

Phenology and social biology of two sibling species of *Halictus* in an area of sympatry

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Abstract: Fortnightly samples of foragers of *Halictus ligatus* Say and its recently distinguished sibling species *Halictus poeyi* Lepeletier were collected in an area of sympatry. Both species were active from late April until autumn, although *H. ligatus* ceased foraging about 1 month earlier than *H. poeyi*. Phenological differences were minor and insufficient to preclude hybridization opportunities between the species. The two had a similar proportion of ovarially developed workers, but the proportion that mated in *H. poeyi* was double that found in *H. ligatus*, and size dimorphism between castes was greater in *H. poeyi* than in *H. ligatus*. When these data are compared with data from other populations, in sympatry the two species appear to be more similar to each other in several sociobiological parameters than each does to allopatric conspecific populations. This suggests a prime role for ecological factors in determining details of social organization in halictine bees.

Résumé : Des échantillons bimensuels de récolteuses de l'abeille *Halictus ligatus* Say et de son espèce soeur reconnue depuis peu *Halictus poeyi* Lepeletier ont été recueillis dans une zone où les deux espèces vivent en sympatrie; elles sont toutes deux actives de la fin d'avril à l'automne, mais *H. ligatus* cesse sa quête de nourriture environ 1 mois plus tôt que *H. poeyi*. Les différences phénologiques sont mineures et insuffisantes pour prévenir les occasions d'hybridation des deux espèces. Chez les deux espèces la proportion d'ouvrières à ovaires développés était la même, mais la proportion d'ouvrières qui se sont accouplées a été deux fois plus importante chez *H. poeyi* que chez *H. ligatus* et le dimorphisme entre les castes quant à la taille, plus important chez *H. poeyi* que chez *H. ligatus*. Par comparaison avec des données sur d'autres populations, ces deux espèces qui vivent en sympatrie paraissent plus semblables l'une à l'autre par plusieurs de leurs paramètres sociobiologiques que chacune d'elle à des populations allopatriques conspécifiques. Cette situation semble souligner l'importance des facteurs écologiques dans la mise en place des détails de l'organisation sociale chez les abeilles halictinées.

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Introduction

Halictine bees are an enormous and abundant group found on every continent except Antarctica (Michener 1990). Among social insects, they display the broadest range of social behaviours; eusociality (sensu Michener 1974) is exhibited by many genera and has arisen at least several times, with solitary and eusocial species often found within the same subgenus (Packer 1997). Geographic variation in social behaviour has been noted in most halictine species studied in sufficient detail and many aspects of their sociality seem environmentally determined (Richards and Packer 1995; Wcislo 1997), although genetic influences cannot be discounted (Plateaux-Quénu et al. 1998).

Halictus ligatus has been considered one of the most widespread and frequently studied halictines. However, Carman and Packer (1997) found that it comprises two distinct species, one in the southeastern United States and one to the north and west, with sympatry of the two throughout the Piedmont region from at least Raleigh, North Carolina,

to Auburn, Alabama (Packer 1998). *Halictus ligatus* Say is probably the more northerly species, for which data are available from Indiana (Chandler 1955), California (Eickwort 1985), New York (Litte 1977; Boomsma and Eickwort 1993), and Ontario (Knerer 1980; Packer 1986a, 1986b; Richards and Packer 1995, 1996; Richards et al. 1995). In all of these areas, it has an archetypal, primitively eusocial annual colony cycle.

The newly discovered sibling species provisionally referred to as *Halictus poeyi* Lepeletier has been studied in Florida (Packer 1986c; Packer and Knerer 1986, 1987; Carman and Packer 1997). In the central and northern regions of the state, it has an annual, although somewhat extended, colony cycle with periods of inactivity lasting from late November to early March (Packer and Knerer 1987). In contrast, in the subtropical climate of the Florida Keys, *H. poeyi* nests may be initiated at any time of the year, with the entire colony cycle lasting less than 6 months (Packer and Knerer 1986).

Here we investigate possible differences between the two species in an area of sympatry. In particular, we wanted to see (i) if there are seasonal phenological differences that may preclude hybridization between the species, (ii) whether the long colony cycles of *H. poeyi* and the shorter ones of *H. ligatus* are at least partially retained in sympatry, and (iii) whether the reduced social level apparent in *H. poeyi* in the south in comparison with *H. ligatus* in the north applies also where the two are sympatric. Lastly, we compare our

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data for the two species where they are sympatric with previously published information for them where they are allopatric.

Methods

Sampling

Bees were collected along railroad tracks on the west side of the campus of Winthrop University in Rock Hill, South Carolina. Collections were made about every 2 weeks from May to October 1996 and again in April and May 1997, usually for a period of 1 h in the early afternoon. The bees were found foraging on wild flowers, such as *Aster* sp. (white daisy), *Helenium* sp. (bitterweed), *Heterotheca* sp. (camphorweed), *Solidago* sp. (goldenrod), *Senecio* sp. (ragwort), *Erigeron* sp. (fleabane), and *Coreopsis* sp. (tickseed). Following field collection, samples were stored in a -75°C freezer in Rock Hill and then transported to York University, Toronto, Ontario, on dry ice or liquid nitrogen. In total, 223 females and 87 males were collected in 1996. Because sample sizes for overwintered gynes were small, additional collections were made in April and May 1997 at a time when all females were overwintered reproductives. An additional 4 *H. ligatus* and 30 *H. poeyi* were obtained.

Species identification

As the two species are presently morphologically indistinguishable (Carman and Packer 1997), gel electrophoresis was used for identification. Carman and Packer (1997) found seven fixed differences between the two, including loci for the enzymes esterase, glucose-6-phosphate isomerase, glycerol-3-phosphate dehydrogenase, and malate dehydrogenase (NADP). Further studies indicate that fumarate hydratase is also diagnostic in areas of sympatry (Packer 1998). Following the methods of Carman and Packer (1997), we used three to five of these loci to identify each specimen. There was complete agreement among loci for all individuals: in these samples we found no heterozygotes at any of the approximately 1000 diploid bee loci investigated and all individuals were (genetically) either pure *ligatus* or pure *poeyi*.

Sociobiological data

Detailed study requires observations of marked bees and nest excavations, but we have yet to discover nest sites where the two species are sympatric. Nonetheless, sociobiologically relevant information can be obtained from dissection and measurement of bees. We collected data on (i) the percentage of workers mated, (ii) the percentage of workers with ovarian development, and (iii) the size dimorphism between castes, variables known to be relevant to social evolution in halictines (Breed 1976; Packer and Knerer 1985).

Following standard techniques (Ordway 1965), wing wear and mandibular wear were used to estimate the comparative age of specimens and were summed to provide an estimate of total wear. We checked every female collected in 1996 for the presence of sperm in the spermatheca and assessed ovarian development using the index of summed oocytes (ISO) (Goukon et al. 1987) as follows. Each of the six ovarioles was assigned a developmental stage from I to IV or a resorption stage from I to III; ISO is the sum of development and resorption indices and varies from 0 to 6 (for further details see Goukon et al. 1987). Note that when we analyzed data from developing or resorbing stages only, the same patterns were found as presented for ISO below. Oophagy (egg cannibalism) is known in social halictines (Michener 1990; Kukuk 1993) including *H. ligatus/poeyi* (Packer 1987) and was detected by the presence of pasty white masses identical in consistency with a crushed fully developed oocyte in a bee's gut. The presence of yellow bodies, or corpora lutea, yellow deposits laid down after

oviposition (Billen 1985), or oocyte resorption (Pabalan 1998) was recorded for each female.

Caste was determined from a number of variables taken together for whole samples. Foundresses were identified from the combination of being the earliest bees foraging, all mated, usually with high ISO, often rather large, and with increasing wear over time early in summer (see Figs. 1A and 1B). Workers were obtained later in the year, initially with little or no wear, and were unmated and (or) had undeveloped ovaries. Only six bees seemed to be prediapause gynes (all were *H. poeyi*), but as they may have been young late-emerging workers, they were removed from all analyses. Caste size dimorphism was expressed as the mean size difference between the castes divided by mean queen size expressed as a percentage.

Weather data for Rock Hill were obtained from the Winthrop University Station of the National Oceanographic and Atmospheric Administration.

Results

Phenology

Overwintered foundresses were collected in May and early June and workers thereafter. Very few completely unworn individuals were found in any of our samples, suggesting unusually rapid development of wing wear in particular. Nonetheless, unworn bees were found in each month of sampling, and in late August unworn females and individuals of both species with completely abraded wings were flying simultaneously. Female *H. poeyi* were generally two to three times as numerous as those of *H. ligatus* and were sampled later into the autumn (Fig. 1A). The bimodal pattern of male abundance (Fig. 1C) seems to be consistent, with one "worker" brood containing some males followed by a reproductive brood. However, the lack of marked variation in worker wear (Fig. 1B) suggests a fairly constant turnover of foragers through more than one brood; August workers with little or no wear could not have been produced by foundresses foraging in May, and worn foragers in autumn are unlikely to have been from the first worker brood.

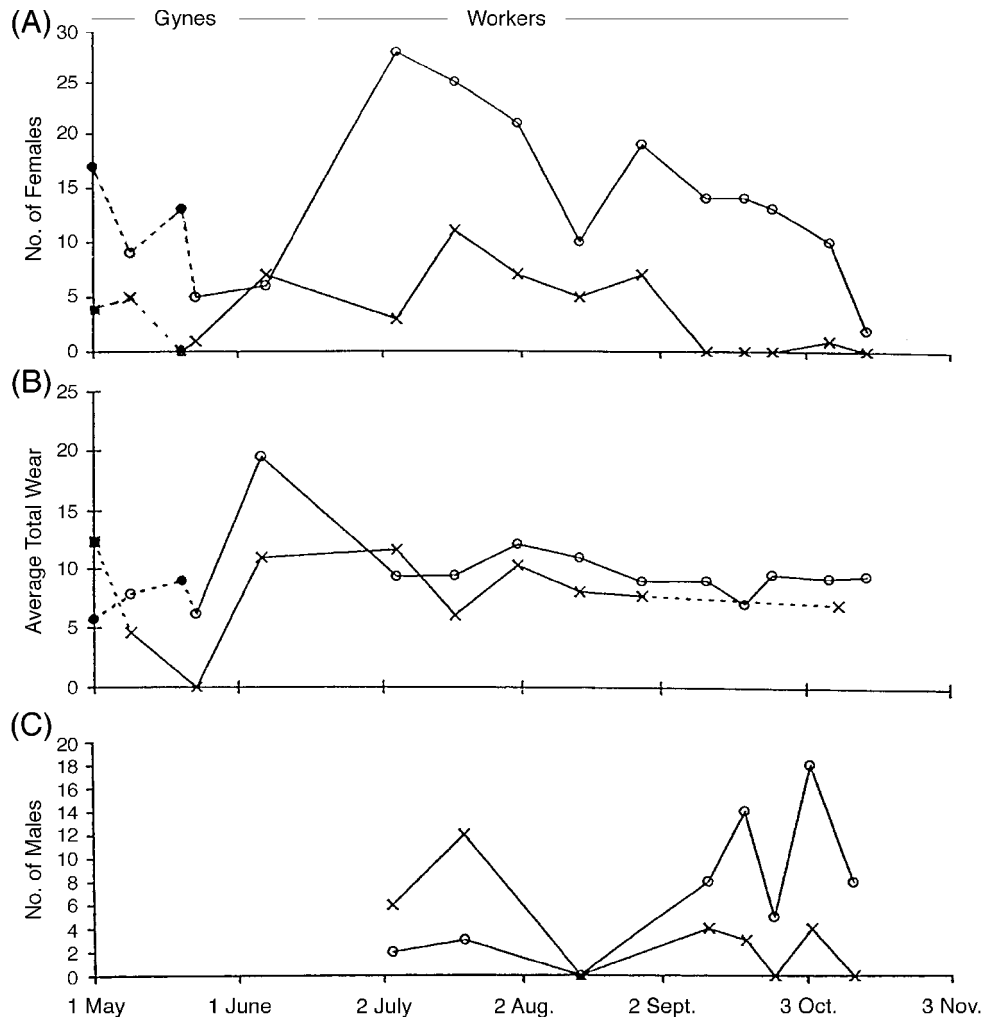
Sociobiology

Halictus poeyi is generally larger than its sister species, although there is a continuum in size, with no caste-based bimodality (Fig. 2). Female *H. poeyi* are significantly larger both for gynes (*H. ligatus*: mean = 2.72 mm, SE = 0.02 mm, $n = 17$; *H. poeyi*: mean = 3.04 mm, SE = 0.04 mm, $n = 48$; $t = 7.04$, $p < 0.001$) and for workers (*H. ligatus*: mean = 2.64 mm, SE = 0.03 mm, $n = 33$; *H. poeyi*: mean = 2.90 mm, SE = 0.03 mm, $n = 142$; $t = 7.52$, $p < 0.001$). Wing lengths are similar for gynes (*H. poeyi*: mean = 6.02 mm, SE = 0.13 mm; *H. ligatus*: mean = 5.74 mm, SE = 0.16 mm; $t = 2.33$, $p = 0.015$) and workers (*H. poeyi*: mean = 5.76 mm, SE = 0.08 mm; *H. ligatus*: mean = 5.44 mm, SE = 0.06 mm; $t = 5.6$, $p < 0.001$). *Halictus ligatus* gynes had a bimodal size distribution, four of them being below average for a worker (Fig. 2A). One *H. poeyi* gyne was also extremely small (Fig. 2B).

Caste size dimorphism was small: 2.6% for *H. ligatus* and 4.6% for *H. poeyi*.

Of the 34 putative workers of *H. ligatus*, 29.4% were fecund (i.e., they had some ovarian activity), and in *H. poeyi*, 28.3% of 152 workers had ovarian activity ($\chi^2 = 0.0148$, $df = 1$, $p > 0.9$). Workers with some ovarian activity were,

Fig. 1. Phenological data for *Halictus ligatus* (×) and *H. poeyi* (○) at Rock Hill in 1996. (A) Female abundance throughout the sampling period. (B) Variation in total wear for females. (C) Male abundance. ● and ■ denote data for *H. ligatus* and *H. poeyi*, respectively, in May 1997. The broken lines at the left-hand side join data points from different years and therefore may not represent comparative abundance as accurately as the rest of the data. The line at the top of the figure shows the time periods during which overwintered gynes and workers were active.



on average, almost significantly larger than those without (*H. ligatus*: mean wing length of workers *with* ovarian activity = 5.53 mm, SE = 0.04 mm, $n = 8$; mean wing length of workers *without* ovarian activity = 5.40 mm, SE = 0.07 mm, $n = 18$; $t = -1.38$, $p = 0.09$; *H. poeyi*: mean wing length of workers *with* ovarian activity = 5.80 mm, SE = 0.06 mm, $n = 39$; mean wing length of workers *without* ovarian activity = 5.72 mm, SE = 0.09 mm, $n = 62$; $t = -1.54$, $p = 0.06$). Ovarian activity in workers peaked slightly earlier in *H. ligatus* than in *H. poeyi* (Fig. 3A).

Halictus poeyi workers were twice as likely to be mated (61.2%) than those of *H. ligatus* (32.4%, $\chi^2 = 9.34$, $df = 1$, $p < 0.01$). Mated workers were significantly larger than unmated workers in both species (*H. ligatus*: mean wing length of *mated* workers = 5.62 mm, SE = 0.02 mm, $n = 7$; mean wing length of *unmated* workers = 5.37 mm, SE = 0.03 mm, $n = 16$; $t = -3.14$, $p = 0.002$; *H. poeyi*: mean wing length of *mated* workers = 5.84 mm, SE = 0.06 mm, $n = 60$; mean wing length of *unmated* workers = 5.63 mm, SE = 0.09 mm, $n = 41$; $t = -3.76$, $p = 0.0001$). The proportion of mated *H. poeyi* workers varied around 60% but generally increased from mid-August onwards (Fig. 3B). In contrast, the propor-

tion of mated *H. ligatus* workers decreased as the summer progressed.

There was no significant difference in the frequency of workers with either oocytes (17% in *H. ligatus* and 9% in *H. poeyi*; $\chi^2 = 2.357$, $p > 0.1$) or yellow bodies (32% in *H. poeyi* and 22% in *H. ligatus*; $\chi^2 = 1.65$, $p > 0.1$) in their gut.

Weather data from Winthrop University for autumn 1995, when the gynes collected in spring 1996 were produced, and for summer 1996 are shown in Table 1. August 1995 was warmer and much wetter and September cooler and much drier than usual. In contrast, May–July 1996 was not much different in temperature but much drier than normal, whereas August and September were close to average for both variables (Table 1).

Discussion

Comparison of the two species in sympatry

Two main differences in phenology are apparent (Table 2): *H. poeyi* continues foraging much later than *H. ligatus* and its males become most numerous later in the year. Nonethe-

Fig. 2. Size variation in *H. ligatus* (A) and *H. poeyi* (B). Open bars represent individuals collected after 1 June and solid bars those collected before 1 June.

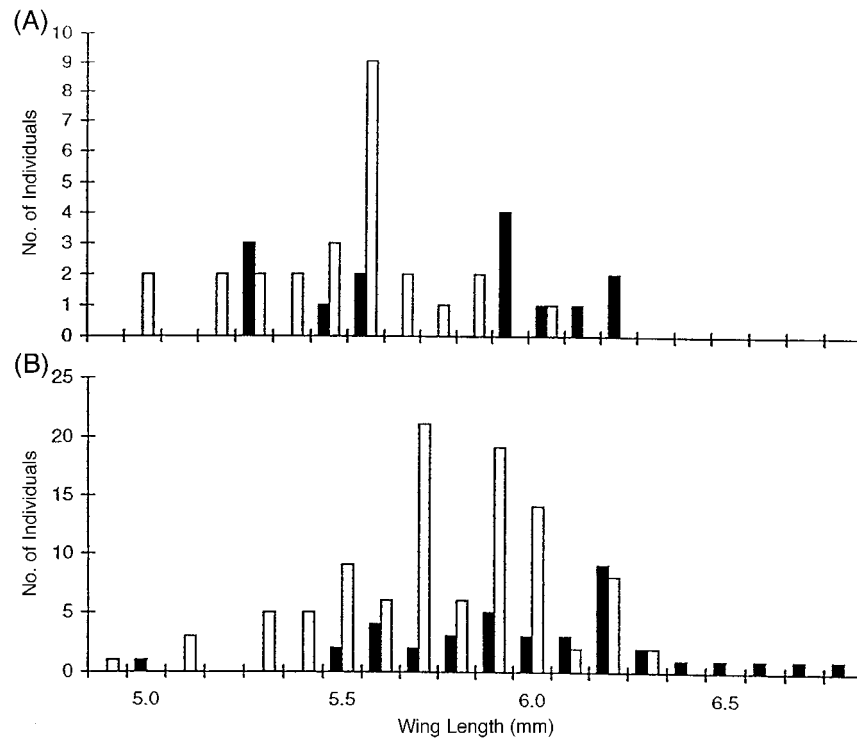
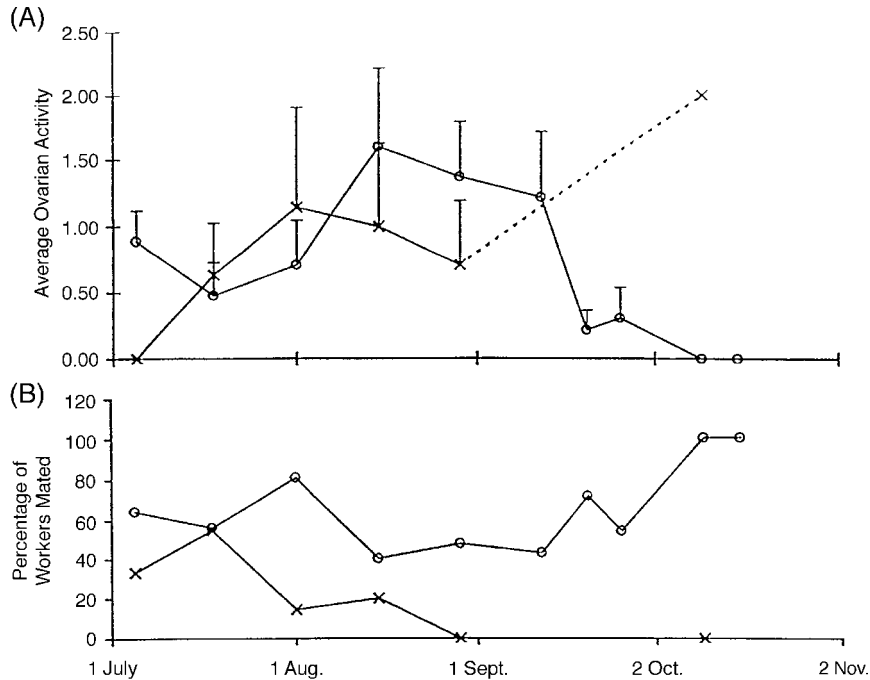


Fig. 3. Variation in reproductive status of workers throughout the period of worker activity. (A) Ovarian development (ISO is the index of summed oocytes (see the text)). (B) Proportion of workers mated. For sample sizes see Fig. 1.



less, males of the two species are active simultaneously from July until October, so hybridization between the species is not precluded by seasonal allochrony. Although males were collected more or less simultaneously, we cannot discount some diel allochronic reproductive isolation, as is known, for example, in *Apis* spp. (e.g., Koeniger et al. 1996). The

longer colony cycle of *H. poeyi* in allopatry remains (albeit less marked) in sympatry.

Halictus ligatus foundresses exhibit size bimodality (Fig. 2), four of them being smaller than the average worker. This pattern has been found in Ontario, where most unusually small foundresses became subordinate females in multiple-

Table 1. Weather data for Rock Hill for times relevant to the data discussed here, with percent deviation from average conditions estimated over 30 years.

	1995		1996				
	Aug.	Sept.	May	June	July	Aug.	Sept.
Temperature (°C)							
Mean	27.0	21.4	21.4	25.0	25.9	25.2	22.1
Percent deviation	+5.1	-4.4	+4.1	+2.9	-1.1	-1.5	-1.3
Rainfall (mm)							
Mean	194.8	33.0	35.0	70.9	52.1	109.7	132.6
Percent deviation	+78.4	-69.8	-63.3	-35.5	-52.3	+0.5	+14.8

Table 2. Summary of biological differences found between the two species in sympatry at Rock Hill.

	Period of foraging activity	Peak male abundance	Percent caste size dimorphism	Percentage of workers	
				Mated	Fecund
<i>H. ligatus</i>	May–Aug.	July–Aug.	2.6	32.4	29.4
<i>H. poeyi</i>	May–Oct.	Oct.–Nov.	4.6	61.2	28.3

foundress associations (Packer 1986b, 1993). The small overwintered females may have been subordinate cofoundresses in the Rock Hill population of *H. ligatus*, as could the one very small *H. poeyi* gyne.

Of the variables related to social level, only the proportion of mated workers differed significantly between the species. More *H. poeyi* workers were mated throughout the period of worker activity despite the fact that its males were less common in our samples. This could result from behavioural differences in males or workers. Male *H. poeyi* may have been more numerous but much more active around the nest site and not so readily sampled. Alternatively, *H. poeyi* workers may have a greater propensity for mating, perhaps indicative of a higher proportion of replacement queens (Packer 1986a) or worker-laid diploid eggs (Richards et al. 1995). In both species, mated workers were significantly larger than unmated ones, presumably because these females are more likely to be gynes or workers that will oviposit, as was suggested in a detailed study of mating in *H. poeyi* (Packer 1986c).

Although interesting differences between the species in sympatry have been noted, it should be remembered that these differences are of the same sort as those found in comparisons of conspecific allopatric populations or years of study for the same population. Such differences are often considered to have a direct environmental cause (Richards and Packer 1995; Eickwort et al. 1996; Wcislo 1997; but see Plateaux-Quénu et al.)² We cannot discount the role of the environment in causing the differences observed between the two species here because, although they were sampled sympatrically, it is possible that they have slightly different nesting sites and experience different microclimates. For example, if one species were to nest in shadier places, it would experience lower temperatures in the nest and, based upon interyear comparisons of *H. ligatus* (Richards and Packer

1996), would have smaller colonies and larger caste differences.

Comparison of allopatric conspecific populations

Halictus poeyi

The most detailed published information available is in Packer and Knerer (1986) for a Florida Keys population, with additional data from elsewhere in Florida (Packer and Knerer 1987) (see Table 3). Note that many of the values provided in Table 3 differ from those originally published because samples are often combined or subsampled here to make the data from different localities as comparable as possible.

All but Knights Key samples were obtained from flowers and are thus more directly comparable with those from Rock Hill, although sampling took place over a shorter time period and sample sizes were smaller. Because data from different localities are not directly comparable, no formal statistical analysis is presented. Nonetheless, it seems clear that the size difference between the castes is markedly reduced in the Rock Hill sample and workers and especially gynes are smaller. It is possible that some large foundresses in multiple-foundress associations were not sampled; if so, our caste dimorphism value would be an underestimate. All populations had a high proportion of mated workers, but the proportion of workers with developed ovaries is very variable, with a pattern perhaps more influenced by sample size and date than location.

Halictus ligatus

All the data presented in Table 4, except those for Rock Hill, are from nest excavations, so detailed comparisons with the Rock Hill data are unwarranted. Nonetheless, caste size dimorphism is lowest in Rock Hill, although not markedly lower than in California and Kansas (but see the caveat

²C. Plateaux-Quénu, L. Plateaux, and L. Packer. Differentiation between solitary and social populations of *Evylaeus albipes* (F.) (Hymenoptera: Halictidae). I. Behaviour under experimentally reversed conditions. Submitted for publication.

Table 3. Comparison of sociobiological variables for various populations of *H. poeyi* data from Packer and Knerer (1986, 1987).

	Period of foraging activity	Percentage of workers		Mean head width (mm)		Percent caste size dimorphism
		Mated	Fecund	Workers	Queen	
Knights Key, Fla. (24°42'N)	All year	50.3	76.0	3.64	3.11	14.6
Zephyrhills, Fla. (28°14'N)	Mar.–Nov.	51.1	17.0	3.41	2.96	13.2
Yankeetown, Fla. (29°01'N)	?–Oct.	36.4	52.0	3.41	2.93	14.1
Apalachicola, Fla. (29°26'N)	?–Oct.	57.8	19.0	3.38	3.10	8.3
Rock Hill, S.C. (34°22'N)	May–Oct.	61.2	28.3	3.04	2.90	4.6

Table 4. Comparison of sociobiological variables for various populations of *Halictus ligatus*.

	Period of foraging activity	Percentage of workers		Size		Caste size differentiation	Source
		Mated	Fecund	Queen	Workers		
Rock Hill (34°22'N)	May–Sept.	32.4	29.4	2.71	2.64	2.72	This paper
California (38°33'N)	Apr.–?	na	na	na	na	4.4	Eickwort 1985
Kansas (39°N)	Apr.–Sept.	7.3	35.8	2.58	2.41	6.6	Michener and Bennett 1977
Indiana (40°30'N)	Apr.–Oct.	na	na	2.42	2.04	15.7	Chandler 1955
New York (42°30'N)	May–Sept.	17.0	35.8	2.91	2.49	14.4	Litte 1997
Toronto, Ont. (43°40'N)	May–Oct.	16.0	25.0	na	na	16.0	Knerer 1980
Victoria, Ont. (43°50'N)	June–Sept.	14–50.0	62.3	2.83	2.51	11.3	Packer 1986a

on sampling bias above). The reduced size dimorphism is due to the large size of workers, not the small size of queens. The percentage of workers mated varies considerably according to the time of year when sampling was done, but neither this nor the percentage of workers with ovarian development is unusual in Rock Hill.

Overall, the data suggest decreasing caste size dimorphism with increasing latitude in *H. poeyi* and increasing size dimorphism with latitude in *H. ligatus*. Much more detailed field study is required to explain this pattern.

Extrapolation from annual variation within a locality

Richards and Packer (1996) compared sociobiologically relevant parameters from a single aggregation of *H. ligatus* in Ontario over 5 years and found significant weather-induced variation. Cool wet weather resulted in smaller colony sizes and greater morphological and physiological differentiation between the castes. In comparison with average conditions, the drier weather in Rock Hill in 1996 suggests somewhat lower caste differentiation than usual in the year of this study, assuming that the weather-induced differences found in *H. ligatus* in Ontario also apply to both species here.

The two species appear more similar to each other than to allopatric conspecific populations. Only the California data for *H. ligatus* seem similar. This is intriguing, as character displacement may be expected in sympatric populations of sibling species (see Grant 1986). However, such divergence generally arises in characters related to the use of resources over which competition occurs. It is not easy to envisage

competition arising over most of the sociobiological parameters that we have measured. Size might be an exception if it were to influence competition over flower resources; however, as the data in Tables 3 and 4 indicate, the two species are more similar in size in sympatry than in allopatry. Overall these data suggest a large role for the environment in determining details of the social organization of halictine bees (Wcislo 1997). Much more detailed analysis will be required to determine the extent to which any sociobiological variation induced by weather factors is mediated by differences in the relative benefits and costs associated with Hamilton's Rule under different environmental conditions.

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