genera may not be independent data points for statistical purposes (see Harvey and Pagel, 1991), I reduced the original data set to six pairs of closely related taxa which differ in nest site and analyzed the frequency of parasitism using a sign test for the pairs (Siegel, 1956).

Following peer review by the journal, I attempted to gather more data for the reduced data set. To minimize observer bias, I searched through an additional 10 years of the *Journal of the Kansas Entomological Society* (1975-1984) and 10 years each (1970-1979) of *Psyche*, *Pan-Pacific Entomologist*, and *Proceedings of the Entomological Society of Washington*, or references therein. These additional taxa are not included in the Appendix (Table AI).

RESULTS

Based on this survey (Table AI), the overall rate of cell parasitism per species was not significantly different for ground- and twig-nesting apoid species (Table I). Differences were also not significant at the generic level (Table II; Kruskal-Wallis $U = 228.5$, χ^2 approximation = 0.1, $P = 0.751$). For bees alone, there also were no significant differences in parasitism rates with respect

Table I. Summary Statistics for Mean Rates \pm SE of Cell Parasitism for Species of Twig- and Ground-Nesting Apiform ("Bee") and Spheciform ("Wasp") Apoidea^a

	Twig-nesting	Ground-nesting	Pooled
Bees	29.2 \pm 4.37 (25)	29.9 \pm 4.61 (27)	29.6 \pm 3.15 (52)
Wasps	20.8 \pm 3.94 (18)	18.9 \pm 2.9 (22)	19.7 \pm 2.37 (40)
Pooled	25.7 \pm 3.06 (43)	24.9 \pm 2.94 (49)	25.3 \pm 2.1 (92)
	Source	F ratio	P
	Taxon	5.319	0.023
	Site	0.023	0.881
	Taxon * Site	0.094	0.759

^aF values are from a one-way ANOVA. Sample sizes are in parentheses.

Table II. Summary Statistics for Mean Rates \pm SE of Cell Parasitism for Genera of Twig- and Ground-Nesting Apiform ("Bee") and Spheciform ("Wasp") Apoidea^a

	Twig-nesting	Ground-nesting	Pooled
Bees	30.5 \pm 6.97 (13)	29.4 \pm 3.9 (16)	29.9 \pm 3.75 (29)
Wasps	22.1 \pm 3.84 (9)	19.6 \pm 3.5 (6)	21.1 \pm 2.63 (15)
Pooled	27.0 \pm 4.4 (22)	26.7 \pm 3.17 (22)	26.9 \pm 2.68 (44)

^aFor genera with more than one species per genus included (see Appendix), an unweighted mean was used. Sample sizes are in parentheses.

to nest site at the species level ($U = 338.5$, $P = 0.99$; Table I) or at the generic level ($U = 97.5$, $P = 0.77$; Table II). For wasps, there also were no significant differences, at either taxonomic level (species, $U = 198.5$, $P = 0.989$, Table I; generic: $U = 26$, $P = 0.91$, Table II), although as defined here this group is probably paraphyletic (see Alexander, 1992), so the result is ambiguous.

The original data set contained six phylogenetically related pairs with which to compare rates of parasitism between taxa that differ in nest site. In five of six comparisons ground-nesters had higher rates of parasitism than twig-nesters (sign test, $P = 0.109$). Following this analysis, a subsequent literature search gave additional comparisons (from Hunt, 1993; Hager and Kurczewski, 1986; Freeman, 1982; Taffe and Ittyeipe, 1976; Krombein 1964). For 9 of 11 comparisons (Table III), ground-nesters had higher rates of parasitism than twig-nesters (sign test, $P = 0.033$).

For the species surveyed, bees are more heavily parasitized than wasps (Mann-Whitney $U = 781.5$, $P = 0.042$), and there is no significant interaction between site and taxon which influences parasitism rates (Table I). At the generic level, however, these statistical differences between rates of parasitism for bees and wasps are not significant (Table II; Kruskal-Wallis $U = 161.5$, χ^2 approximation = 1.923, $P = 0.17$).

For twig-nesting forms at the generic level, artificial nests had higher rates of parasitism ($\bar{x} = 35.4 \pm 6.2$, $N = 10$) than did natural or manipulated nests ($\bar{x} = 21.9 \pm 8.0$, $N = 5$, and $\bar{x} = 13.7 \pm 2.9$, $N = 7$, respectively) (Kruskal-Wallis = 6.09, $P = 0.047$).

DISCUSSION

The most conservative analysis supports Michener's hypothesis (see Introduction). Paired comparisons of related taxa show that ground nests more often have higher rates of parasitism than do twig nests. The small sample size and

Table III. Taxa Used for Comparisons of Related Taxa Differing in Nest Site; Values for Parasitism Rates Are Given in the Appendix

Taxon	Rate of parasitism: Ground-nester > aerial-nester?
Osmiini	
<i>Osmia sanrafaelae</i> (intraspecific)	+
<i>Osmia nigrifrons</i> vs other <i>Osmia</i>	-
Colletidae: <i>Scapter</i> vs other colletids	+
Apidae	
Xylocopini vs (Exomalopsini, Emphorini, Eucerini)	+
Crabronini	
<i>Crabro</i> vs <i>Crossocerus</i> or <i>Rhopalum</i>	+
<i>Crabro</i> vs. <i>Ectemnius paucimaculatus</i> ^a	-
Larrinae	
<i>Tachytes</i> vs other larrines	+
Sphecini	
<i>Sceliphron fistularum</i> (intraspecific) ^a	+
<i>Ammophila</i> vs <i>Sceliphron</i> ^a	+
Eumenidae	
<i>Pachodynerus nasidens</i> (intraspecific) ^a	+
<i>Zeta abdominale</i> (intraspecific) ^a	+

^aPair added following the initial analyses.

other caveats (below) suggest that this conclusion should be accepted with caution. The results are, however, concordant with studies on birds showing that ground-nesting taxa, on average, are more frequently preyed upon than those nesting in trees (Martin, 1995).

Intraspecific comparisons also support Michener's hypothesis, although these comparisons are confounded by density effects (see Molumby, 1995) since nests on flat surface are often at higher densities than those on roots and vines. For example, trap-nests of *Pachodynerus nasidens* placed directly on rocks and masonry were more heavily parasitized (27.5%) by *Melittobia* wasps than free-hanging ones (0%) (Jayasingh, unpublished data, in Taffe and Ittyeipe, 1976). Similarly, mud nests on flat surfaces were more heavily parasitized by wasps than those on roots [*Zeta abdominale* (Eumenidae) (Taffe and Ittyeipe, 1976), *Sceliphron fistularum* (Sphecidae) (Freeman, 1982)]. In contrast, for *Z. abdominale* there were no consistent nest-site differences in parasitism rates by satellite flies (*Amobia*, Diptera: Miltogramminae). The search behavior of the two parasites differs, which may help account for these findings. *Melittobia* lands on a substrate, and walks or jumps to host nests (references in Ittyeipe, 1976). Taffe and Ittyeipe (1976) suggest that flying wasps are more likely to be intercepted by rock faces and flat surfaces than by dangling vines or rootlets. In contrast,

Amobia follows flying adult hosts (reference in Wcislo 1986), so nest location may be relatively unimportant.

Less conservative analyses, which treat species or genera as independent data points, do not support the hypothesis that nests in the ground are subject to higher levels of parasitism than those in twigs. Weaving (1996) also compiled published data on parasitism rates for sphecid, eumenid, and pompilid wasps. An analysis of data in his Appendix A shows no significant differences in mean rates of parasitism for ground-, twig-, or mud-nesting forms (Wcislo, unpublished). All these analyses probably violate statistical assumptions of independence, since some species may share an immediate common ancestor (see Harvey and Pagel, 1991).

The following caveats suggest further reasons why results from this kind of a survey should be cautiously interpreted and emphasize the preliminary nature of the conclusions.

(i) Many data on twig-nesters came from "trap-nesting" studies (see Krombein, 1967). These artificial nests are often bundled together, effectively creating an aggregation and a larger target for a searching parasite. Group size or density can influence parasitism rates (see Wcislo, 1984; Rosenheim, 1990; Molumby, 1995; Weaving, 1996), and parasitism rates are sometimes lower under more natural nest densities. Ground-nesting species which nest in aggregations are probably overrepresented in the literature, since they are easier for biologists to locate and study. Such aggregations may attract more parasites on a *per capita* basis, relative to isolated nests (Wcislo, 1984; Rosenheim, 1990).

(ii) I tallied total rates of parasitism, even though Michener (1985) originally proposed his hypothesis for *wingless* parasites; later he (Michener, 1990) included predators and parasites in general. I included both winged and wingless parasites because few published reports made the distinction between the two classes. Some parasites (e.g., certain parasitic Hymenoptera) attack only twig-nesters, and others (e.g., some meloid beetles) attack only ground-nesting forms (see Wcislo and Cane, 1996). In tallies of total rates of parasitism, these habitat specialists may counterbalance each other.

(iii) The assumption that the ground or a rock face is strictly a two-dimensional surface is probably not always true, since microtexture and vegetation will perturb a planar surface. No attempt was made to account for that variability.

(iv) Current taxonomy may not always reflect phylogeny, and the higher classification of Apoidea is not well understood (see Alexander, 1992; Roig-Alsina and Michener, 1993). Our current understanding means that we do not know to what extent phylogenetic relatedness is a confounding variable in the analyses. Moreover, host species are from lineages of different evolutionary ages, which may have different numbers of specialized parasites (cf. Brooks and McLennan, 1993).

(v) Most included species have Nearctic distributions, and different regions could have different abundances and diversities of natural enemies (see Hawkins, 1994).

(vi) Finally, the data included in the Appendix (Table AI) are not a true random sample drawn without observer bias, as required for the statistical analyses. The decision to search a predetermined number of journal issues was an attempt to avoid observer bias, yet the publication process itself introduces a bias that is usually neglected in comparative studies. As pointed out by a reviewer, this study, like other comparative studies (e.g., references in Harvey and Pagel, 1991), neglected sampling procedures and simply included all relevant data from the publications surveyed, violating a basic statistical assumption. A valid approach would use all the relevant data to form a "study population" and, from this population, draw at random a specified number of data points appropriate for the statistical analyses.

Based on this sample, bees (at the species level) are more heavily parasitized than spheciformes. Due to the paraphyletic nature of the latter, it is not clear if these differences are real or artifactual. Some parasites that attack bees do not attack wasps, and vice versa. Cleptoparasites, for example, are common among bees relative to spheciformes (Wcislo, 1987), yet other parasitic taxa attack both bees and wasps [e.g., many miltogrammines (Wcislo, 1986)]. If supported, however, this observation may help explain why group-living has evolved more frequently in bees relative to spheciformes (references in Michener, 1974; Wcislo, 1992), by analogy to Michener's (1985) original hypothesis.

A proper test of the relationship between parasitism rates and nest habitat (i) should be based on closely related taxa with host species nesting both in the ground and in twigs [e.g., some megachilid, xylocopine, or colletid bees; *Rhopalum* (Crabronini) or eumenid wasps (see O'Toole and Raw, 1991; Bohart and Menke, 1976; Evans, 1978)] and (ii) utilize only data from enemies which attack both twig- and ground-nesters. In practice, however, this hypothesis (see Introduction) is a slippery one to test, using the following logic (C. D. Michener, *in litt.*). Ground-nesting species may survive only in areas where enemies are not too abundant. Additionally, all species have some defenses against natural enemies. These behaviors range from hiding nest entrances under rocks or at the base of plants, to closing the entrances, to group-living so there can be guards at entrances. If natural enemies are especially abundant, and nests are easy to locate, then defenses of extant species must be better ipso facto. But because defenses are better, parasitism rates may be the same. If this "circularity" is true, then a more definitive comparative prediction derived from Michener's hypothesis is that populations of ground-nesting aculeates should be more frequently extirpated by natural enemies than twig-nesting ones. A still more definitive test is to assess directly the search capabilities of parasites and predators.

APPENDIX

Table AI. Rates of Parasitism for Nesting Hymenoptera^a

Species and site	% parasitism	Reference	Generic mean
Spheciformes			
Pemphredoninae			
Psenini			
T <i>Psenulus concolor</i>	0.0	Danks (1971)	
T <i>P. schencki</i>	1.2	Danks (1971)	
T <i>P. pallipes</i>	50.0	Krombein (1967)	20.1
Pemphredonini			
T <i>Pemphredon lethifer</i> + <i>Pemphredon</i> sp.	20.2	Danks (1971)	
T <i>P. shuckardi</i> (gen I)	23.0	Danks (1971)	21.6
T <i>Passaloeocus gracilis</i>	8.7	Danks (1971)	
T <i>P. cuspidatus</i>	42.0	Krombein (1967)	25.4
T <i>Spilomena</i> spp.	15.7	Krombein (1967)	15.7
Crabroninae			
Crabronini			
T <i>Rhopalum coarctatum</i>	9.1	Krombein (1967)	
T <i>R. clavipes</i>	20.4	Danks (1971)	14.8
T <i>Crossocerus capitosus</i>	19.7	Krombein (1967)	19.7
G <i>Crabro advena</i>	25.0	Evans <i>et al.</i> (1980)	
G <i>C. cribrellifer</i> (NY)	42.0	Evans <i>et al.</i> (1980)	
G <i>C. cribrellifer</i> (MI)	30.8	Wcislo <i>et al.</i> (1985)	26.6
Larrinae			
Trypoxylini			
T <i>Trypoxylon</i> spp.	17.2	Krombein (1967)	
T <i>T. frigidum</i>	3.8	Medler (1967)	
T <i>T. rubrocinctum</i>	16.4	<i>Op. cit.</i>	
T <i>T. striatum</i>	5.9	<i>Op. cit.</i>	10.8
Miscophini			
T <i>Solierella blaisdellia</i>	20.0	Krombein (1967)	20.0
Larrini			
G <i>Tachytes validus</i>	20.8	Kurczewski & Ginsburg (1971)	20.8
Sphecinae			
Sphecini			
T <i>Isodontia mexicana</i>	51.1	Medler (1965)	
T <i>I. auripes</i>	50.0	Krombein (1967)	50.6
Philanthinae			
Cercerini			
G <i>Cerceris fumipennis</i>	1.9	Evans (1971)	
G <i>C. fumipennis</i>	62.0	Hagar & Kurczewski (1984)	
G <i>C. californica</i>	>20.0	Linsley & MacSwain (1956)	29.9

Table AI. Continued^a

Species and site	% parasitism	Reference	Generic mean
Sphéciformes Continued			
Philanthinae Continued			
Philanthini			
<i>G Philanthus bicinctus</i>	7.5	Gwynne; in Evans & O'Neill (1988)	
<i>G P. basilaris</i> (Chimney R.)	27.7	Evans & O'Neill (1988)	
<i>G P. basilaris</i> (Great Sand Dunes)	0.0	<i>Op. cit.</i>	
<i>G P. zebratus</i>	15.6	<i>Op. cit.</i>	
<i>G P. sanborni</i>	41.3	<i>Op. cit.</i>	
<i>G P. gibbosus</i> (New York)	29.7	<i>Op. cit.</i>	
<i>G P. gibbosus</i> (Bedford, MA)	35.7	<i>Op. cit.</i>	
<i>G P. gibbosus</i> (Fort Collins)	18.9	<i>Op. cit.</i>	
<i>G P. crabroniformis</i>	21.3	<i>Op. cit.</i>	
<i>G P. barbatus</i>	3.1	<i>Op. cit.</i>	
<i>G P. inversus</i>	4.3	<i>Op. cit.</i>	
<i>G P. pulcher</i>	25.9	<i>Op. cit.</i>	
<i>G P. politus</i>	25.0	<i>Op. cit.</i>	
			21.3
Nyssoninae			
Bembicini			
<i>G Bembix comata</i>	30.0	Bohart & MacSwain (1940)	
<i>G B. hinei</i>	0.0	Evans (1957)	
<i>G B. dentilabris</i>	0.0	Evans (1957)	
<i>G Stictia heros</i>	8.7	Sheehan (1984)	10.0
			8.7
Apiformes			
Apidae			
Xylocopinae			
<i>T Xylocopa</i> spp. ^b	44.0	Watmough (1983)	44.0
<i>T Ceratina calcarata</i>	10.0	Rau (1928)	10.0
Apinae			
Centridini			
<i>G Centris flavofasciata</i>	59.0	Vinson <i>et al.</i> (1987)	59.0
Eucerini			
<i>G Melissodes rustica</i>	47.0	Clement (1973)	47.0
Exomalopsini			
<i>G Exomalopsis solani</i>	50.0	Rozen (1984)	
<i>G E. solidaginis</i>	7.0	Rozen (1984)	
			28.5
Emphorini			
<i>G Diadasia bituberculata</i>	51.0	Linsley & MacSwain (1952)	
<i>G D. consociata</i>	47.0	Linsley <i>et al.</i> (1952)	
<i>G Diadasia</i> sp.	27.0	Linsley (1958)	
			41.7
<i>G Melitoma marginella</i>	59.0	Linsley <i>et al.</i> (1980)	
<i>G M. segmentaria</i>	0.0	<i>Op. cit.</i>	
			29.5
Anthophorini			
<i>G Anthophora linsleyi</i>	43.0	Linsley & MacSwain (1942)	
<i>G A. linsleyi</i>	52.0	<i>Op. cit.</i>	
<i>G A. bomboides</i>	6.0	Brooks (1983)	
			33.7

Table AI. Continued^a

Species and site	% parasitism	Reference	Generic mean
Apiformes Continued			
Megachilidae			
Megachilinae			
Anthidiini			
T <i>Dianthidium heterulkei</i>	16.0	Krombein (1967)	16.0
T <i>Callanthidium formosum</i>	14.3 ^c	Parker (1987)	14.3
Osmiini			
T <i>Ashmeadiella meliloti</i>	100.00	Krombein (1967)	100.0
T <i>Osmia lignaria</i>	25.0	Krombein (1967)	
T <i>Osmia georgica</i>	12.3	Hawkins (1975)	
T <i>Osmia rufa</i>	28.0 ^d	Raw (1972)	
T <i>Osmia sanrafaelae</i>	36.8	Parker (1986)	
T <i>Osmia ribifloris</i>	11.0	Rust (1986)	
T <i>Osmia tersula</i>	48.0	Arduser (ms.)	
			26.8
G ^f <i>Osmia sanrafaelae</i>	51.8	Parker (1986)	
G ^f <i>Osmia nigrifrons</i> (1969)	2.9	Rust and Thorp (1973)	
G <i>Osmia nigrifrons</i> (1970)	42.8		
			32.5
T <i>Hoplitis fulgida</i>	32.4	Tepedino & Parker (1984)	
T <i>Hoplitis cylindrica</i>	40.0	Medler (1967)	
			36.2
T <i>Chelostoma phaceliae</i>	36.3 ^c	Parker (1988)	36.3
Megachilini			
T <i>Megachile mendica</i>	26.0	Krombein (1967)	
T <i>Megachile xylocopoidea</i>	25.0	<i>Op. cit.</i>	
T <i>Megachile brevis</i>	35.0	Michener (1953)	
			28.7
T <i>Chalicodoma georgica</i>	43.0	Krombein (1967)	
T <i>C. campanulae</i>	55.0	<i>Op. cit.</i>	
			49.0
Colletidae			
Xeromelissinae			
T ^g <i>Chilicola ashmeadi</i>	0.0	Eickwort (1967)	0.0
Hylaeinae			
T <i>Hylaeus asininus</i>	10.0	Krombein (1967)	
T <i>H. modestus</i>	20.0	<i>Op. cit.</i>	
			15.0
T <i>Prosopis brevicornis</i> (I)	7.5	Danks (1971)	
T <i>P. brevicornis</i> (II)	55.0	<i>Op. cit.</i>	
T <i>P. communis</i>	0.0	<i>Op. cit.</i>	
			20.8
Colletinae			
G <i>Scapter longula</i>	47.0	Rozen & Michener (1968)	47.0
Halictidae			
Halictinae			
G <i>Halictus rubicundus</i> ^h	15.5	Eickwort <i>et al.</i> (1996)	15.5
G <i>Lasioglossum sakagami</i>	27.9	Sakagami <i>et al.</i> (1982)	27.9
G <i>L. figueresi</i>	21.0	Wcislo <i>et al.</i> (1993)	
G ⁱ <i>L. coeruleum</i>	0.0	Stockhammer (1967)	
			16.3

Table AI. Continued^a

Species and site	% parasitism	Reference	Generic mean
Apiformes Continued			
Halictidae Continued			
Rhopitinae			
G <i>Dufourea trochantera</i>	10.0	Torchio <i>et al.</i> (1967)	10.0
Nomiinae			
G <i>Nomia melanderi</i>	6.6	Bohart & Cross (1955)	
G <i>N. melanderi</i> (Washington)	91.0	Bohart <i>et al.</i> (1960)	
			48.8
G <i>Dieunomia triangulifera</i>	16.4	Wcislo <i>et al.</i> (1994)	16.4
Andrenidae			
Panurginae			
G <i>Perdita nuda</i> (1970)	5.7	Torchio (1975)	
G <i>Perdita nuda</i> (1973)	10.3		
			8.0
G <i>Calliopsis andreniformis</i>	9.0	Shinn (1967)	9.0

^aG, ground-nesting; T, twig-nesting or trap-nesting. A few species are not strictly ground- or twig-nesting, as explained in the subsequent footnotes; the symbol indicates which group the species was placed in for statistical comparisons. For genera with more than one species, a mean for the genus is also given. Classification follows Bohart and Menke (1976) for Spheciformes and Roig-Alsina and Michener (1993) for Apiformes.

^bData pooled for uni- and multivoltine species; presumably these have different parasites.

^cMortality from unknown causes.

^dExcludes mortality from unknown causes.

^eMud nests built on ground substrata.

^fThese mud cells were aggregated within the entrance of a drain pipe.

^gThese bees nested in twigs of dead trees which had fallen to the ground.

^hData from nests in a population of solitary bees.

ⁱThese bees nested within logs of dead trees on the ground.

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