Dynamics of a Host-Cleptoparasite Relationship: *Holcopasites ruthae* as a Parasite of *Calliopsis pugionis* (Hymenoptera: Anthophoridae, Andrenidae)

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ABSTRACT *Holcopasites ruthae* Cooper is a cleptoparasite of *Calliopsis pugionis* Cockerell. At five sites, parasitism rate of host cells varied from 0 to over 30%, with an overall parasitism rate of 6.6% when data from all sites were combined. Significant influences on parasitism rate included site, nest density, and date of excavation, and density had a significant interaction with date. Together these factors account for 97% of the variance in parasitism rate. The sex ratio of the host bee was significantly influenced by parasitism rate, host nest density, and date, which together explain 88% of the variance in host sex ratio. Possible explanations for the dynamics of this host–parasite relationship are discussed. Host nest density may influence parasitism via predator confusion or selfish herding. The influence of parasitism on sex ratio is probably not directly a result of differential parasitism reducing the number of surviving females. However, both equal vulnerability by sex and differential vulnerability resulting from differences in the time spent by females provisioning male and female cells remain possibilities: the latter could indirectly influence sex ratio through facultative behavioral changes in the host bee.

KEY WORDS cleptoparasitism, host–parasite relationship, sex ratio

THE GENUS *Holcopasites* includes ≈15 species of North American cleptoparasitic bees whose hosts include species of the panurgine genera *Calliopsis* (sensu Ruz 1991) (Shinn 1967), *Pseudopanurgus* (Hurd & Linsley 1972), *Heterosaurus*, *Metapsaenythia*, and probably *Pterosaurus* (Rozen 1989, 1993). *Holcopasites* belongs to the monophyletic anthophorid subfamily Nomadinae (Alexander 1990, Roig-Alsina 1991). All nomadine bees are cleptoparasites of pollen-collecting bees (Bohart 1970). Female nomadines enter open, partially provisioned cells within the nests of their hosts and deposit one or more highly modified eggs in the wall of the host cell (Rozen 1992). These eggs hatch and the nomadine first instar destroys the host egg or first instar (Linsley & MacSwain 1955; Rozen 1965, 1991; Bohart 1970; Rozen et al. 1978). The *Holcopasites* larva thereafter feeds on the pollen and nectar provisions.

Because most cleptoparasitic bees are quite rare in comparison with their hosts, the majority of studies have focused only on establishing the host-parasite association. Almost no data exist on the factors shaping the host-parasite interaction, either spatially or temporally, for cleptoparasitic bees. In this study, thanks to the help of many people (see Acknowledgments), we were able to investigate parasitism of *Calliopsis pugionis* Cockerell by *Holcopasites ruthae* Cooper over the course of the entire 1992 nesting season at six widely scattered sites in Riverside County, California. Our results indicate that parasitism is correlated with several factors, such as nest density, date, and host sex ratio.

C. pugionis, the host of *H. ruthae*, has been collected in coastal sage scrub habitats of cismontane southern California, including sites in Riverside, Los Angeles, and San Diego counties, and in adjacent areas of the Colorado desert from late March until the beginning of June (Visscher & Danforth 1993). Both *Encelia* (*E. farinosa* Gray) and *Hemizonia* (*H. laevis* [Keck] Keck) served as pollen and nectar sources for *C. pugionis* (Visscher & Danforth 1993) and as nectar sources and mating sites for *H. ruthae*.

Materials and Methods

Study sites. This study was carried out from 2 May until 12 June 1992 at six localities in Riverside County, California. Four of the sites are located along railroad beds: three sites at the foot of the Box Springs Mountains (Manfield Road, Gernert Road, SP & Santa Fe) and one site (San Timoteo Canyon) ≈15 km east of Riverside. The other two sites are the Biological Control Groves

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Table 1. Parasitism rate by site

Site	No. of *Calliopsis*	No. of *Holcopasites*	Parasitism rate, %
Gernert Road	236	12	4.8
Manfield Road	234	44	15.8
SP & Santa Fe	56	0	<1.8
San Timoteo Canyon	44	8	15.3
San Jacinto Wildlife Area	337	0	<0.3
Total	907	64	6.6

on the University of California, Riverside, campus, where the first specimens of *H. ruthae* were collected (Cooper 1993), and the San Jacinto Wildlife Area, ≈20 km ESE of Riverside. Visscher & Danforth (1993) gave a map and a more detailed description of the study sites.

Nest Excavations. We excavated some individual nests to evaluate *C. pugionis* nest architecture (see Visscher & Danforth [1993]). Larvae of both *C. pugionis* and *H. ruthae* from these excavations were used in calculating the overall parasitism rate by site (Table 1) but could not be used in the data set on correlates of parasitism (Table 2), because accurate measures of cell density were not possible with such small samples. Hence these data are presented separately.

For estimates of parasitism rate we excavated nests of *C. pugionis* at all sites except the University of California, Riverside, campus, where nests occurred at very low density. To quantify the extent of parasitism and factors correlated with the rate of parasitism (such as nest density and *C. pugionis* sex ratio), we excavated nests in groups by choosing an area (from 225 to 900 cm^2) and excavating all cells without regard to the nest associations. Nest density can be quantified using nearest neighbor distances (e.g., Wcislo 1984), but in our case nest entrances were not always conspicuous and we reasoned that cell density would be an accurate, though indirect, measure of nest density. In areas of the lowest nest density (<4 per m^2), we had to lump data from several 225-cm^2 areas to accumulate total numbers of cells that would allow statistically meaningful estimates of sex ratio and parasitism rate. Cells containing fungi were not included in the measures of cell density because it was often impossible to determine whether fungus-infected cells were provisioned in the year of our study or in previous years.

When closed cells were discovered in nest excavations, the contents were transfered to 96-well tissue culture trays. Cell depth and diameter were treated as possible correlates of parasitism and were measured for each cell excavated. The cell diameter was measured by inserting a machinist's hole gauge (Precision Brand Small Hole Gauge Set no. 69925) along the long axis of the ellipsoidal cell and expanding it until it fit snugly against the lateral walls. The hole gauge was then removed and the diameter measured with digital calipers to the nearest 0.01 mm. Cell depth was measured with a ruler to the nearest 0.1 cm.

Larvae. The contents of all cells were brought to the laboratory for identification, sex determination, and weighing. Bee larvae were identified using keys in Rozen (1966a,b). Sex of larvae was determined for all *Holcopasites* and *Calliopsis* feeding last instars and prepupae using Carnoy's fixative, as described in Duchateau & van Leeuwen (1990). While still alive, 122 *Calliopsis* and 29 *Holcopasites* prepupae were weighed and sex was later determined. All specimens were ultimately fixed in Kahle's solution.

Table 2. Parasitism rate, sex ratio, and cell density

Site	Date	Area excavated, cm^2	No. cells excavated[a]	Density, cells per m^2	Parasitism rate, %	Sex ratio[b], % male (*n*)
Gernert Road	16 May	1,575	45	286	28	82 (11)
	7 June	400	46	1,150	0	70 (33)
	8 June	225	101	4,489	1	84 (81)
Manfield Road	9 May	900	160	1,778	14	68 (81)
	9 May	900	60	667	30	80 (68)
	1 June	225	90	4,000	8	79 (84)
SP & Sante Fe	15 May	400	30	750	0	18 (17)
	15 May	900	34	377	0	48 (25)
San Timoteo	21 May	625	17	272	33	na (0)
	6 June	400	41	1,025	10	69 (29)
San Jacinto	29 May	225	54	2,400	0	63 (24)
	29 May	225	212	10,613	0	73 (146)
	9 June	2,975	87	292	0	55 (42)

[a] Only cells clearly from the year of the study were counted. It was impossible to assess with moldy cells whether they had come from the year of the study or previous years.

[b] Some cells in excavations contained eggs or early instars whose sex could not be determined. Therefore, the data on sex ratio are based on a subset of the total cells excavated that contained viable offspring (no. cells excavated). Sample sizes are for total larvae whose sex was determined.

Because our study concerned the relationship between sex of larvae, cell diameter, cell depth, and weight of larvae, sex determination of larvae was done "blind" with respect to these measurements.

Voucher Material. Voucher specimens of adult *C. pugionis* and *H. ruthae* are deposited at the University of California, Riverside. Voucher specimens of larval *C. pugionis* and *H. ruthae* were deposited at the American Museum of Natural History, New York, NY and the National Museum of Natural History, Smithsonian Institution, Washington, DC.

Throughout this paper, means, standard deviations and sample sizes are denoted by the following format: mean ± SD (*n*).

Results

Mode of Parasitism. The most detailed observations of adult *H. ruthae* behavior were made at an area of high nest density at Manfield Road (>60 nests per m^2). Typically, female *H. ruthae* flew low over the nest site and periodically entered *Calliopsis* nests, with intermittent periods of perching on small rocks and prominent features in the vicinity of nests. Although most visits were of short duration (<1.0 min), some lasted up to 10 min. Female *H. ruthae* appeared attentive to the behavior of female *C. pugionis*. On two occasions we observed *H. ruthae* entering *Calliopsis* nests almost immediately after the departure of the resident, and female *H. ruthae* were commonly seen perched on small rocks within nest sites apparently watching for female *C. pugionis* leaving their nests.

A total of 17 female *H. ruthae* were marked on the scutum with paint in individual color combinations at Manfield Road and the University of California campus (MR, 6; UCR, 11) from 6 to 17 May. Five were resighted on at least one subsequent day, and all five were resighted at the same site from which they were originally marked (up to 11 days after original marking). The return of female *H. ruthae* to sites from which they were previously marked with paint suggests that females may learn the locations of host nest sites, but we have no evidence that cleptoparasites learn the locations of individual nests, as has been suggested for *Epeolus minimus* (Robertson) (Graenicher 1906), *Nomada opacella* Timberlake (Linsley & MacSwain 1955), *Protepeolus singularis* Linsley & MacSwain (Rozen et al. 1978), and *Melecta separata callura* (Cockerell) (Thorpe 1969) and demonstrated for a chrysidid wasp, *Argochrysis armilla* Bohart (Rosenheim 1987).

As in other nomadine bees, female *H. ruthae* laid eggs in the walls of open, partially provisioned cells. Two cells containing *Holcopasites* larvae were brought to the laboratory and the *H. ruthae* oviposition sites located. The egg was deposited in soil beneath the hydrophobic cell lining at roughly the midpoint along the cell's length and in the upper surface or "roof" of the cell. The first-instar *Holcopasites* had forced open the cover or operculum (as described by Rozen [1992] for other nomadines) and crawled onto the pollen ball, where the host egg or first instar was killed. We found one first-instar *H. ruthae* with its mandibles imbedded in a deflated *Calliopsis* egg, although first instars are probably equally vulnerable to *Holcopasites* first instars.

Determinants of Parasitism Rate. Data on parasitism rate are presented in Tables 1 and 2. To analyze variation in the rate of parasitism, we performed an analysis of covariance (ANCOVA) on data presented in Table 2. The ANCOVA consists of a linear model with percentage parasitism as the dependent variable, a nominal factor of site, and continuous regressors of *ln* density (the natural log of cell density), date, and date**ln* density interaction. The overall model explains 96.9% of the variance in parasitism rate and is highly significant ($P = 0.0018$). The null hypotheses that there is no difference in parasitism due to differences in site, *ln* density, date, and the date**ln* density interaction can also be rejected ($P = .0022, .0127, .0113$, and $.0238$, respectively).

Although we observed *H. ruthae* at flowers and nest aggregations at all sites, we found no *Holcopasites* larvae at SP & Santa Fe or San Jacinto (Table 1). However, even just for those sites where *H. ruthae* larvae were collected, site remains a significant predictor of parasitism rate in the ANCOVA model ($P = 0.0236$). It is not surprising to find different levels of parasitism at widely separated nest aggregations.

Fig. 1A shows the relationship between density and parasitism rate by site. When variation accounted for by site, date, and date*density interaction are removed, there is a highly significant overall inverse linear effect of *ln* density.

Parasitism rate and date of excavation were inversely related at all sites (Fig. 1B). This relationship has several components. In part it is due to the relationship between density and parasitism, because later excavations were made at sites that had a higher density of nests, but also because later excavations for a given nest density had more cells per nest. The model factors out this correlation, and when the other factors in the model are taken into account, date still had a highly significant effect on parasitism rate. This probably arises because cells provisioned late in the season are less likely to be parasitized. The flight season of *C. pugionis* is considerably longer than that of *H. ruthae*. At all sites we observed cessation of *Holcopasites* visitation while foraging by *Calliopsis* females continued. Later excavations included cells parasitized early in the season, but these composed a lower

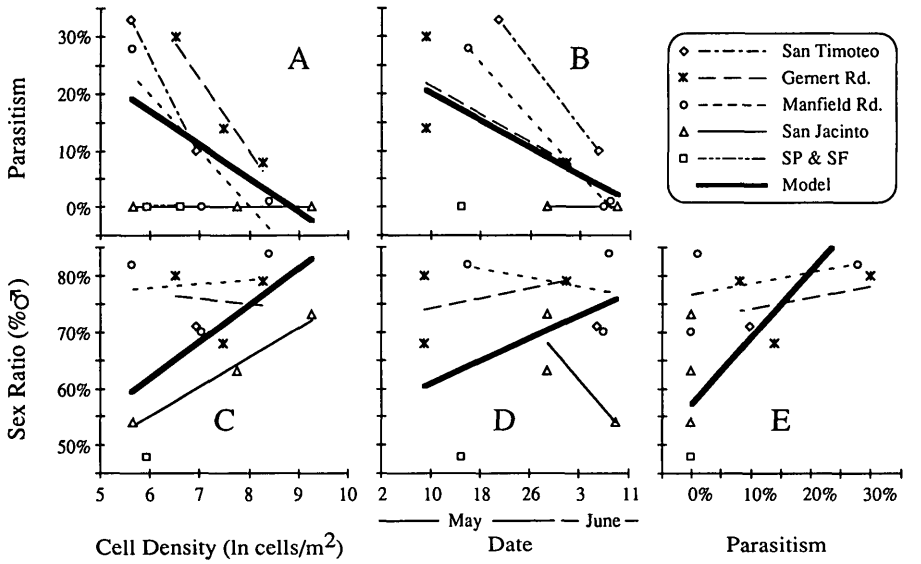

Fig. 1. Influence of cell density and date on parasitism rate (A, B), and effects of cell density, date, and parasitism rate on the sex ratio of the host bee (C, D, E). Each plot shows the effects within sites, with by-site lines of least squares fit to the raw data. The heavy lines are projections from our multivariate models, holding all independent variables except the ones shown in each plot at their overall means. For the regression model of sex ratio, the intercepts, but not the slopes of the model lines shown, change as one changes other variables. For the ANCOVA model of parasitism rate, site-to-site changes affect only the intercepts, and the density*date interaction causes the slopes as well as the intercepts to vary as either of these variables is changed. All of the effects shown by the model lines are highly significant (see text).

proportion because of cells added after parasite activity ceased.

The significant date*density interaction indicates that the slope of the relationship between parasitism and density varies with date. Probably this effect is an artifact of using cell density to estimate nest density. At a given nest density, cell density increases with time, but the expected nest density effects do not change (and the effect of time per se is accounted for separately). This leads to the flattening of the parasitism/density slope with time when density is measured as cell density rather than nest density.

Relationship Between Parasitism and *Calliopsis* Sex Ratio. The sex ratio of *C. pugionis* larvae shows considerable variation among excavations (Table 2). We analyzed this variation with a multiple regression of sex ratio on parasitism rate, cell density, and date of excavation. This model accounted for 88% of the observed variation in sex ratio and was highly significant overall (P = 0.0013). The hypotheses that the slopes of the relationships between sex ratio and parasitism rate, *ln* cell density, and date were each zero can be rejected at alpha levels of 0.0004, 0.002, and 0.013, respectively. In this analysis, the sample from SP & Santa Fe with a very low sex ratio (18% male) was a stong outlier, and, because it also was based on a small sample (Table 2), we omitted it from the analysis. However, the qualitative results of the analysis do not change if it is included: the model is still significant overall (P = 0.0049), as are the effects of parasitism rate (0.0012), *ln* density (0.025), and date (0.014).

The effect of each of these variables can be seen in Fig. 1C-E. The effect of date was the least important, and the effects of the remaining two variables are significant without it. Changes in sex ratio with season have been reported in other solitary bees (Tepedino & Torchio 1982), but the effect is weak in *C. pugionis*. As discussed in Visscher & Danforth (1993), there was no apparent correlation of depth of cell with sex, as would be expected if females usually provisioned female larvae early in the season and male larvae later. Nonetheless, when variation due to parasitism rate and cell density is removed, there is significant effect of date, with higher proportions of males than expected in nests excavated later in the season.

The strongest effect on sex ratio appears to be parasitism rate. We observed a positive relationship between parasitism rate and the percentage of male larvae in nests of the host bee (Fig. 1E). Two hypotheses might account for this relationship. First, female cells might be more frequently parasitized than male cells, and hence the sex ratio of larvae surviving parasitism might be male–biased. Differential vulnerability to parasitism might arise because of sexual size dimorphism, which is pronounced in *C. pugionis*. Female *C. pugionis* are larger than males in adult dry body weight (Visscher & Danforth

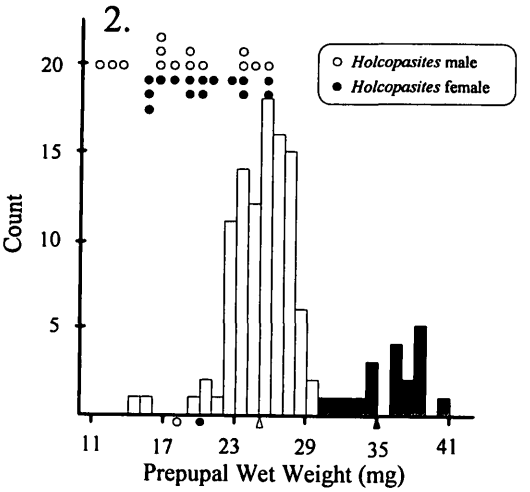

Fig. 2. Histogram of prepupal wet weights for male (open bars) and female (shaded bars) *C. pugionis*. Data for *H. ruthae* are shown above as open (male) and shaded (female) circles (one individual per symbol). Means for *C. pugionis* are indicated by triangles and means for *H. ruthae* are indicated by circles along the abcissa.

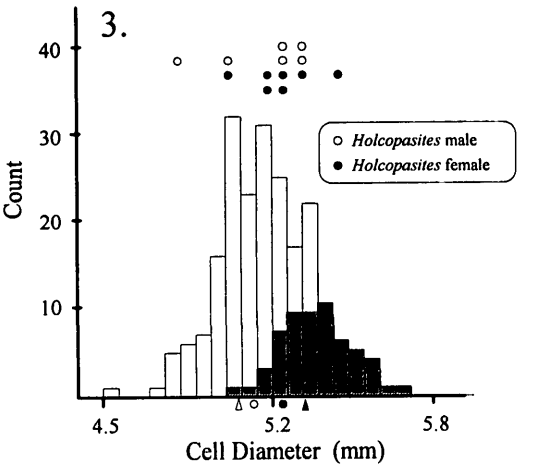

Fig. 3. Histograms of cell diameter for male (open bars) and female (shaded bars) *C. pugionis*. Data for *H. ruthae* are shown above as open (male) and shaded (female) circles (one individual per symbol). Means for *C. pugionis* are indicated by triangles and means for *H. ruthae* are indicated by circles along the abcissa.

1993) and prepupal wet weight (Fig. 2; Table 3; $t = 15.34$, df = 120, $P < 0.001$). Female *C. pugionis* larvae also receive more food than males, based on the dry weights of meconia and the total time spent foraging for male and female cells (Visscher & Danforth 1993). To the extent that time spent away from the nest foraging is proportional to the risk of parasitism, one might expect female *C. pugionis* cells to be more vulnerable to parasitism than males.

The second hypothesis is that adult female *Calliopsis* might respond facultatively to the presence of adult *H. ruthae* by changing the frequency with which they produce sons and daughters. Such behavior might be adaptive if producing the less costly sex, males, decreases the vulnerability to parasitism. Both hypotheses predict an association between parasitism rate and *C. pugionis* sex ratio; however, the first hypothesis predicts a tighter correlation.

Table 3. Comparisons, mean ± standard deviation (*n*), of *C. pugionis* and *H. ruthae* in overall body size

	C. pugionis		*H. ruthae*	
	Males	Females	Males	Females
Prepupal wet wt (mg)	25.24 ± 2.80 (103)	35.94 ± 2.74 (19)	18.45 ± 4.48 (14)	19.86 ± 3.62 (15)
Cell diam (mm)	5.12 ± 0.17 (205)	5.33 ± 0.14 (57)	5.17 ± 0.15 (6)	5.22 ± 0.10 (7)

See text for statistical comparisons.

We set out to evaluate the first hypothesis: that male and female *C. pugionis* differ in vulnerability to parasitism. Direct identification of the sex of *C. pugionis* larvae following parasitism was impossible, for obvious reasons. However, because male and female *C. pugionis* differed significantly in cell diameter (Fig. 3; Table 3; $t = 8.50$, df = 260, $P < 0.001$), differential parasitism of male and female cells might be tested by comparing the cell diameters of parasitized cells with the diameters expected if vulnerability of the two sexes were indeed different. We derived the expected diameters with a Monte Carlo simulation program.

In each simulation the program selected 13 cells (the number of parasitized cells for which we had diameter measurements; cf. Table 3) from the observed distribution of *C. pugionis* cell diameters (Fig. 3), according to one of four hypotheses of the likelihood of parasitism of female versus male cells. A hypothetical sample mean was calculated from this sample, and the process was repeated 1,000 times to determine the distribution of expected means under the hypothesis. We then compared the observed mean parasitized cell diameter (5.20 ± 0.12 mm) with the resulting distribution of expected means (Table 4). The proportion of expected means in either tail of the distribution that lie farther from this distribution's mean than does our observed mean represents the alpha level of the two-tailed test. For each hypothesis, a 1,000–sample simulation was run five times to evaluate the distribution of its estimates for the expected mean cell diameters and the alpha level. We based our simulations on four hypotheses: (1) only female cells are parasitized;

Table 4. Tests of hypotheses of differential and random parasitism, with Monte Carlo simulations as described in the text

Hypothesis generating expected diam	Mean ± SD of distribution of 1,000 expected mean diam of parasitized cells, mm (*n*)	Alpha level for observed 5.20-mm mean diam, from simulation (*n*)
(1) Only female cells parasitized	5.33 ± 0.001 (5)	$P < 0.001$
(2) Female cells 1.27 times more likely to be parasitized[a]	5.20 ± 0.002 (5)	$P = 0.957 \pm 0.03$ (5)
(3) Female cells 1.35 times more likely to be parasitized[b]	5.21 ± 0.001 (5)	$P = 0.885 \pm 0.012$ (5)
(4) Male and female cells equally vulnerable	5.19 ± 0.002 (5)	$P = 0.880 \pm 0.035$ (5)

[a] Differential vulnerability is estimated as the ratio of foraging times for female to male offspring. Provisioning females were away from their nest for 73.72 ± 16.32 min (6) while provisioning male cells, and for 93.33 min (1) while provisioning female cells, yielding an exposure ratio (female/male) of 1.27.

[b] Differential vulnerability is estimated as the ratio of the weights of 14 female and 50 male meconial masses (Visscher & Danforth 1993). These comprise the remains of all the food provided to each larva by its mother, and indicate that daughters receive 1.35 times the food of sons, and presumably require foraging times in the same ratio.

(2) female cells are more likely to be parasitized than male cells in proportion to the extra time during which they are open while being provisioned, a factor of 1.27; (3) same as (2), but with a different estimate of vulnerability, a factor of 1.35; and (4) male and female cells are equally vulnerable. Based on the Monte Carlo analysis, the observed diameters of parasitized cells are incompatible with the hypothesis that only female cells are parasitized, but are compatible with both the hypothesis that all cells are equal in vulnerability and the hypothesis that female cells are slightly more vulnerable as a function of the longer time spent provisioning them (Table 4).

In contrast to *C. pugionis*, larvae of *H. ruthae* showed no sexual size dimorphism, as measured by prepupal wet weight (Fig. 2; Table 3; $t = 1.158$, df = 26, $P = 0.257$). There is no evidence that female *H. ruthae* differentially lay male eggs in cells destined to contain male *C. pugionis* or female eggs in cells destined to contain female *C. pugionis*, because the cells of male and female *H. ruthae* larvae did not differ in diameter (Fig. 3; Table 3; $t = 0.641$, df = 11, $P = 0.534$).

Holcopasites Sex Ratio. Table 5 summarizes the data on *H. ruthae* sex ratio. Neither the numerical sex ratio nor the investment sex ratio differed significantly from the hypothesis of equal investment.

Discussion

Determinants of Parasitism Rate. Rosenheim (1990) reviewed studies on density-dependent parasitism in the solitary Hymenoptera. The majority of studies he surveyed ($n = 8$) showed a positive association between nest density and parasitism rate (direct density dependence), whereas a minority (2) showed inverse density dependence (Freeman 1981, Wcislo 1984). The results of our study fall into the latter catagory, at least at sites with detectable levels of parasitism (Fig. 1). Factors that could account for such inverse density dependence are parasite limitations and nest defense, which includes predator confusion, active group defense, selfish herding, and parasite detection (Rosenheim 1990).

Table 5. *Holcopasites* sex ratio data (sex ratio as percentage males)

Males	Females	Observed sex ratio	χ^{2a}	χ^{2b}
23	24	48.9%	0.021 NS	0.192 NS

[a] Null hypothesis is a numerical sex ratio of 1:1 (50% male).

[b] Null hypothesis is a numerical sex ratio of 51.8% males, which is the hypothesis of equal investment when prepupal wet weight is used as the measure of offspring "cost."

Parasite limitations refer to processes that limit the number of host individuals parasitized, including physiological limits on the number of mature oocytes or behavioral limits on the minimum handling time. Studies of parasitoid wasps have shown that even when adult parasite activity is concentrated in areas of highest host density, the resulting pattern of parasitism may be inversely density dependent because of parasite limitations, such as egg number (Hassell 1982). We suspect that female *H. ruthae* are not egg-limited, because, like many nomadine parasites (Alexander & Rozen 1987), females have numerous ovarioles per ovary. However, without actual data on the potential parasitism rate and oocyte numbers we cannot assess the importance of this factor.

Although we did not observe *C. pugionis* actively defending their nests, the presence of a strong lemony scent in females (and not males) suggests that chemical defense of nests is at least a possibility. Gas chromatography and mass spectroscopy of samples extracted from air around living *C. pugionis* females indicated the presence of neral, geranial, nerol, geraniol, nonanaldehyde, decanaldehyde, and dodecanaldehyde. Hefetz et al. (1982) reported neral and geranial from other *Calliopsis* species and suggested that they function as defensive chemicals.

The two "passive defense" hypotheses, predator confusion and selfish herding, seem more likely explanations in our study. Predator confusion results when the density of host individuals

and their rate of movement is high enough to make tracking individual hosts difficult. In *Calliopsis* nesting aggregations we suspect that predator confusion may result primarily from the dense clouds of males flying over the areas of high nest density. We quantified the abundance of *C. pugionis* males over nest sites by counting the number of males to fly across a 40-cm tape placed on the ground during 1 min. in areas of high nest density at Manfield Road (see Visscher & Danforth [1993] for complete data). At peak activity we counted 40–60 male crosses per minute. Male *C. pugionis* pounce on each other as well as on female *C. pugionis* and remain in copula until females enter their nests. Couples flying in copula are frequently hit by solitary males apparently trying to dislodge the male in copula, and we have seen female *H. ruthae* pounced on by male *Calliopsis*. The intensity of activity over such areas makes it difficult for a human observer to follow individual female *C. pugionis* and therefore may deter *H. ruthae,* to the extent that nest searching is based on visual tracking of female hosts. Even if nest searching is not based on visual tracking of host females, female *H. ruthae* entering regions of high nest density, and therefore high male activity, may find it difficult to search for nest entrances by flying over the ground because of frequent pouncing by male *C. pugionis*.

Selfish herding (Hamilton 1971), or taking cover from natural enemies through proximity to neighboring conspecifics, may also explain the observed pattern of inverse density dependence. Wcislo (1984) attributed the inverse density-dependent parasitism found in *Crabro cribrellifer* (Packard) (Sphecidae) to this phenomenon.

Most models of insect host-parasite relationships indicate that inverse density-dependent parasitism has a destabilizing effect on host populations (Hassell & May 1973, 1974; Hassell 1978). Such instability may be a normal component of *C. pugionis* populations, as suggested by the apparent preference for highly disturbed nesting sites such as vacant lots and railroad beds in this species. We suspect that individual populations of *C. pugionis* and *H. ruthae* are short-lived, and establishment of new nest sites may be required for long-term viability of these species.

Relationship Between Parasitism and *Calliopsis* Sex Ratio. We attempted to evaluate the hypothesis that female *C. pugionis* are more vulnerable to parasitism than males by using our data on the diameters of parasitized and unparasitized cells. Using the Monte Carlo simulations, we were unable to reject the hypothesis that male and female *Calliopsis* are equally vulnerable to parasitism, but also failed to reject the hypothesis that they are differentially vulnerable according to differences in the time spent in cell provisioning. The lack of evidence in favor of differential parasitism of the sexes suggests that the bias toward males in areas of high parasitism (Fig. 1E) may result from a facultative response on the part of female *C. pugionis*. Such a facultative response, producing an excess of the lower-cost sex in areas of highest exposure to parasites, might be selected for when there are slight differences in vulnerability and the costs associated with a male-biased brood are small.

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