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Source: *Journal of the New York Entomological Society*, Vol. 94, No. 4 (Oct., 1986), pp. 458-466
Published by: New York Entomological Society
Stable URL: http://www.jstor.org/stable/25009564
Accessed: 14-02-2016 04:10 UTC

J. New York Entomol. Soc. 94(4):458–466, 1986

THE BIOLOGY OF A SUBTROPICAL POPULATION OF *HALICTUS LIGATUS* IV: A CUCKOO-LIKE CASTE

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Abstract.—Intraspecific cleptoparasitism is described in a subtropical population of the social sweat bee *Halictus ligatus.* Cuckoo-like individuals are, on average, larger than workers but smaller than queens. Behavioral modifications resulting in the cleptoparasitic behavior are quite minor: forced entry and sneaky oviposition are activities possessed by non-parasitic members of this population. Only the trap-lining and host nest choice behaviors are new. Intraspecific cleptoparasitism has not been recorded from any of the temperate populations of this species that have been studied. It is argued that the continuously brooded, multivoltine phenology of this population has been a necessary prerequisite for the origin of this pattern of cleptoparasitism.

A large number of bees exhibit obligatory cleptoparasitic behavior, that is they do not provision their own nests but lay eggs in those built and provisioned by other species (Bohart, 1970). The success of this strategy is indicated by the fact that whole genera and even tribes of bees are obligate cuckoos (Michener, 1944; Bohart, 1970). Most cleptoparasites lay their eggs in the nests of solitary hosts. However, cleptoparasitism of social hosts is a fairly common condition, exhibited particularly frequently by parasitic species of the subfamily Halictinae whose hosts are usually other species of this taxon (Michener, 1977). Over half of the records assembled by Michener involve hosts that are known to exhibit eusocial behavior. However, most halictines that have been studied in any detail are social species, therefore the sample is biased in favor of cleptoparasites of social hosts. True social parasitism, in which the intruding parasite becomes an integral part of the host society, is a rarer phenomenon in bees: known in the cuckoo bumble bees of the genus *Psithyrus,* various allodapines (Wilson, 1971) and in *Microsphecodes* (Eickwort and Eickwort, 1972) and some *Sphecodes* (Knerer, 1980).

Although there are several reports of intraspecific nest usurpation within the Halictinae (Knerer, 1973) and elsewhere amongst the social Hymenoptera (Archer, 1980; Fisher, 1985; Richards, 1978; Turilazzi, 1985) intraspecific cleptoparasitism has not been recorded for any social species, but is known in solitary forms (Eickwort, 1975). Emery's rule: "that parasitic species tend to resemble their host species more than any other free-living form" (Wilson, 1971) seems to hold true for most cleptoparasitic halictine taxa. Apparent exceptions, such as the large and cosmopolitan genus *Sphecodes,* result from a long evolutionary history of cleptoparasitism: the ancestral *Sphecodes* almost certainly parasitized a host that was a closely related halictine species. Thus, intraspecific cleptoparasitic behavior should provide important clues as to the origin and further elaboration of this mode of life.

Detailed field investigations were carried out on the bionomics and social organization of *H. ligatus* at Knights Key, Monroe County, Florida between February

1981 and February 1984 (see Packer and Knerer, 1986a for an account of the general biology of this population). This paper is an account of cuckoo-like behavior in a small proportion of the individuals in this subtropical population.

METHODS

On the 22nd of December 1981 a large individual of *H. ligatus* was observed to circle around the entrance of a conspecific nest. Several times on that day this bee flew to the nest from the north east, flew around the entrance several times and then circled around another nest two meters away. This trap-lining behavior is characteristic of cleptoparasitic species and was observed as closely as possible thereafter.

Trap-lining behavior was distinct from other types of searching behavior exhibited by young gynes looking for a suitable nest site or lost foragers attempting to find their nest. Searching young gynes carefully inspected certain areas, first whilst on the wing and then by walking. They then moved on a short distance (rarely more than 30 cm unless suitable substrate was absent) and repeated the process. Eleven such searching young foundresses were captured, although more were seen (Packer and Knerer, 1986a). Lost foragers would repeatedly search the same area in flight, alight frequently but fly off every now and then only to return after re-orientation. This type of searching behavior was observed on many occasions in the course of this study but always after a bee had been disoriented by capture or after its nest entrance had been obstructed.

The behavior of trap-lining individuals was very different from either of these searching activities. Trap-liners flew low over the ground, from nest entrance to nest entrance, without any hesitation. The paths that they took appeared stereotyped, as if they "knew" where the nest entrances were, and were repeated several times daily, and on at least two occasions, over several successive days. Additionally, most of the observations of trap-lining took place before any nest excavations had been performed and in a comparatively undisturbed part of the study site: these were not lost bees.

During the course of the rest of the study, some 24 trap-lining individuals were caught and preserved in Kahle's solution. Their head widths, wing and mandibular wear and reproductive condition were noted as described by Packer and Knerer (1986a). Ovarian status was assessed following Litte (1977) and Michener and Bennett (1977). Thus, females were divided into categories with five or six (A), three or four (B), one or two (C) or no (D) developed ovarioles. Furthermore, each ovariole was assessed as to whether its contents were developing or being resorbed, these conditions being distinguished by shape and coloration (Packer and Knerer, 1986a). These data were used to compare trap-lining bees with queens and workers from excavated nests.

RESULTS

Trap-lining females were significantly smaller in size than queens (*t* test with Sidak's multiplicative inequality [Rohlf and Sokal, 1981], $t = 2.45$, $P < 0.05$), and significantly larger than workers (same test as above, $t = 7.63$, $P < 0.01$) excavated from nests (mean head width of queens = 3.63 mm, SD = 0.19, N = 50; trap-lining bees 3.49 mm, SD = 0.25, N = 24; workers = 3.09 mm, SD = 0.20, N = 322). The size variation of these three categories of female can be seen in Figure 1.

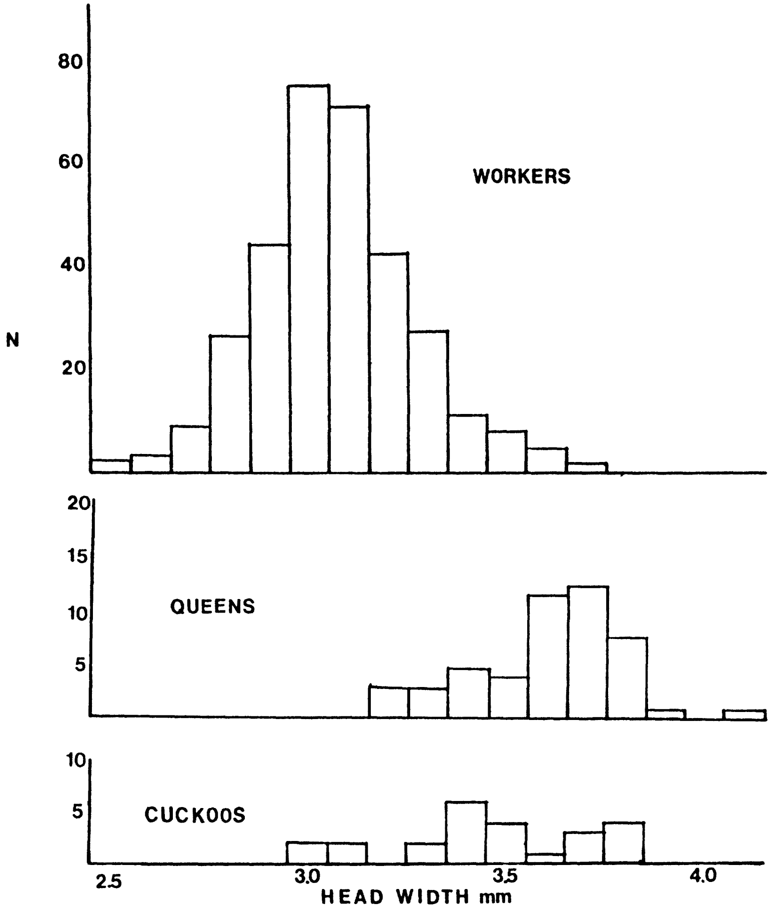

Fig. 1. Size variation in queens, workers and cleptoparasitic females of *H. ligatus* at Knights Key, Florida.

Only 2 of the 24 trap-lining individuals had any mandibular wear, significantly fewer than queens or workers (Fisher's exact test, $P = 0.0009$ and $P = 0.015$ respectively). In contrast, 13 of the 24 trap-liners had some wing wear, varying from one or two nicks in the wing margin to having the complete margin frayed away. There was no significant difference in the degree of wing wear between these individuals and queens and workers from nests.

Like queens, all of the trap-lining females were mated (in this population 58% of the workers were mated). Trap-lining bees differed in the number of developed ovarioles when compared to workers but not when compared to queens (Table 1). No queens or trap-lining bees had fewer than two developed ovarioles and the relative frequency of occurrence of ovarian categories A, B and C did not differ significantly between the two groups ($\chi^2 = 3.09$, $P > 0.1$). Worker individuals showed a much higher proportion of ovarian categories C and D than trap-lining bees ($\chi^2 = 20.05$,

Table 1. Variation in the frequency of ovarian categories in queens, workers and cuckoos of *H. ligatus* at Knights Key. Figures in brackets are percentages. With ovarian categories A and B, and C and D combined, differences between queens and cuckoos are not significant (Fisher's exact test, $P = 0.34$), those between workers and cuckoos are highly significant ($\chi^2 = 18.5$, $P < 0.0001$).

	Ovarian category			
	A	B	C	D
Workers	22 (8.3)	78 (29.4)	85 (32.1)	80 (30.2)
Queens	25 (62.5)	11 (27.5)	4 (10.0)	0 (0.0)
Cuckoos	8 (33.3)	12 (50.0)	4 (16.7)	0 (0.0)

$P < 0.0001$). Queens and workers did not differ significantly in the relative proportions of ovarioles with developing or resorbing contents (with 42.4 and 39.5% of enlarged ovarioles containing developing contents respectively). However, trap-lining bees had mostly developing oocytes (67.7% of enlarged ovarioles), differing significantly from workers and queens combined ($\chi^2 = 14.81$, $P < 0.0001$).

The following sequence of events was observed around the entrance of one nest which was situated in an unusually open position: in an area of very short and sparse grass cover. This nest was comparatively populous: nine foragers had been marked and the duration of their pollen foraging trips was being recorded when these observations were made. Another two, small, unmarked bees were also foraging from this nest. On the 23rd of December 1981 the same large bee that was first observed trap-lining on the 22nd regularly visited the same nest between 1115 and 1320 hrs. It was first observed at 1115, and then at 1149, 1225 and lastly at 1310 hrs. During each visit, it entered the nest entrance briefly before leaving. On the 29th of December a large bee (quite probably the same individual, judging by relative size and details of flight behavior) entered the nest, flying from a height of 30 cm straight down into the entrance at 1232 hrs. Only one forager left the nest after this and the nest was plugged at 1329 hrs (it is not known which bee was responsible for the nest closure). On two other occasions the nest was observed to be still open at 1500 and 1530 hrs. At 0900 hrs the following morning a large bee was gradually forced out of the nest; it was captured and preserved. Upon dissection this individual appeared to have oviposited recently: one ovariole remained oocyte-shaped but was empty. It seems likely that it was the intruder observed the day before.

On the 5th of January at 1210 pm the same type of rapid entrance was again exhibited by a trap-lining individual. Three bees that had been observed foraging earlier in the day were evicted and the nest entrance was plugged soon afterwards. An additional three returning pollen-laden foragers joined the evicted bees in trying to locate the nest entrance, succeeding approximately 15 minutes later. At this point I attempted to excavate the nest but unfortunately the burrow went down a narrow fissure in the coralline substrate and complete excavation was impossible. Other interactions between trap-lining bees and individuals at nests were restricted to brief encounters at nest entrances before the former were captured.

Nests of *H. ligatus* at this locality are frequently guarded although no individuals seemed to be specialized in this task. Most guarding bees stayed at the nest entrance for only short periods of time, often returning deeper into the nest or leaving to forage. Individuals spend longer periods of time guarding as a result of disturbances at the nest entrance—caused by ants, cuckoo bees or returning young gnyes; such individuals would rarely be observed guarding with such intensity for more than a few hours. Guarding seems to be facultative in this population.

DISCUSSION

Trap-lining *H. ligatus* females at Knights Key have a relatively high degree of ovarian development with very little ovarian resorption compared to queens and workers in nests. They exhibit hardly any mandibular wear, a wide range of wing wear and all of them are mated. Observations at one particular nest entrance indicate that these bees forcibly enter populous nests. It seems probable that these individuals represent a cleptoparasitic subpopulation of this species. They are clearly not searching young foundresses, as indicated by the difference in searching behavior and the high degree of ovarian development and, in many individuals, large amount of wing wear in the trap-lining bees. It is noteworthy that the trap-lining bees had as much ovarian development as queens in nests with active foragers, more than gynes that were provisioning their first brood. Trap-lining bees were not foraging workers as they did not carry pollen loads, were in general much larger and seemed to have a clear route between nests that they would follow over several days. Neither were they lost bees, the behavior patterns of which are very different.

Intraspecific nest usurpation is a well known phenomenon in social Hymenoptera (Archer, 1980; Fisher, 1985; Plowright and Laverty, 1984; Turilazzi, 1985) and has been recorded from social halictines (Knerer, 1973). The behavior reported here for *H. ligatus* is thought to represent cleptoparasitism and not nest usurpation for several reasons. Firstly, halictine females do not undergo ovarian development until they have a nest suitable for provisioning. This is shown by the results of dissections of searching young foundresses from the same locality (Packer and Knerer, 1986a). It is unlikely that a usurping individual of *H. ligatus* will develop oocytes until after a nest is usurped. All of the trap-lining females that were dissected had at least two ovarioles with well developed contents. Furthermore, usurpers may be expected to oust an original owner before reaching a comparatively old age. The fact that several of the trap-lining bees had very worn wings indicates that if they were usurpers, they must be comparatively unsuccessful ones. In addition, the only forced nest entrances observed took place in populous nests, this would not be the strategy that one might expect a usurper to adopt. For these reasons it is thought that the observations recorded here represent cleptoparasitic behavior. Nonetheless, the possibility that usurpation occurs at this locality cannot be disproven; however, it was not observed.

It has been shown that the amount of mandibular wear correlates well with the amount of excavation performed by individual females of this species (Packer and Knerer, 1986b). The low degree of mandibular wear in cuckoo-like individuals of *H. ligatus* at Knights Key indicates that they perform little or no excavation. The large proportion of searching cuckoos with a high degree of wing wear indicates that they probably do not stay in one nest for any great length of time, unlike *Psithyrus* species (Fisher, 1984) or some species of *Sphecodes* (Knerer, 1980). Rather, it seems more likely that they oviposit in several nests over a protracted period of time, as appears to be the case with *Microsphecodes kathleenae* (Eickwort and Eickwort, 1972).

Trap-lining *H. ligatus* females are comparatively large and therefore, the egg that produced them must have been laid upon a large pollen mass. Large provision masses are characteristic of the queen production phase of colony development. In this population, gyne production occurs when the nest population is near its maximum (Packer and Knerer, 1986a). Therefore, if the tendency towards cleptoparasitism is heritable, such individuals must attempt to enter the more populous nests. Alternatively, if this behavior is facultative, forced entry into the more easily invaded smaller nests may be expected. In such instances, the cleptoparasite could lay male-producing haploid eggs on the smaller male or later worker-producing pollen balls. In addition, the oviposition of diploid eggs on smaller provision masses may not be particularly disadvantageous because of the high degree of worker oviposition at this locality. In either case, trap-lining is the mechanism allowing repeated assessment of potential host colonies. Large colonies were the targets of both of the invasion attempts that were observed. Although obtaining entry into populous colonies may be more difficult, the complexity of the nest burrows and general social chaos that may characterize these nests probably makes it more likely that oviposition by a cuckoo will pass undetected than in a younger, less populous nest.

Of particular interest is the low degree of ovarian resorption in the cuckoo individuals. Two reasons may be suggested for this. Firstly, it may be expected that cleptoparasitic individuals are selected to be able to retain developed oocytes for a comparatively long time before they begin resorption. This would allow them more time to find a suitable nest to parasitize. Secondly, the high degree of ovarian resorption in queens and workers in nests may result from mutual inhibition (and there is clear evidence that this is the case; Packer, in prep.). Clearly, solitary cleptoparasites do not suffer such inhibitory influences.

H. ligatus has been the subject of more hours of field research than any other New World halictine species (for summaries of this information see Michener and Bennett, 1977, and Packer, in prep.). Most studies have been of temperate populations and not one author has mentioned trap-lining or possible cleptoparasitism within the species. Detailed field work by the author in Ontario during 1983 and 1984 would certainly have showed up the presence of this behavior unless it were extremely rare. Observations involving hundreds of marked bees were carried out in these two years and no behaviors consistent with cleptoparasitism were ever observed. There is reason to believe that the form of intraspecific cleptoparasitism described here may be restricted to subtropical and tropical climes. This is because only where the colonies are continuously brooded and multivoltine is it probable that newly emerged cuckoo individuals will be able to find nests that are at the reproductive phase of colony development. Cleptoparasites in temperate populations would require different behaviors. If they were of the gyne generation they would have to remain inactive until the emergence of workers in other nests, otherwise their ovipositions would result in workers with reduced reproductive success. Cleptoparasites of the worker generation would have great difficulty in entering active summer nests because of their comparatively small size.

"Lost" bees are frequently mentioned in the sweat bee literature. It is possible that such individuals are not lost, but represent a cleptoparasitic subpopulation. Collections of such individuals should be made in order to assess their levels of ovarian development. If they are more fecund than other individuals flying at the time this would be evidence that they are indeed cleptoparasites. Observations of marked individuals would verify such claims; such detailed investigations are badly needed.

The cleptoparasitic individuals of *H. ligatus* parasitize the nests of conspecifics. They seem to possess no special adaptations to parasitic behavior other than the ability to detect and trap-line host nests and recognize nests that should be preferentially parasitized. Secretive oviposition and techniques for assuring entry into defended nests are almost certainly abilities that are possessed by nonparasitic individuals in this population: egg-laying workers and returning young gynes respectively (Packer and Knerer, 1986a). Returning young gynes often have to fight their way past bees at entrances to their natal nest. The ability to forcibly re-enter natal nests could have served as a preadaptation to cleptoparasitic behavior.

Two alternative strategies will not co-exist in a population unless they are, on average, equally successful (Brockmann et al., 1979). The advantage to pursuing a cleptoparasitic strategy at this locality is easy to see. Knights Key is a coral island and *H. ligatus* foundresses have to locate earth filled fissures in the bedrock that are hidden beneath the shallow soil surface. Many unsuccessful nest initiation attempts probably result causing these females to be at risk from ant predation for a prolonged time. Although not investigated in any detail, it seems certain that mortality during the early stages of nest initiation are much higher in this population than in that studied in Ontario (Packer, in prep.). Under these circumstances, cleptoparasitism may be particularly favored.

Because most cleptoparasitic species are closely related to their hosts, it has been suggested that sympatric speciation must have been involved in their origin. A hypothesis that does not invoke sympatric speciation has been suggested by Wilson (1971). If speciation occurs as a result of geographic isolation and the barrier between the newly diverged populations is removed it is possible that one species could evolve to be parasitic upon its recently diverged sibling. It should be noted that parasitic behaviors could have arisen in the ancestral population or in either or both of the daughter populations before becoming fixed in one of them when they became sympatric once more. In this regard it is worth noting that many bees live in small, localized aggregations that would facilitate such a mechanism. Additionally, this study was carried out on one of a series of small islands—the Florida Keys. It is interesting to speculate that the observations made here represent the first stages in the incipient differentiation of a cleptoparasitic species.

What effect this parasitic strategy has upon the social organization of *H. ligatus* at this site will depend upon the nature of the basis of cleptoparasitic behavior. If this is a genetic strategy then it is likely that a proportion of the female offspring of cuckoo mothers will also be parasites (the exact proportion, clearly, depending upon the mode of inheritance). The remaining female offspring of cuckoo mothers, those not manifesting cuckoo behavior themselves, should presumably start their own nests or become laying individuals in the host colony. In the latter instance they would decrease the mean coefficient of relatedness among the females in the nest. The powers of dominance exhibited by *H. ligatus* foundresses at Knights Key are reduced in comparison to more northern populations. It will be argued elsewhere that this may be the result of a reduced degree of relatedness among nestmate females, clearly the presence of cuckoo offspring may play a part in this. It is too early for any precise statements on the exact nature of cleptoparasitism or the effect of cuckoos on sociality to be made: more field observations on the frequency of cleptoparasitism and the fate of cuckoo-laid eggs are required.

Eickwort and Eickwort (1972) have described three types of host nest entry in *Sphecodes.* 1) Sneak attack, in which the cleptoparasite enters the nest while the rightful occupant is absent; this is generally restricted to attacks on solitary host species or social species during the spring (often monogynous) phase. 2) Colony attack, in which the intruder has to force its way into the nest, fighting and killing the occupants as it does so; this has been described for *Sphecodes monilicornis, S. minor* and *S. gibbus* attacking *Lasioglossum* (*Evylaeus*) *malachurum, L.* (*E.*) *cinctipes* and an unnamed species of *Halictus* respectively. 3) Host impersonation, in which the parasite gains entry to the nest as if it were a member of the host colony and elicits few, or no aggressive responses from the hosts that it encounters. This entry technique was described for *Microsphecodes kathleenae* entering the nests of its eusocial host *Lasioglossum* (*Dialictus*) *umbripenne* (Eickwort and Eickwort, 1972).

S. pimpinellae has been recorded as eliciting unusual escape responses in its host *Augochlorella striata* (Ordway, 1964). This should perhaps be regarded as a fourth type of entry type—a host repellant strategy.

The cuckoo-like behavior exhibited by some individuals of *H. ligatus* at Knights Key would seem to be a more primitive and generalized strategy than any of these. They do not sneak into empty nests or engage in fatal battles in the host colony nests. Rather, they seem to enter nests, cause confusion and probably sneak in an oviposition or two during the ensuing melée, this being facilitated by the comparatively anarchic social organization of the host at this locality.

This paper describes the first recorded example of cleptoparasitism between conspecifics of a social insect. It indicates that, in this instance at least, the amount of behavioral modification required for this strategy to be successful may be quite small.

ACKNOWLEDGMENTS

The author would like to thank Dr. Richard Fisher and two anonymous referees for commenting upon an earlier version of the manuscript and thereby greatly improving the final version. Financial support for field work was obtained from an NERC NATO scholarship and an NSERC operating grant awarded to G. Knerer. The field assistance of Michelle Smith is very gratefully acknowledged. The paper was written while the author was supported by an Ontario Graduate Scholarship and publication charges were borne by a NSERC grant to Professor G. Knerer.

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Received October 2, 1985; accepted January 3, 1986.

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