# Reproductive Biology of Two *Coelioxys* Cleptoparasites in Relation to Their *Megachile* Hosts (Hymenoptera: Megachilidae)

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**ABSTRACT**   We report the results of an 8-yr trap nesting study on the reproductive behavior of two cleptoparasite bees, *Coelioxys funeraria* Smith and *Coelioxys moesta* Cresson. This study provided a unique opportunity to examine parasite-host adaptation within a species, in which two different size classes of *C. funeraria* consistently laid eggs in the nests of the two different sized *Megachile* hosts, *M. relativa* Cresson and *M. inermis* Provancher. Additionally, we compared the behavior of *C. funeraria* to another *Coelioxys*, *C. moesta*, which also parasitized the nests of *M. relativa.* One striking pattern we found was the tight concordance of emergence times between hosts and parasites. The emergence patterns of individual *C. funeraria* parasitizing *M. relativa* nests closely matched that of the host, as well as that of *C. moesta*, which parasitizes the same host. These emergence patterns were significantly different from those of *C. funeraria* on *M. inermis*. We also found that *Coelioxys* and *Megachile* apportioned male and female offspring in the same parts of the linear nests and at similar times of the season. Female offspring tended to be placed in the innermost cells early in the season and males in outer cells later in the season. Because emergence patterns can severely affect offspring survival in these linear nesting situations, we suggest that the emergence times of males and females have determined the patterns of sex placement in both host and parasites.

**KEY WORDS**   Apoidea, behavior, parasitism, cleptoparasite, sex ratio

STUDIES OF PARASITOID insects have generally revealed that parasitoid behavior and physiology closely tracks the biology of their hosts (Rosenheim 1990, Brodeur et al. 1996, Hedlund et al. 1996, Brodeur et al. 1998, Dippel and Hilker 1998, Henneman 1998, Yongjun et al. 1998). Parasitoids are defined as insects that lay their eggs on other insects and develop on or inside the bodies of these insects, killing the host insect in the process. Parasitoids are so dependent on their hosts, like other specialized parasites, they should possess adaptations allowing them to take advantage of these hosts (Price 1980, Thompson 1994). Studies of parasitoids have discovered that these insects are adept at tracking and finding their hosts, and the more specialized the parasitoid, the more their behavior tends to match that of the particular host (Brodeur et al. 1996, Hedlund et al. 1996, Brodeur et al. 1998, Geervliet et al. 1998).

One unique group of parasitoids, the cleptoparasitic bees, has received very little behavioral or physiological study (Danforth and Visscher 1993). Rather than building nests and gathering provisions, these cleptoparasites oviposit in the nests of other, often closely related, bee species (Michener 2000). As they develop, cleptoparasite offspring consume the pollen and nectar stores gathered by the host species, and in

the process they destroy the host egg or larva (Graenicher 1905, Graenicher 1927, Bohart 1970). Surveys of bee species diversity have estimated that 15–20% of all bee species are cleptoparasites (Wcislo and Cane 1996). Although cleptoparasitic bees are abundant and have a broad, mostly temperate, distribution (Bohart 1970), relatively little is known about their nesting behavior because their population sizes rarely become very large (Cane 1983, Rosenheim 1987, Danforth and Visscher 1993). Thus, the opportunity to study cleptoparasitic bees in numbers sufficient to allow statistical analyses is limited to very few studies (Torchio 1989, Danforth and Visscher 1993).

Because cleptoparasitic bees reproduce by ovipositing in the nests of particular bee species, cleptoparasitic bees should be attuned to the nesting biology of their hosts (Wcislo 1987, Danforth and Visscher 1993). In particular, comparative analyses have suggested that there should be a great deal of temporal synchrony between the nesting times of cleptoparasites and that of their hosts (Wcislo 1987). As Wcislo (1987) pointed out, there is a narrow "window of opportunity" for cleptoparasites to complete their egg-laying and development within the nests of their hosts. Researchers studying cleptoparasitic bees have recorded a number of nest-finding and oviposition behaviors that allow these parasites to successfully rear offspring in the nests of other bees. For instance, bees of the genus *Coelioxys* (Hymenoptera: Megachilidae), parasites of leaf-cutting bees in the genus *Megachile* (Hymenoptera: Megachilidae), are not only able to locate

the nests of specific host species (Cane 1983), but they also await the departure of the host to gather more provisions and oviposit through a slit they pierce in the leaf-lining of the reproductive cell, thus hiding their egg (Graenicher 1927, Baker 1971, Michener 2000).

In this study, we examined the reproductive biology of two cleptoparasitic species of the genus *Coelioxys* to determine how closely certain aspects of their behavior and development matched that of their *Megachile* hosts. Specifically, we examined how closely the emergence times of the cleptoparasites matched those of their hosts, and what factors influenced the distribution of offspring sex in both hosts and parasites. The two species of *Coelioxys* we chose for this study, *C. funeraria* Smith and *C. moesta* Cresson, provided a unique opportunity to study the adaptation of cleptoparasites to their hosts. Previous studies of *C. funeraria* uncovered two different size classes (hereafter referred to as "morphs") within the species that exclusively parasitize the nests of two different species of *Megachile* (Packer et al. 1995). The smaller female morph lays her eggs in the nests of the smaller *M. relativa* Cresson, whereas the larger female morph lays her eggs in the nests of the larger *M. inermis* Provancher. Genetic tests have confirmed that both of these morphs belong to the same species, so this is not a case of undiscovered cryptic species (Packer et al. 1995). Thus, we asked whether individual morphs within a single species were adapted differently to the biology of two different hosts. We were also able to compare the biology of these morphs to that of another *Coelioxys* species, *C. moesta*, which lays eggs only in the nests of *M. relativa.*

The two *Megachile* species in this study nest within preexisting holes in logs or branches. The nests consist of a linear series of reproductive cells sometimes followed by an empty vestibular space and then capped with leaves, soil, or decaying wood (Strickler et al. 1996). The reproductive cells are lined with oblong pieces of leaves cut from plants growing near their nests (Krombein 1967, Strickler et al. 1996). After completing the cell lining, these *Megachile* species make a number of trips to gather pollen and nectar. When sufficient pollen has been deposited in the cell, the female *Megachile* oviposits onto the pollen mass and caps the cell with round leaf pieces. In the process of parasitizing *Megachile* nests, female *Coelioxys* deposit a single egg into the leaf lining of individual host cells. *Megachile* and *Coelioxys*, like all Hymenoptera, are haplo-diploid and can control the sex of their offspring. Fertilized eggs develop into females, and unfertilized eggs develop into males (Gerber and Klostermeyer 1970). The *Coelioxys* offspring hatches, and the second instar, armed with large mandibles, destroys the host egg or larva and any other rival *Coelioxys* larvae in the cell (Baker 1971). The surviving *Coelioxys* offspring then molts and consumes the pollen and nectar originally stored for the host's offspring (Krombein 1967). *Coelioxys* and *Megachile* both complete development within their cells and emerge as adults.

## Materials and Methods

**Study Sites and Trap Nesting.** This study of *Coelioxys* began in the summer of 1983 and continued from the summer of 1986 through the summer of 1992 in Dickinson and Iron Counties in the Upper Peninsula of Michigan. At the beginning of each summer, newly drilled trap nests were placed no later than the first week of June at four sites: Camp 5 (C5), County Line (CL), Ford 1 (F1), Ford 2 (F2) (see Strickler et al. [1996] for a map of the sites). During 1983, 768 trap nests were placed at each site, and 1,152 trap nests were placed at each site in the following years. All study sites were located in open meadows surrounded by second growth northern hardwood forest. Trap nests consisted of blocks of white pine 19 mm square by 153 mm long into which a hole was drilled lengthwise to a depth of ≈142 mm. (Some of the 1983 season nests were shorter because of the paucity of drill bits. For analyses of cell depth, adjustments were made to account for the shorter bore lengths.) The diameter of the nesting holes was 5.5, 6.0, or 11.0 mm for all years after 1986. During the 1983 and 1986 nesting seasons, several other bore diameters of smaller or intermediate sizes were also provided to encourage other species to nest in the traps. Trap nests were checked every other day to see if they contained nests. Completed nests were replaced with empty trap nests and moved to a holding area at each study site where they remained until the following spring. More complete trap nesting procedures and methodologies can be found in Strickler and Scriber (1994) and Strickler et al. (1996).

**Nest Dissections and Architecture Measurements.** *M. inermis* and *M. relativa* nests were retrieved from the study sites in the year after their construction, 1–2 mo before offspring emergence. Cells were removed from the nests before offspring emergence and placed in separate rearing dishes or tubes. Offspring from individual cells were reared at room temperature in a laboratory in Channing, MI (1983), Crystal Falls, MI (1986–1987), or at an unheated shed located in a jack-pine plantation 6.4 km south of Crystal Falls (1988–1992). Cells were checked daily for emergence, and date, species, and sex were recorded for each offspring. All *Coelioxys* were retained as well as selected *Megachile* offspring for species identification and dry weight measurements. Measurements of dry weights were taken from offspring reared from nests constructed between 1989 and 1991. After individual bees were desiccated in a $P_2O_5$ chamber for a period of 2–4 d, specimens were weighed to the nearest 0.1 mg, and reweighed after a second desiccation period. The smaller of the two weights obtained for a specimen was used to calculate the dry weight used in the analyses. Voucher specimens were deposited at the entomological collections of Michigan State University.

**Field Observations.** All field observations are those of V.L.S. and were recorded at the time of observation either directly onto paper or onto a tape recorder. In-nest behavioral observations of *Coelioxys* were made by direct observation while reflecting light with

**Table 1.  Number of cells and nests constructed by *Megachile* and parasitized by *Coelioxys* for each year of the study**

| Year | *M. inermis* | | *C. funeraria* on *M. inermis* | | *C. funeraria* on *M. relativa* | | *C. moesta* on *M. relativa* | | *M. relativa* | |
|------|------|-------|------|-------|------|-------|------|-------|------|-------|
|      | Cells | Nests | Cells | Nests | Cells | Nests | Cells | Nests | Cells | Nests |
| 1983 | — | — | — | — | 45 | 34 | 10 | 8 | 833 | 172 |
| 1986 | 538 | 126 | 5 | 5 | 38 | 28 | 40 | 33 | 906 | 228 |
| 1987 | 1,539 | 311 | 59 | 47 | 44 | 36 | 45 | 38 | 1,113 | 254 |
| 1988 | 927 | 218 | 18 | 16 | 27 | 23 | 56 | 42 | 794 | 283 |
| 1989 | 2,598 | 563 | 98 | 76 | 28 | 22 | 54 | 38 | 961 | 248 |
| 1990 | 3,693 | 834 | 76 | 64 | 62 | 54 | 33 | 27 | 998 | 331 |
| 1991 | 3,477 | 753 | 52 | 48 | 63 | 42 | 46 | 34 | 805 | 224 |
| 1992 | 1,829 | 409 | 145 | 121 | 69 | 52 | 13 | 11 | 615 | 216 |
| Total | 14,601 | 3,214 | 453 | 377 | 376 | 291 | 297 | 231 | 7,025 | 1,956 |

a mirror down the bore of a nest. Observations of the large *C. funeraria* morphs were made without prior species identification of most individuals, whereas the small *Coelioxys* morphs were netted at the CL site and identified to species in the field (V.L.S.). The smaller *Coelioxys* were marked with either a blue Testors paint dot on the scutum, for small *C. funeraria,* or with an orange paint dot for *C. moesta.*

**Host Sex Determination.** Because *Coelioxys* offspring kill the host offspring, the sex of the host for the cell in which *Coelioxys* developed is unknown. However, in many cases, it is possible to predict the sex of the host that would have been reared had the *Megachile* offspring survived. *Megachile* follow the general rule of placing their female offspring in the innermost cells followed by male cells (Krombein 1967), which is a pattern also common to other leaf-cutting bees (Tepedino and Parker 1984). We assumed that any parasitized cell occurring basal (inner) to a cell containing a female *Megachile* was provisioned for a female host offspring, whereas a parasitized cell constructed after a cell containing a male *Megachile* was provisioned for a male host offspring. For some cells it was not possible to predict host sex because these cells occurred between female and male host cells, or occurred in the basal most cell of an all-male nest. Those cells for which a host sex could not be confidently predicted were not used in analyses requiring knowledge of host sex.

**Statistical Analyses.** All statistical analyses were performed using the SAS software package version 6.03 (SAS Institute, Cary, NC). We compared adult female and adult male dry weights using Kruskal–Wallis tests. To examine parasite sex ratios as a function of cell position, nest depths were divided into four categories for *M. inermis,* and five categories for *M. relativa:* cells 1 and 2 (most basal), cells 3 and 4, cells 5 and 6, and cells 7 through 9 (for *M. inermis*) or 7 and 8, and 9–12 (for *M. relativa*). This was done to ensure adequate sample sizes for analyses and still retain information on cell depth. Because the first date and the length of the cleptoparasite oviposition season varied substantially from year to year, we standardized the years by dividing each summer season into four quarters based on the percentage of the total *Coelioxys* produced on each host. To determine the effects of season and cell position on sex ratios, we performed simple linear regressions of season and cell depth on sex ratios, and

a multiple regression analysis that included the effects of both season and cell depth on sex ratios.

## Results

*Coelioxys funeraria* were reared from 453 cells in 377 *Megachile inermis* nests and from 376 cells in 291 *M. relativa* nests. *C. moesta* were reared from 297 cells in 231 *M. relativa* nests. Table 1 shows the number of cells and nests constructed by each *Megachile* species and the number of cells and nests parasitized by *Coelioxys.* We treated the *C. funeraria* populations from the two *Megachile* hosts separately, because the individuals parasitizing the two *Megachile* hosts are considerably different in both size and behavior. Only the large morph was observed inspecting and ovipositing in the large diameter *M. inermis* nest, whereas the small morph restricted its activities to the small diameter *M. relativa* nests, despite the fact that they each could physically fit into nests of both *Megachile* species. *C. moesta* restricted its activities to the smaller bores, and thus, *M. relativa.*

**Coelioxys Oviposition Behavior.** The following descriptions are based on field observations made by V.L.S. Oviposition of the large morph *C. funeraria* in *M. inermis* nests was observed hundreds of times, and always occurred immediately after oviposition by *M. inermis. C. funeraria* oviposited into the leaf lining of a complete reproductive cell, and the female *M. inermis* was collecting leaf pieces to cap the cell. If *M. inermis* was successful in getting the first several capping leaf pieces in place before *C. funeraria* oviposition, then the cleptoparasite almost always abandoned the nest. On one occasion, V.L.S. observed a *C. funeraria* ovipositing in a nest that had eight capping leaf-pieces in place. The *C. funeraria* did not remove the leaves from the nests, but simply moved them out of the way to gain access to the cell, and left the nest immediately after ovipositing into the side wall of the cell's leaf lining without trying to reposition the capping leaf pieces. V.L.S. observed the small morph of *C. funeraria* ovipositing a few times in nests of *M. relativa,* and in each case the *C. funeraria* female oviposited onto the leaf lining of a cell containing a nearly complete pollen-nectar mass. This occurred while *M. relativa* was collecting pollen, and before *M. relativa* oviposition. *C. moesta* was also observed, on a few
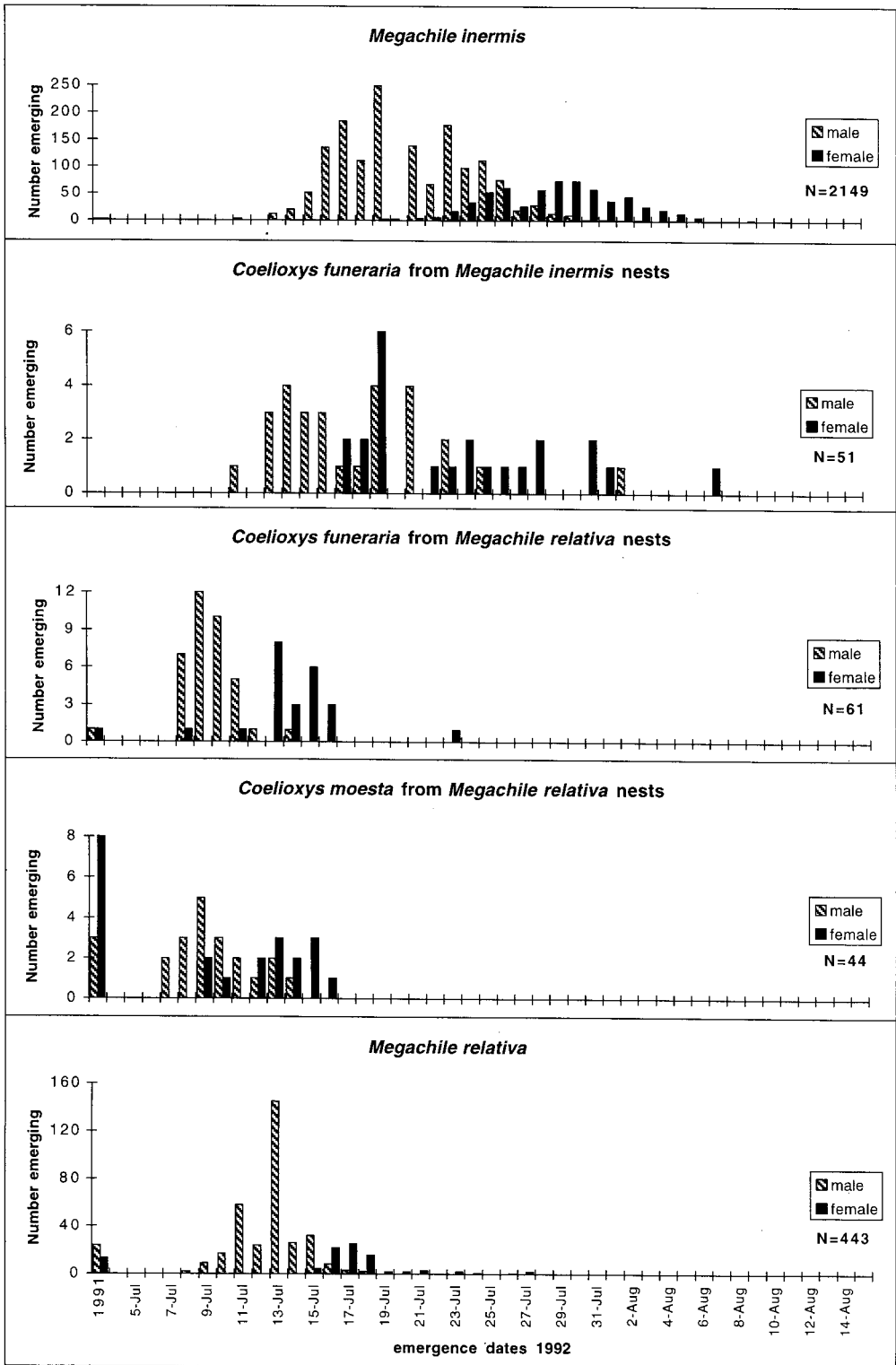
**Fig. 1.** Emergence pattern data for host and cleptoparasite offspring from nests constructed during 1991, a typical year for this study. Males emerge before females in every species, and the *Coelioxys* tend to match the host emergence (shifted forward by a day or two).

**Table 2.**   Average dry weights in milligrams ± 1 SD of female and male *Coelioxys* and *Megachile* adults

| Sex | M. inermis | C. funeraria on M. inermis | C. funeraria on M. relativa | C. moesta on M. relativa | M. relativa |
|---|---|---|---|---|---|
| Females | 54.73 ± 9.81 | 29.44 ± 7.33 | 11.59 ± 2.49 | 9.95 ± 2.16 | 14.34 ± 2.72 |
| | n = 505 | n = 98 | n = 57 | n = 47 | n = 252 |
| Males | 35.98 ± 6.96 | 22.99 ± 5.13 | 9.52 ± 2.17 | 8.37 ± 2.09 | 11.05 ± 2.45 |
| | n = 2,851 | n = 106 | n = 90 | n = 57 | n = 1,152 |

occasions, ovipositing in the nests of *M. relativa*. In each case the *C. moesta* entered a reproductive cell that was empty, or contained at most two loads of pollen (<10% of a full provision). Oviposition by this *Coelioxys* species occurred into the base of the *M. relativa* cell. Later dissection of all *Coelioxys* parasitized cells showed that the placement of oviposition was consistent with field observations.

**Emergence.** *M. inermis* and the *C. funeraria* that parasitized it were univoltine, producing no second-

generation. *M. relativa* and both *Coelioxys* species parasitizing it often had some individuals emerging the same year as nest construction. Fig. 1 shows the emergence patterns for offspring from nests constructed during 1991, a typical year. In each year of the study, both *Coelioxys* and *Megachile* males emerged earlier than females (Kruskal–Wallis test; $P < 0.0001$ for all years). Using the emergence data, we performed a series of *a priori* Kruskal-Wallis tests on Julian dates. These tests were performed separately for each year of the study and then combined in the final analysis using Fisher's combined $P$ value test. We found significantly different emergence times for individuals of *C. funeraria* on the two different hosts ($P < 0.0001$, df = 14, $\chi^2 = 118.1$). The emergence times of the hosts, *M. inermis* versus *M. relativa*, were also significantly different ($P < 0.0001$, df = 14, $\chi^2 = 128.9$). Although the emergence times of the parasites corresponded well with that of the hosts, *C. funeraria* offspring
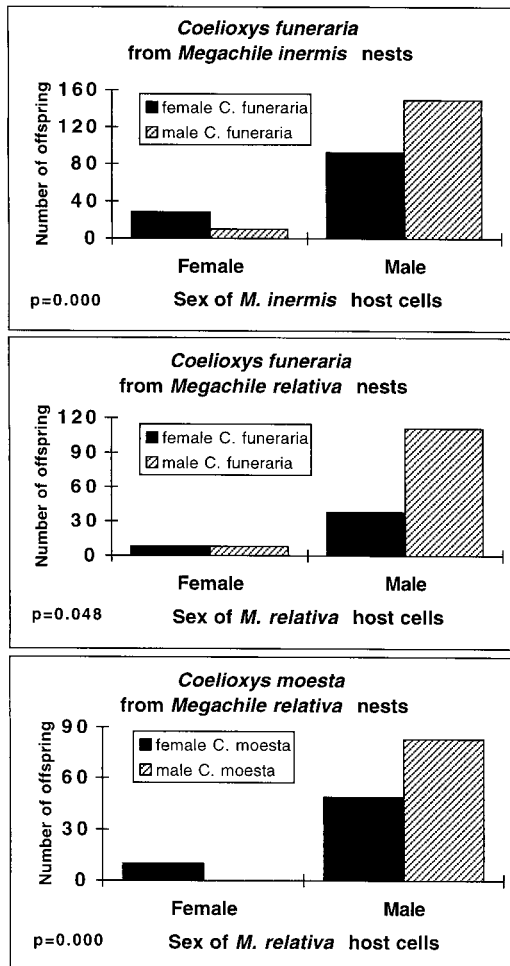


**Fig. 2.**   Number of female and male *Coelioxys* offspring produced from host cells predicted to have been provisioned for either female or male *Megachile*.
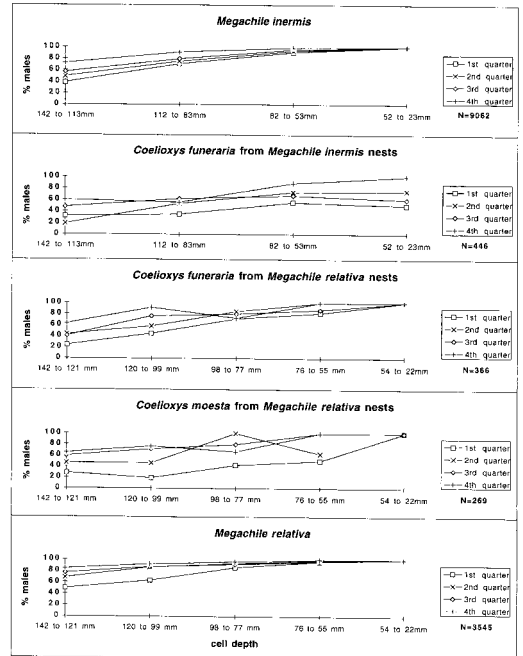


**Fig. 3.**   Regression analyses for the percentage males in each cell depth category for all species of host and cleptoparasite. On the x-axis, the larger cell depth values indicate cells that are deeper in the nest. The four lines indicate the percentage of males for each quarter of the year (see *Results*).

**Table 3. Multiple and linear regression analyses, with cell depth and season as the independent variables, and percentage males as the dependent variable**

| Species | M. inermis | C. funeraria on M. inermis | C. funeraria on M. relativa | C. moesta on M. relativa | M. relativa |
|---|---|---|---|---|---|
| Multiple regression | | | | | |
| Cell depth | $P = 0.0001$ | $P = 0.0060$ | $P = 0.0001$ | $P = 0.0120$ | $P = 0.0003$ |
| Season | $r^2 = 0.94$ | $r^2 = 0.82$ | $r^2 = 0.88$ | $r^2 = 0.78$ | $r^2 = 0.86$ |
| Linear regression | | | | | |
| Cell depth | $P = 0.0001$ | $P = 0.0074$ | $P = 0.0001$ | $P = 0.0150$ | $P = 0.0001$ |
| Season | $P = 0.0395$ | $P = 0.0170$ | $P = 0.0471$ | $P = 0.0309$ | $P = 0.0242$ |

The $r^2$ values are only included for the multiple regression analyses, and they were always higher than with the linear regression analyses.

emerged significantly earlier than the hosts. *C. funeraria* from *M. relativa* emerged earlier than *M. relativa* ($P < 0.0001$, df = 14, $\chi^2 = 38.9$), and *C. funeraria* from *M. inermis* emerged earlier than *M. inermis* ($P < 0.0001$, df = 14, $\chi^2 = 56.3$). A posteriori tests comparing the emergence of *C. moesta* from *M. relativa* versus *M. relativa* were not significantly different at the $P = .05$ level for any individual year, as was the case for *C. funeraria* from *M. relativa* versus *C. moesta* from *M. relativa*.

**Adult Dry Weights.** *Coelioxys* and *Megachile* females were always heavier than their male counterparts (Table 2). Sex of offspring had a significant affect on the weight of *Coelioxys* in all cases (Kruskal–Wallis test; *C. funeraria* from *M. inermis* $P < 0.0001$; *C. funeraria* from *M. relativa* $P < 0.0001$; *C. moesta* from *M. relativa* $P < 0.0007$).

Because it was possible to predict the host sex for approximately half the *Coelioxys* offspring, and because female *Megachile* cells are more abundantly provisioned (i.e., larger) than male *Megachile* cells, we asked whether *Coelioxys* offspring that developed in the better provisioned (i.e., larger) female host cells were significantly heavier than offspring that developed in the less well provisioned (i.e., smaller) male host cells (Strickler et al. 1996). The effects of host sex was only significant for the weights of *C. moesta*, in which offspring reared out of female host cells were heavier than those reared out of male host cells (Kruskal–Wallis test; $P < 0.05$), but it should be noted that all *C. moesta* reared from female host cells were female.

**Coelioxys Sex Versus Host Sex.** We were able to predict host sex for 62% of *C. funeraria* from *M. inermis*, 44% of *C. funeraria* from *M. relativa*, and 48% of *C. moesta* from *M. relativa*. As seen in Fig. 2, the sex ratios for *Coelioxys* reared in male host cells were more male biased than those in female host cells (goodness-of-fit test; *C. funeraria* from *M. inermis* $P < 0.0001$; *C. funeraria* from *M. relativa* $P < 0.048$; *C. moesta* from *M. relativa* $P < 0.0001$). In the case of *C. moesta* from *M. relativa*, no male offspring were produced in cells predicted to contain female hosts. However, the bulk of *Coelioxys* offspring, both male and female, were produced in male host cells (Fig. 2).

**Effects of Cell Depth and Season.** The results of a simple linear regression analysis found that both *Megachile* species produced more female offspring early in the summer than late in the summer, and

placed female offspring deeper in the nests than male offspring (Fig. 3; Table 3). This was also the case with *C. moesta* and *C. funeraria* on each of the two host species (Fig. 3; Table 3). Multiple regression analyses, including both cell depth and season as variables, were highly significant in most cases, and explained from 78 to 94% of the variation (Table 3).

**Effects of Cell Length.** *C. moesta* was observed ovipositing into the leaf lining at the base of *M. relativa* cells that were either empty or had at most two pollen loads in each cell. *M. relativa* constructed longer cells for female offspring than for male offspring (Strickler and Scriber 1994, Strickler et al. 1996). Therefore, it might be possible for *C. moesta* to use cell length as a determining factor in whether or not to fertilize eggs. In our analyses, however, we found no effect of cell length on the sex placement of *C. moesta* offspring (Kruskal–Wallis test; $P > 0.05$). *C. funeraria*, however, oviposited either immediately after the oviposition of *M. inermis*, or just before *M. relativa* oviposition. *C. funeraria*, therefore, would be unable to use cell length as a factor in determining which sex to produce in a cell, and cell length analyses were not performed for this species.

## Discussion

We found that the nesting behavior of *Coelioxys* mirrored that of their *Megachile* hosts to a considerable degree. One remarkable finding of this study was how well the emergence times of the parasites matched those of the hosts. In each case, the cleptoparasite offspring emerged just before the hosts. This was even true of individual *Coelioxys funeraria* parasitizing two different host species: *C. funeraria* on *M. relativa* emerged significantly earlier than did *C. funeraria* on *M. inermis*. In fact, the emergence times of *C. funeraria* on *M. relativa* were much more similar to *C. moesta*, also a cleptoparasite of *M. relativa*, than to individuals of *C. funeraria* that emerged from *M. inermis*. Because *Megachile* nests are made in linear series, offspring emerging within these nests must chew their way out of the nests through the cells constructed after theirs. Tepedino and Frohlich (1984) showed that if the cell positions in nests are experimentally reversed, emerging *Megachile rotundata* will chew their way through their own siblings. Thus, there should be strong selection pressure for the cleptoparasites to match their host's emergence patterns. The fact that the emer-

gence times of the cleptoparasites matched those of the hosts so closely, even within a species that used two hosts with different emergence times, strongly indicates the action of natural selection in molding the emergence patterns of the parasites to fit those of the specific hosts. These results conform to the general patterns of cleptoparasite nesting behavior reviewed by Wcislo (1987).

Another remarkable similarity between the nesting behavior of host and cleptoparasites was the pattern of sex placement within the nests and over the nesting season. Both *Coelioxys* species placed their sexes in similar positions within the nest as their *Megachile* hosts. *Coelioxys* placed a greater proportion of female offspring in female host cells and a greater proportion of male offspring in male host cells (Fig. 2). We also discovered that the ratio of female to male *Coelioxys* and *Megachile* was higher in the inner cells, and the percentage of males increased in the outer cells (Fig. 3). There was also a significant effect of season on sex placement of both *Coelioxys* and *Megachile* species, with more females being produced early in the season and more males produced later in the season (Table 3; Fig. 3). Tepedino and Torchio (1982) found a similar seasonal pattern of sex ratios in another nonsocial wood-nesting bee, *Osmia lignaria propinqua* (Hymenoptera: Megachilidae), which suggests that such patterns may be common in linear wood-nesting bees. Multiple linear regression analyses, including both season and cell placement as factors, were highly significant in all cases, and explained more of the variation than cell placement alone (Table 3; Fig. 3).

Because cells provisioned for *Megachile* females tend to contain greater amounts of pollen and nectar than male *Megachile* cells, presumably because the larger females require more nutrition (Trivers 1972), there could be an advantage for *Coelioxys* to place females in female host cells. *M. inermis* and *M. relativa* are known to lay female eggs in cells with greater resource provisioning (Strickler et al. 1996). *Coelioxys* females are also larger than males (Table 2). The similarity of the sex placement behavior between hosts and parasites suggests that *Coelioxys* might be able to determine the sex of the *Megachile* offspring before parasitizing the cell. However, observations by V.L.S. of *Coelioxys* behavior revealed that only *C. funeraria* parasitizing *M. inermis* enter the host nest and oviposit after the *Megachile* egg has been laid. Thus, it appears unlikely that *Coelioxys* knows the sex of the host offspring before parasitizing a cell (with the possible exception of *C. funeraria* on *M. inermis*). However, by placing females in more basal host cells, *Coelioxys* are more likely to place females in better-provisioned female host cells (Strickler et al. 1996). In this way, the parasites might ensure that, on average, the larger and longer developing females receive adequate nutrition. However, several lines of evidence argue against resources being the most important influence on the sex placement strategy of *Coelioxys* bees. First, although *Coelioxys* females are larger than males, female *C. funeraria* offspring emerging from female hosts cells were not larger than female *C. fu-*

neraria offspring emerging from male host cells. Second, *C. funeraria* in *M. inermis* nests quite often left some of the pollen unconsumed, indicating that pollen was probably not a limiting resource for *Coelioxys* (V.L.S., personal observation). Finally, *Coelioxys* individuals tend to be much smaller than *Megachile* (Table 2), and probably require significantly less pollen and nectar.

Differential resource provisioning does not seem to adequately explain the offspring sex placement of *Coelioxys*. Instead, we suggest that the emergence times of the sexes may be a much more important factor in determining the placement of *Coelioxys* sexes in this study. Because larger females typically have longer development times than males, they also emerge later than males (Fig. 1). If *Coelioxys* females were placed distally to males, the males would emerge first and chew their way out through the female cells, possibly destroying the female offspring. As mentioned earlier, Tepedino and Frohlich (1984) discovered that when males emerged from cells deeper in the nest before females (or other males), they would often chew their way through the outer cells, killing the other offspring. This would put strong selection pressure on both hosts and parasites to place females basal to males (Fig. 1). Interestingly, in another study of cleptoparasitic bees, *Holcopasites ruthae* (Hymenoptera: Anthophoridae), Danforth and Visscher (1993) did not find that female cleptoparasites tended to emerge from female host cells. However, the cleptoparasitic bees they studied were ground nesting bees in which cells were arranged at random (i.e., not in a linear series), and exact emergence times would be much less important in this scenario. It appears that the linear nest architecture, per se, may have a strong influence on cleptoparasite biology in terms of oviposition behavior (sex placement) and emergence.

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