Superparasitism and larval competition in conopid flies (Dipt., Conopidae), parasitizing bumblebees (Hym., Apidae)

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We have collected data on the distribution of parasitoid brood (Conopidae, Diptera) in populations of their bumblebee hosts ((Bombus, Apidae) in two localities (Huggerwald, Allschwil) in Northwestern Switzerland. Conopid flies are solitary parasitoids of aculeate hymenoptera. The larvae live endoparasitically in the abdomen of adult bees and, after completing their larval development, pupate in situ. Only one progeny per host emerges, but superparasitism, i. e. more than one brood per infested host, is now being shown to occur regularly. Bees were sampled in regular intervals throughout summer 1988 and either immediately dissected to check for the presence of parasitoid brood (eggs and larvae) or kept in the laboratory until the animal died naturally to check for the presence of a conopid puparium (successful pupation). On average, 1.78 brood per infested bee was observed at site Huggerwald (371 brood in a total of 469 bees, 209 infested), and 1.19 brood at site Allschwil (62 brood in a total of 343 bees, 53 infested); 32.3% of all bees contained parasitoid brood; in 28.5% of the cases a puparium was found after the natural death of the animal. The distribution of parasitoid brood among hosts is not different from Poisson. Prevalence of successful pupation usually equals prevalence of parasitoid brood in samples collected on the same occasion. At very high infestation intensities, however, prevalence of puparia drops as compared to brood prevalence. As a result, the percentage of killed hosts is close to a negative exponential function of infestation intensity, i. e. number of brood per average host. This kind of relationship is known from theory to enhance the stability of the host-parasitoid interaction.

INTRODUCTION

Parasitoids compete for hosts intra- and interspecifically. In contrast to predators that remove a victim from the pool of available prey, parasitoids leave parasitized hosts vulnerable for further discovery and attack. Superparasitism thus occurs when an egg is placed on a host that already contains eggs from a previous oviposition of the same or another individual. As a consequence, fitness of an individual parasitoid depends not only on discovery of a host, i. e. the effect of across-host competition (TAYLOR, 1988), but also on whether or not the encountered host is already parasitized (within-host competition).

Although parasitoids are known to be able to discriminate between parasitized and unparasitized hosts (VAN LENTEREN, 1981), superparasitism is often found in nature. Superparasitism need in fact not always be disadvantageous as long as an egg has a finite probability of survival in competition with other brood. This is likely to be the case when the availability of unparasitized hosts is low and/or discrimination costs are prohibitive (VAN ALPHEN & NELL, 1982; CHARNOV & SKINNER, 1985; PARKER & COURTNEY, 1984; IWASA *et al.*, 1984; BAKKER *et al.*, 1985).

On the other hand, competition among individual parasitoids and heterogeneity in distribution of attacks among hosts must have important consequences for the population dynamics of the host-parasite interaction (e. g. HAS-

SELL & MAY, 1983; BEDDINGTON et al., 1978; MAY, 1978; HASSELL & ANDERSON, 1984; HASSELL, 1986; CHESSON & MURDOCH, 1986; TAYLOR, 1988). However, data on superparasitism and its consequences on offspring production in field populations are scarce, despite the potential significance in evolutionary and ecological terms. Here, we report on observations of superparasitism in a host-parasitoid system that holds promise for further investigation in the field.

Conopid flies are parasitoids of other insects, usually aculeate hymenoptera, with a worldwide distribution (e. g. SMITH, 1966; ASKEW, 1971) and we are currently studying the interaction with their bumblebee hosts. Female flies oviposit on adult bumblebees that venture outside the nest while in flight or while the bee stays on a flower. To our knowledge, only one egg is inserted inside the host's abdomen upon any one attack (DE MEIJRE, 1904, 1912; ASKEW, 1971).The larva soon afterwards hatches and, passing through three successive stages, reaches pupation within some 10 days after the egg is placed (POUVREAU, 1974). The host dies before pupation (SMITH, 1966) which then takes place in situ. The fly overwinters in its puparium inside the dead host to give raise to a new generation next summer, usually in June–July.

Our previous studies have shown that the probability of a host bee to contain a conopid puparium depends on time of the year (with peak prevalences of over 50% during summer), sex (with workers more infested than males) and species (conopids mostly affect the later-season species such as *Bombus pascuorum* or *B. lapidarius*) (SCHMID-HEMPEL et al., 1989). We identified *Sicus ferrugineus* L., *Physocephala vitata* Fabr. and *Physocephala rufipes* Fabr. as the three conopid species parasitic on *Bombus* in our areas in Northwestern Switzerland (SCHMID-HEMPEL et al. 1989). Moreover, prevalence of *Physocephala* peaks somewhat later than that of *Sicus* and, consequently, *Physocephala* is more prevalent among later-season host species (and males) which are produced towards the end of the colony cycle (for a review of bumblebee biology see ALFORD, 1975).

Although it is invariably the case that only one puparium is present when the host is dissected after its death (SCHMID-HEMPEL et al., 1989), hints in the literature did suggest the possibility that more than one egg may be inserted in a host (SEVERIN, 1937; POSTNER, 1951; KNERER & ATWOOD, 1967; POUVREAU, 1974). These authors, however, seemed to accept that superparasitism is a rare phenomenon and thus not typical for the interaction between conopids and bumblebees. Here, we present data that suggest the contrary and that superparasitism may be an important and regularly occurring element of this host-parasitoid interaction.

MATERIAL AND METHODS

Host bees were sampled in regular censuses during summer 1988 (June to August) in two study areas, Huggerwald (HU, elevation 570 m) and Allschwil (AL, elevation 320 m), near Basel, Switzerland. The bees were immediately transferred to the laboratory. A first subsample was dissected to check for the presence of parasites. For this purpose, bees were freeze-killed and their abdomen opened in physiological Ringer solution under a stereo microscope. This procedure ensured that parasites were still alive and that the highly mobile and active larvae inside the body cavity could readily be detected under the microscope. Because even eggs of conopids are quite large, we are confident to here report the true occurrence of all stages within a host bee. Morphology of eggs and

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the different larval stages is given by SMITH (1966) and POUVREAU (1974). We used these sources, together with our own records, to identify the different larval instars in freshly dissected hosts. Thus, the dissected sample provided data on prevalence (i. e. percentage of hosts containing at least one brood) and infestation intensity (i. e. the number of brood per host) of parasitoid brood, i. e. eggs and larvae, in host bees at time of their capture.

The bees of the second subsample were individually kept with food ad libitum in small glass jars and their subsequent survival time measured (similar to Schmid-Hempel & Schmid-Hempel, 1988). Not until a few days after their natural death (which allows eventual larva to develop and pupate), they were dissected to check for the presence of puparia. The presence of a puparium suggests that the host must have contained parasitoid brood at time of capture in the field. Therefore, these observations provided data on the prevalence of puparia finally produced (i. e. the percentage of hosts containing a puparium when dissected after their death) and can be compared with the presence of brood at time of capture. Freshly extracted puparia were weighed with a precision balance to the nearest mg.

Conopid puparia are very conspicious and fill the entire abdomen of the host bee. Moreover, external morphology is diagnostic such that *Sicus* can be distinguished from *Physocephala*. We here discuss our results for all species of *Bombus* and the three conopid species together. Little difference in many of the ecological characteristics among the conopid species is apparent, such that for most questions, pooling data seems appropriate. At present, sample sizes would also not allow to analyze data separately for each of the host and parasitoid species.

RESULTS

In the two areas, we sampled at total of 1470 bees (1125 workers, 288 males and 34 females). With the flip of a coin, about half of them (N = 812) were selected to be checked for parasites immediately by opening the body cavity. In this subsample, 32.3% (N = 262) were found to be infested by parasitoid brood, i. e. containing at least one parasitoid egg or larva. Another N = 635 of the bees from the total sample were kept until their death to check for conopid puparia (further 23 animals yielded no data). On average, 28.5% (N = 181) of these bees contained a puparium (Tab. 1). The following host species were encountered: *Bombus terrestris, B. lucorum, B. pascuorum, B. lapidarius, B. hortorum, B. pratorum, B. humilis.*

Superparasitism

Fig. 1 summarizes the observations for sites HU and AL, respectively, during the entire summer study period. On average, we found a total of 371 brood in 209 infested host bees in HU (average intensity 1.78 brood/infested host), and 62 brood in 53 infested bees in AL (intensity 1.19 brood/host).

For further analysis, only workers are considered. Parasitoids distributed themselves among workers as shown in Fig. 1. This observed distribution was compared to the expectation from a Poisson. However, for this purpose observations from each census day had to be analyzed separately, because average infestation intensity was known to vary with season (SCHMID-HEMPEL *et al.*, 1989) and

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Table 1. Summary of observations used in this study. Bees from the pupae sample were kept in the laboratory and dissected after their natural death to check for conopid puparia, whereas the larvae sample was opened immediately (see text). Workers (W), Males (M) and females (overwintered and virigin queens, F) of all species of Bombus are summarized here. N = sample size, n = number of infected bees, k = number of brood found. Prev = 100 N/n and Int = k/n. Census days were June 12, 24, July 8, 13, 19, 26, August 2, 10, 17, 24, 31 for HU and June 13, 23, July 4, 14, 17, 25, August 3, 9, 14, 19 and 28 for AL.

	Larvae sample				Pupae sample			
	W	M	F	Total	W	M	F	Total
Huggerwald:								
N	377	76	16	469	215	36	1	252
n	181	22	6	209	106	6	1	113
k	328	24	19	371				
Prev (%)	48.0	30.0	37.5	44.6	49.3	16.7	-	44.8
Int	1.81	1.09	3.17	1.78				
Allschwil:								
N	238	100	5	343	295	76	12	383
n	39	14	0	53	54	13	1	68
k	46	16	0	62				
Prev (%)	16.4	14.0	0	15.5	18.3	17.1	8.3	19.3
Int	1.18	1.14	0	1.17				

hence would generate different expectations from a Poisson process that cannot simply be pooled. Furthermore, only data from site HU could be used in the statistics, because expected frequencies at site AL were too small. The respective X^2-values from the goodness-of-fit statistic for each period were then subsequently added (together with the degrees of freedom) to provide a test-statistics for the entire observation period (Sachs 1978, p. 285). With this procedure, we found that the distribution of parasitoids was not different from Poisson expectation (Fig. 1).

Superparasitism and prevalence of puparia

More than one conopid egg or larva may be present within a single host (Fig. 1), but at most one will eventually manage to pupate. We therefore compared prevalence of puparia (as estimated from the kept bees) with prevalence and intensity of infestation among the immediately dissected bees that were sampled on the same occasion to elucidate possible consequences for host and para-
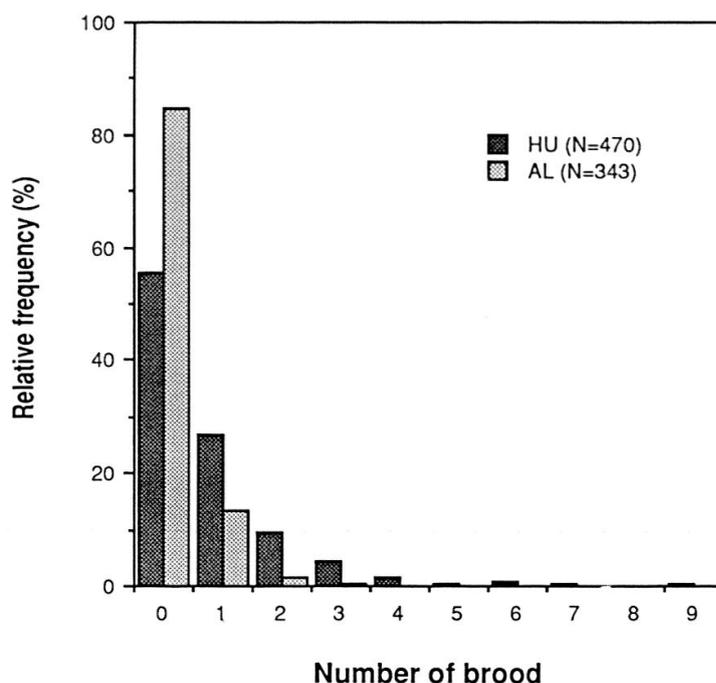
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Fig. 1. Distribution of parasitoid brood among hosts; for worker bees sampled during this study. All host and parasite species pooled. For site HU, the observed distribution of brood was compared to the expectations from a Poisson (see text). Altogether, data from 9 census days (between 7 July and 31 August; 321 brood in 175 infested hosts) could be used for this analysis. No deviation from Poisson was found ($X^2 = 21.0$, df $= 17$).

site (Fig. 2). This comparison demonstrated that the percentage of bees eventually yielding a puparium when kept in the laboratory (i. e. prevalence of puparia) corresponds to the percentage of bees containing at least one brood (brood prevalence). Deviations seem to occur at high infestations, i. e. when most bees in the population contain at least one parasite brood, such that at very high infestation levels perhaps no brood may succeed (Fig. 2). Furthermore, infestation intensity can now directly be plotted against prevalence of puparia (Fig. 3) to show what percentage of hosts will eventually be killed (and thus produce a pupa) as a function of parasite pressure.

As mentioned above, the distribution of brood among hosts follows a Poisson distribution. Note that in this case, the pattern displayed in Fig. 3 is a corollary of the data presented in Fig. 2. This follows because, under a Poisson, prevalence *(P)* of the parasite is a function of mean intensity *(q)* such that $P = 1 - e^{-q}$.

Association among larval stages

We checked the association among different developmental stages of conopid brood (eggs, first, second, and third larval instars) in individual hosts that contained exactly two broods. A similar analysis was carried out for hosts containing three or more brood, but sample size did not allow for statistical tests. The chances of finding within a single host any combination of two out of the four developmental stages of the parasite can be derived from a multinomial distribution (here with four different stages «competing» for two places in a host, regardless
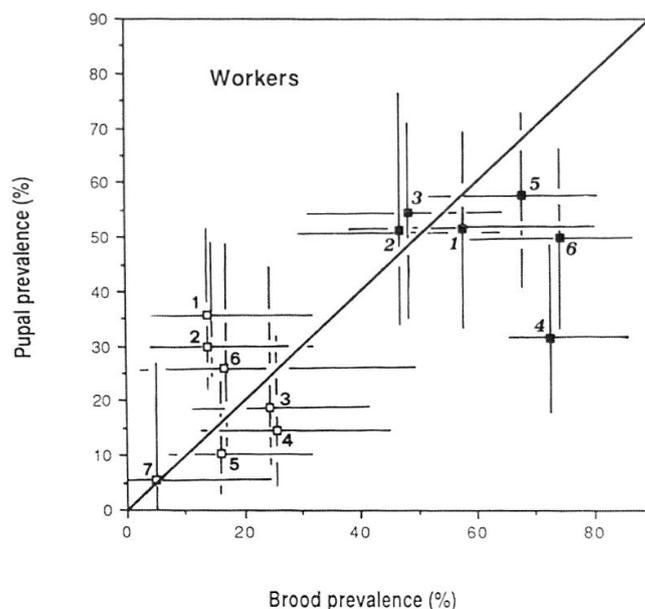
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Fig. 2. Prevalence of puparia in worker bees (ordinate) plotted against prevalence of parasitoid brood (abscissa) for sites HU (closed symbols) and AL (open symbols). Each dot is a different sampling occasion. The two prevalences were correlated (Spearman's r = 0.655, N = 13, z = 2.268, P = 0.012) and not different from one another (Wilcoxon's signed-rank test, z = 0.699, P = 0.24). A similar but non-significant correlation was found for males with r = 0.110 (N = 11, z = 0.348, P = 0.36), but also with no difference between pupal and brood prevalence present (Wilcoxon's signed-rank test, z = 1.274, P = 0.15). Bars denote 95%-confidence intervals; small figures indicate sample dates in HU: 1 (23.6.), 2 (4.7.), 3 (14.7.), 4 (25.7.), 5 (3.8.), 6 (9.8.), 7 (28.8.), and in AL: 1 (13.7.), 2 (19.7.), 3 (26.7.), 4 (2.8.), 5 (10.8.), 6 (17.8.).
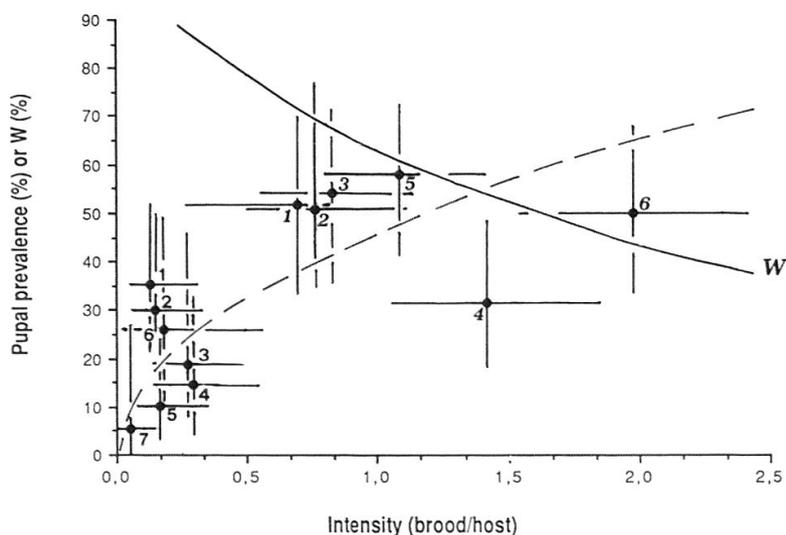

Fig. 3. Prevalence of puparia (ordinate, P, in percent) as a function of infestation intensity (average number of brood per average host, abscissa, I) for worker bees and all sampling occasions. Data were log-log transformed to give the fitted regression line $P = 45.76\ I^{0.496}$ ($r^2 = 0.595$, N = 13, P < 0.001). Bars denote 95%-confidence intervals (ordinate binomial, abscissa Poisson). Figures refer to sampling dates in site HU (italics): 1 (13.7.), 2 (19.7.), 3 (26.7.), 4 (2.8.), 5 (10.8.), 6 (17.8.) and in site AL (normal): 1 (23.6.), 2 (4.7.), 3 (14.7.), 4 (25.7.), 5 (3.8.), 6 (9.8.), 7 (28.8.). Infestation in males is generally lower, therefore, no such relationship could be established. W indicates the chances of leaving progeny (i. e. successful pupation) for a female attacking a randomly selected host as a function of average infestation intensity in the population (see text).

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of order). Such expected frequencies were then compared to observations with a chi-square test. However, no statistical deviation from random association was present (Tab. 2). But it appears from Tab. 2 that second and third larval instars are less often able to coexist, whereas younger stages (i. e. eggs with first and second instar) are more often found together than expected. This pattern is expected for biological reasons, but statistical effects may not have shown up in the data due to limited sample size.

Table 2. Observed frequencies of various combinations of the four developmental stages (egg, first, second, and third larval instar) of conopids found in hosts containing two broods only (N = 48 cases). Small numbers indicate expected relative frequencies as calculated from a multinomial distribution and random association. Expected frequencies were not different from observations (X^2 = 6.69, df = 6, P = 0.3; where cases of second and third instars are pooled). A similar picture also emerges for hosts containing more than two brood.

	Egg	First	Second	Third	Total
Egg	6	6	11	4	27
	0.118	0.097	0.090	0.039	
First	-	4	6	7	17
		0.079	0.073	0.032	
Second	-	-	4	0	4
			0.068	0.030	
Third	-	-	-	0	0
				0.013	
Total	6	10	21	11	48

Observations on life durations

Observation of residual life times for bees kept in the laboratory provided a clue to the nature of larval competition among species of conopids. Average life time for uninfested bees (values for N = 339 out of 350 workers were obtained) was 16.0 ± 15.4 days (S. D.), whereas infested ones survived for only 7.2 ± 3.0 days (N = 159; one worker without data) (t = 7.19, df = 496, P < 0.0001). A similar reduction in life time was demonstrated earlier (SCHMID-HEMPEL & SCHMID-HEMPEL, 1988) and should be indicative of a substantial mortality rate imposed by conopid flies on their host bees in the field.

However, when comparing life times of bees that had died of infestation by *Sicus* (6.4 ± 2.5 days, N = 95) with those that were containing *Physocephala* (8.3 ± 3.4 days, N = 64), a significant difference between the effect of two parasitic

genera emerged (t = 4.01, df = 157, P < 0.001), suggesting that development of *Physocephala* is slower than that of *Sicus*. At the same time, in our sample the average fresh weight of freshly extracted puparia of *Physocephala* (45.86 ± 11.59 mg, S. D., N = 59) was significantly larger than that of *Sicus* (40.12 ± 11.03 mg, N = 91) (t = 3.06, df = 148; P = 0.003).

DISCUSSION

Within-host competition among parasitic larvae as a result of oviposition decisions of the female is an important parameter in the dynamics of host-parasitoid systems (e. g. HASSELL *et al.*, 1983; TAYLOR, 1988). The results reported here suggest that one parasitoid progeny is emerging as a result of parasitic infestation of bumblebees, regardless of how many broods of conopids are present. This allows to predict the prevalence of puparia that will be found after some time (i. e. survival time in the laboratory for this study) from the prevalence of brood alone. However, this simple relationship seems not to hold under very high infestation intensities, where within-host competition may be so intense to prevent any brood from developing.

We have estimated the production of puparia in the sampled populations by keeping the bees alive in the laboratory. Since we have thus removed them from natural sources of mortality other than the parasitoids themselves and perhaps also from food stress associated with infestation, our estimates of pupal prevalence must be upper limits. Under natural circumstances, some hosts might have died after the census day before the parasite larvae could have developed further. This difference would be small, however, if parasitoids are actually the major source of mortality under field conditions.

It is not known whether conopid flies can discriminate between already parasitized or unparasitized host bees. Such discrimination seems not impossible to achieve, however. Although anecdotal evidence suggests that bees apparently behave normally until the parasite larva has reached its last stage, a reduction in pollen collecting behaviour (MÜLLER, 1988) and thermoregulatory deficiencies (HEINRICH & HEINRICH, 1983) seem to occur as a result of infestation, which could in turn be exploited by ovipositing females. Regardless of the possible existence of discriminatory processes, however, the observed outcome is a random distribution of brood among hosts (Tab. 1; Fig. 1). We could observe this pattern at both locations and over successive censuses.

Given a Poisson distribution of broods among host bees (where all parasitoid species are treated as one; Fig. 1), the chances for a female conopid of leaving progeny when attacking a randomly selected host can be estimated. With mean infestation intensity q (i. e. mean number of brood per host, see Fig. 3), the probability of attacking a host that contains k brood is $F(X=k, q)$, where the stochastic variable X is drawn from a Poisson distribution with expectation q. Because only one brood will succeed, a host shared with k other brood yields a chance of $1/(k+1)$ of succesful pupation. Therefore, upon attack in a population of bees where mean infestation intensity is q, the chances of leaving offspring from a randomly selected host can be approximated by

$$W(q) = \sum \frac{1}{(k+1)} F(X=k), \text{ where } F(X=k) = (q^k e^{-q})/k!$$

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Function W(q) can now be calculated for various infestation intensities and is shown in Fig. 3. Thus, in populations where no other females have left brood, the chances for an attacking female of leaving progeny are approximating certainty. If $q = 0.2$, this value drops to W $= 0.906$, whereas with $q = 1.5$ we calculate W $= 0.518$. Thus, non-discriminating females pay a substantial fitness cost by missing some uninfested hosts and placing their eggs into already parasitized hosts, presumably with little chances to leave a progeny. This would make sense if discrimination costs against already infested hosts were prohibitive.

Although the principal aim of this contribution was not to analyze all of the various aspects involved in the dynamics of the interacting host-parasitoid populations, the results shed some light on this issue. It is very likely that in conopids, larval competition acts mainly through depriving competitors from food by consuming the hosts resources faster than others, rather than by aggressive interference (e. g. chopping up rivals, GODFRAY, 1987). In this context, the longer survival times of bees infested by *Physocephala* may demonstrate a competitive disadvantage as compared to *Sicus,* provided that survival time of the host is indicative of the duration of development of the parasite. This hypothesis would at least partly explain why *Physocephala* is found later in the year, i. e. at a time when the occurrence of the "faster" *Sicus* declines. Furthermore, because densities of host and parasites are only imperfectly known, the results in Figs. 2 and 3 cannot readily be translated into dynamic equations of a host-parasite system. However, it is clear from Fig. 3 and the numerical examples shown above, that superparasitism in natural populations represents an important fitness cost to the parasitoids, whereas strong larval competition (and associated overcompensation at high infestation levels) should act to stabilize the interaction (e. g. TAYLOR, 1988).

In conclusion, we find that conopids are solitary parasitoids where superparasitism occurs as a function of overall parasite pressure, and which leads to severe competition among brood present in the same host bee. The natural history of bumblebees and conopids, together with our estimates of densities in the study areas (MÜLLER, 1988), additionally suggests that individual female conopids are very unlikely to attack the same individual host twice. Therefore, superparasitism should mainly affect competition among conspecific and heterospecific individuals but not among close kin.

ZUSAMMENFASSUNG

Die Verteilung von Parasitoiden (Conopidae, Diptera) in Populationen von Wirtshummeln wurde an zwei Orten in der Nordwestschweiz untersucht. Conopiden sind solitäre Parasitoiden von aculeaten Hymenopteren. Die Larven leben endoparasitisch im Abdomen adulter Bienen und verpuppen sich in situ. Nur eine Nachkommenschaft pro Wirt wird produziert, doch ist Superparasitismus, d. h. mehr als eine Parasitenbrut (Larven oder Eier), regelmässig anzutreffen. Bienen wurden in regelmässigen Abständen während des Sommers 1988 gesammelt und entweder sofort seziert, um das Vorhandensein von Parasitenbrut festzustellen, oder die Tiere wurden im Labor bis zu ihrem natürlichen

Tod gehalten, umd das Vorhandensein eines Pupariums nachzuweisen. Durchschnittlich wurden 1,78 Brut (Eier oder Larven) pro Wirtsbiene am Studienort Huggerwald festgestellt (371 Brut in 469 Bienen, 209 davon infiziert). In Allschwil waren es 1,19 pro Biene (62 Brut in 343 Bienen, 53 davon infiziert). 32,3% aller Bienen enthielten mindestens ein Ei oder Larve, 28,5% enthielten ein Puparium nach ihrem Tod im Labor. Die Verteilung der Parasitenbrut auf die Wirte entspricht einer Poissonverteilung. Die Prävalenz (d. h. Prozentsatz von Wirten mit mindestens einem Parasiten) von Puparien ist im allgemeinen gleich der Prävalenz der Brut. Nur bei hohen Befallsintensitäten ist die Puppenprävalenz kleiner als diejenige der Brut. Als Folge davon folgt der Prozentsatz der durch Conopiden getöteter Wirte einer negativ-exponentiellen Funktion der Befallsintensität (d. h. Anzahl Brut pro verfügbaren Wirt). Diese Beziehung sollte, zumindest aus theoretischen Gründen, die Stabilität der Wirt-Parasitoid-Interaktion erhöhen.

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