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The Transition between Annual and Continuously Brooded Colony Cycles

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**The Biology of a Subtropical Population of
Halictus ligatus Say (Hymenoptera; Halictidae).
III. The Transition Between Annual and
Continuously Brooded Colony Cycles**

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ABSTRACT: In north temperate regions *Halictus ligatus* has an annual colony cycle as found in almost all other social sweat bees. However, in the extreme south of Florida, this species is continuously brooded and multivoltine (i.e., it has overlapping colony cycles with one complete cycle lasting for a few months) and the matrifilial societies exhibit a markedly reduced reproductive division of labour. Several series of collections were made along the length of Florida to determine where the transition between the annual and continuously brooded colony cycles occurs. An annual colony cycle seems to be retained at least as far south as Tampa; the continuously brooded populations are restricted to the extreme south of Florida.

Halictus ligatus, a widespread and common social halictine, has been the subject of more field research than any other member of this large and diverse taxon. Studies of north temperate populations indicate that *H. ligatus* has an annual colony cycle very similar to that of many other halictines (Chandler, 1955; Kirkton, 1968; Litte, 1977; Michener and Bennett, 1977; Knerer, 1980; Eickwort, 1985; Packer, 1986a). However, in the subtropical climate of the Florida Keys, matrifilial colonies are continuously brooded and multivoltine (i.e., nests may be initiated at any time of year and the entire colony cycle lasts less than 6 months), although newly emerged gynes may enter a facultative semi-diapause during inclement weather in the winter months (Packer and Knerer, 1986). Workers in queenright subtropical colonies show a high degree of ovarian development and most are mated (Packer and Knerer, 1986). This breakdown in reproductive dominance is even more acute in the tropical populations where colonies may have a "communal-like" organization (Michener and Bennett, 1977). Thus, *H. ligatus* has annual colonies in the north but is continuously brooded in the subtropics. Colonies in tropical regions may enter a dry season aestivation (Michener and Bennett, 1977).

The closest relatives of *H. ligatus* are old world species (Michener, 1978; Psenko, 1985) and it is probably a recent invader of the subtropical and tropical regions (Michener and Bennett, 1977). Its phenology in these zones must be derived from that found further north. An investigation into the pattern of sociality shown by this species along a transect from areas with an annual colony cycle to those where it is continuously brooded should be of interest. A full description of the social organization of a population requires observations at nests coupled with nest excavations carried out during the duration of the colony cycle. None-

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theless, collections of bees from flowers at different times of year will give some insight into the pattern of sociality. Therefore, several series of collections were made along the length of the state of Florida.

Populations of *H. ligatus* with an annual colony cycle, like most other annual social Hymenoptera, initiate nests in spring and produce workers during the summer before switching to male and gyne production in late summer and autumn. Thus, collections of bees made towards the end of the colony cycle should contain a larger proportion of males and young gynes than earlier samples. Studies of temperate populations indicate that there is some overlap in size between gynes and workers and that some of the latter are mated and may have ovarian development. Collections made towards the end of the colony cycle should show the following differences in comparison to earlier samples.

- i) an increase in the proportion of newly emerged “gynes” (where “gyne” is defined as those females that are unworn and have no ovarian development).
- ii) morphological caste differentiation should result in the bees classified as “gynes” being larger than the remainder—hereafter referred to as “workers”. This caste size difference varies from 4 to 16% in different populations of this species (Packer and Knerer, 1986; Packer, 1986a).
- iii) an increase in the proportion of female bees that are mated.
- iv) the sex ratio of bees caught on flowers should show an increase in the proportion of males.

Conversely, collections of bees from populations which are continuously brooded and multivoltine should show none of these differences.

It may seem that these last two factors are confounded. However, Greenberg and Buckle (1981) have shown that queens of a related halictine species can reduce the probability that their workers will accept a mate. Additionally, males of *H. ligatus* at Knights Key have been shown to exhibit mate choice (Packer, 1986b). Thus, an increase in the abundance of males does not necessarily mean that the proportion of females that are mated will increase.

Methods

Samples of *H. ligatus* were collected along the length of the state of Florida during the period October to December 1982. Several additional samples are available from some localities from other times of year. Northern Florida experiences a winter of sufficient intensity and duration to ensure bee inactivity for several months; long enough for mated gynes to be the only survivors in spring. A search for nest aggregations was made at intervals of approximately 100 km along a transect from Apalachicola in the north to Knights Key in the south. Collections of bees were made at each site in at least two out of the three months. Samples were collected as close to mid-day as possible and an effort was made to collect all individuals that were seen. Sample sizes are shown in Table 1.

In addition to Knights Key (24.24°N, 81.14°W); samples were collected at Homestead (25.19°N, 80.19°W), Fort Myers (26.23°N, 81.30°W), Sarasota (27.12°N, 82.20°W), Zephyrhills (28.08°N, 82.29°W), Yankeetown (28.06°N, 82.46°W) and Apalachicola (29.26°N, 85.01°W). The relative position of these collecting sites is shown in Fig. 1.

Bees were preserved in Kahle's fixative. Females were dissected to assess their

Table 1. Data from phenology studies of *H. ligatus* along a north-south transect in western Florida. Note that the data to the right of the "Caste" column refers to the caste and not the month. na, data not available. The N in column three refers to the sample size for females only.

Locality	Month	N	% "gynes"	% mated	% males	"Caste"	N	Head width	SD
Knights Key	Oct.	106	5.7	82.1	na	"Gynes" "Workers"	32	3.02	0.34
	Nov.	52	9.6	69.2	na		216	3.04	0.22
	Dec.	90	23.3 ^a	70.0	na				
Homestead	Oct.	59	1.7	50.3	19.7	"Gynes"	5	2.79	0.21
	Nov.	48	8.3	41.7	25.7	"Workers"	101	2.99 ^a	0.22
Fort Myers	Feb.	34	76.5	100.0	0.0	All bees	34	3.29	0.29
	Nov.	104	22.1	59.6	17.7	"Gynes"	36	3.29	0.30
	Dec.	24	54.2 ^c	87.5 ^a	55.5 ^d	"Workers"	92	3.06 ^d	0.21
Sarasota	Nov.	97	26.8	91.7	23.6	"Gynes"	31	3.14	0.17
	Dec.	22	22.7	95.4	33.3	"Workers"	88	3.07	0.28
Zephyrhills	Mar.	8	100.0	100.0	0.0	Gynes	8	3.41	0.16
	Jun.	48	35.4	51.1	0.0	Workers	48	2.96 ^f	0.15
	Oct.	70	12.9	67.1	1.4	"Gynes" "Workers"	29	3.16	0.30
	Nov.	101	14.8	75.2	15.8				
	Dec.	14	35.7 ^a	85.7	46.2 ^d				
Yankeetown	Oct.	45	2.2	36.4	0.0	"Gynes"	5	3.41	0.25
	Nov.	5	80.0 ^f	100.0 ^c	50.0 ^b	"Workers"	45	2.93 ^e	0.15
Apalachicola	Oct.	80	16.2	63.7	13.1	"Gynes"	25	3.38	0.34
	Nov.	28	42.9 ^c	100.0	54.8 ^c	"Workers"	83	3.10 ^e	0.28

Significance levels: ^a = 0.05, ^b = 0.01, ^c = 0.005, ^d = 0.001, ^e = 0.0001, ^f = 0.00001.

reproductive condition, wing and mandibular wear were recorded to give an estimate of age and head widths measured. The number of males was recorded to give an estimate of the sex ratio.

All unworn bees with no ovarian development were designated as "gynes" and the remainder as "workers". This procedure may result in the misclassification of some late emerging workers in annual colonies. Similarly, "gynes" from continuously brooded populations could also be young workers. However, an increase in frequency of such individuals is only expected towards the end of the season in populations with an annual colony cycle.

Significant changes in the frequency of "gynes", mated females and the sex ratio were detected by means of the chi-squared test. Fisher's exact test was performed when sample sizes were small. Comparisons of size were made using a *t*-test on female head widths. More than two samples are available for the Zephyrhills, Fort Myers and Knights Key localities. Head width data for these sites were subjected to analysis of variance. Chi-squared tests were performed between subsets of the data for the other variables.

Results

Data for Knights Key (Table 1), a locality where *H. ligatus* is known to be continuously brooded and multivoltine (Packer and Knerer, 1986), indicate that there is a significant increase in the proportion of females classified as "gynes" in the December sample in comparison to those of October and November. How-

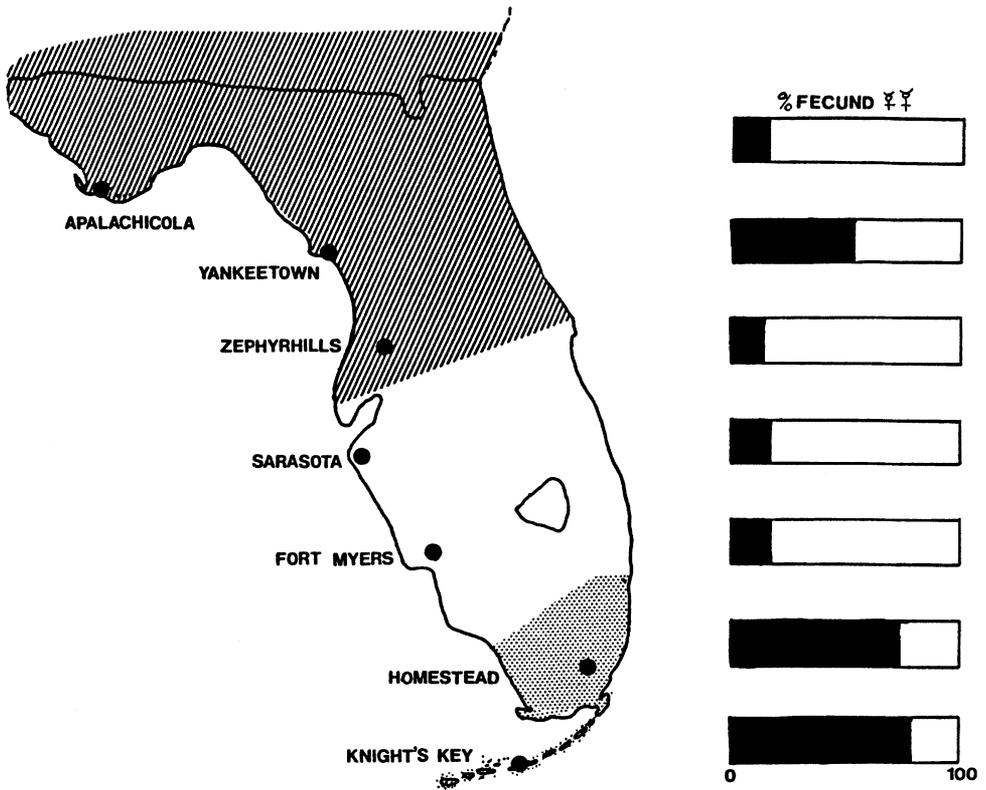


Fig. 1. Map of Florida showing the location of the collecting sites described in the text. The cross-hatched area in the north shows the approximate delineation of *H. ligatus* populations with an annual colony cycle, the dotted area in the south indicates where the species is continuously brooded and multivoltine. The colony cycle in the intermediate, unshaded portion of the map remains unknown. The bar charts to the right show the percentage of worn “worker” bees that exhibited ovarian development for each of the localities shown on the map.

ever, the mean size of these “gynes” is almost exactly the same as that of the “workers”. Therefore, bees classified as “gynes” cannot be true gynes which at this locality average 16% larger than their workers (Packer and Knerer, 1986). None of the other variables show any significant variation confirming that we do not have an annual colony cycle here.

At Homestead, the only significant result is that bees classified as “gynes” are smaller than the “workers”. This could not be the case if the categorization reflects true caste differences and the Homestead population is probably continuously brooded and multivoltine as at Knights Key.

A comparison of the November and December samples from Fort Myers indicates that there is an annual colony cycle here: all four variables show significant differences in the direction expected if this were the case. Thus, there is an increase in the percentage of mated females, an increase in the proportion of males, an increase in the frequency of “gynes” and the bees in this latter category are larger than the “workers”. However, the February 1984 sample indicates that the situation may be more complex. This sample shows a great range in wear and size

such that it is extremely unlikely that all of the bees are young gynes. However, the mean head width of the February sample is exactly the same as that of bees caught in November and December classified as "gynes". Additionally, bees at this locality are active well into December and resume activity at least as early as mid February. It is possible that not all young gynes in this population enter a winter diapause: some may initiate a new nest soon after eclosion and mating. The older bees in this sample were no different in size from the younger ones (bees with an index of wear of zero, mean head width = 3.32 mm, SD = 0.25, $n = 21$; bees with some wear, head width = 3.24 mm, SD = 0.35, $n = 13$; $t = 0.75$, $P > 0.1$). Three of the well worn females had no ovarian development. These individuals are either true workers or subordinates in pleometrotic spring associations. We cannot conclude that this population has a simple, annual colony cycle.

At Sarasota, none of the variables show any significant differences between samples. This would be indicative of a continuously brooded multivoltine colony cycle if it were not for the findings from the more southern Fort Myers population discussed above. More data are required from this locality.

All of the variables except percent mated indicate that the Zephyrhills population has an annual colony cycle. The percentage of females mated does increase from October to December but not significantly. Further evidence that we have an annual colony cycle here comes from samples collected in March and June. All eight individuals caught in March 1982 were mated, none had an index of wear greater than unity and all show little or no ovarian development. Furthermore, the mean size of females in this sample is the largest obtained for this locality and is not significantly different from those bees in the December sample that were classified as "gynes" ($t = 0.61$, $P > 0.05$). Additionally, there were no male bees found at this time. When this locality was visited in February 1984, no bees at all were found and no flowers suitable for *H. ligatus* could be located. It seems highly likely, therefore, that the March sample consists entirely of young gynes in the early stages of nest initiation.

The bees captured in Zephyrhills in June are smaller than the "workers" in the October to December samples but not significantly so ($t = 1.5$, $P > 0.05$) but they are significantly smaller than the "gynes" ($t = 4.1$, $P < 0.001$). The size distribution of the June females is distinctly unimodal with a small range of variation in comparison to the samples collected from October to December. The percentage of females mated is smaller in this sample than in any of the others from this locality and no males were caught. The frequency of "gynes" was quite high but since the bees so classified were small they certainly represent recently emerged workers. In conclusion, we do seem to have an annual colony cycle at this locality.

At both Apalachicola and Yankeetown all four variables show significant differences between October and November samples indicating that *H. ligatus* has an annual colony cycle in the north of Florida.

Discussion

In subtropical and tropical climes, *H. ligatus* has a continuously brooded and multivoltine colony cycle, and, although there may be a break in activity in areas with a pronounced dry season, there is no distinct synchronization of nest initi-

ation. This is in contrast to the north temperate populations in which the cold winter ensures several months of complete inactivity during which only young gynes survive, followed by a burst of nest initiation in spring.

Studies of collections of *H. ligatus* made along the length of Florida indicate that the annual colony cycle occurs at least as far south as Tampa and that continuously brooded populations are restricted to the extreme south of the Florida mainland and the Florida Keys (Fig. 1), where the climate is subtropical. At present it is not possible to describe the colony cycle between these two areas. Collections made at Fort Myers indicate that an annual colony cycle with some gynes initiating a new nest at the end of the season whereas others wait for a month or two may be a possibility. Further work is needed in southern Florida to elucidate the phenology of *H. ligatus* in this area.

The only nest excavation data available from the mainland of southern Florida are those of Drs. G. C. and K. R. Eickwort who studied two nests at the Archbold research station (reported in Michener and Bennett, 1977) in April. This locality is at approximately the same latitude as the Fort Myers site. Both nests seem to represent matrifilial colonies with a dominant queen and a first worker brood with a fair degree of worker ovarian development. These data suggest that new nests are initiated at the end of the short winter in southern Florida, as indicated from the collections made at Fort Myers. Whether the foundresses survive for only a fraction of the entire colony cycle, as seems to occur in California (Eickwort, 1985), remains to be seen. A detailed study of a south temperate population of this species is badly needed.

The Florida Keys population of *H. ligatus* exhibits remarkably poor reproductive division of labor within the matrifilial colonies despite the high morphological caste differentiation—16% based upon head width (Packer and Knerer, 1986). Queen survival until near the end of the colony cycle is no poorer in this population than in others that have been studied (Litte, 1977; Packer, 1986a). As discussed by Packer and Knerer (1986) the degree of sociality exhibited by this species seems to decline from the temperate regions, through the subtropics and down to the tropics where colonies are essentially communal (Michener and Bennett, 1977). Data on worker ovarian development from mainland Florida indicate that poor powers of queen dominance are restricted to the continuously brooded multi-voltine populations in the subtropical zone (Fig. 1). The possible reasons for this will be discussed elsewhere.

Two other halictine species are known to exhibit large differences in social organization over comparatively short distances. Sakagami and Munakata (1972) found that *Lasioglossum (Evyllaesus) calceatum* was social in lowland Japan but solitary in the mountains where the duration of conditions suitable for foraging is brief. Eickwort and Eickwort (1971) compared their findings on *Lasioglossum (Dialictus) umbripenne* at Turrialba, Costa Rica with those of Wille and Orozco (1970) at Damitas in the same country. The two study sites are only 65 km apart but nesting activity was continuous in the damper climate of Turrialba whereas the bees were active only during the dry season at Damitas. Caste differentiation was more highly developed at Damitas and Eickwort and Eickwort (1971) hypothesized that this was an adaptation to the seasonal environment. The findings of the present study indicate that this hypothesis may also hold for geographic variation in sociality in Floridian *H. ligatus*.

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