Predation by Predators of the House Fly in Poultry Manure: Effects of Predator Density, Feeding History, Interspecific Interference, and Field Conditions

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ABSTRACT In laboratory assays over a range of predator densities, the range in number of house fly (*Musca domestica* L.) immatures destroyed per predator per day was as follows: the histerid beetle *Carcinops pumilio* (Erichson) adults, 21-49; *C. pumilio* larvae, 13-26; the histerid *Dendrophilus xavieri* Marseul adults, 5-13; the macrochelid mite *Macrocheles muscaedomesticae* (Scopoli) females, 10-21; the macrochelid *Glyptolapsis confusa* (Foá) females, 4-10; the parasitid mite *Poecilochirus* sp. deutonymphs, 2-5; *Poecilochirus* sp. females, 2-10; and the muscid fly *Ophyra aenescens* Weidemann third instars, 7-18. Adult *C. pumilio* destroyed significantly more house fly immatures per day after 5 d of starvation ($\bar{x} = 104$) than after 5 d of feeding ($\bar{x} = 25$); starvation and feeding treatments had no significant effect on predation by *M. muscaedomesticae* and *Poecilochirus* sp. When *C. pumilio* adults, *M. muscaedomesticae* females, and *Poecilochirus* sp. deutonymphs were tested in various combinations, significant interspecific interference was observed in five of the nine combinations tested and was most pronounced in mixtures of *Poecilochirus* sp. with *C. pumilio*. In an experiment in a poultry house with naturally occurring predator populations in manure, estimated mean daily destruction of fly immatures per predator was as follows: *C. pumilio* adults, 37; *C. pumilio* larvae, 17; *M. muscaedomesticae* females, 8; and *Ophyra* larvae, 25.

KEY WORDS Insecta, house fly, predation, biocontrol

POULTRY PRODUCTION systems, especially caged-layer houses, often produce high densities of flies of economic, public health, and nuisance importance and have been the target of considerable research into the development and implementation of house fly (*Musca domestica* L.) integrated pest management programs (Axtell 1986). Naturally occurring predators in the manure are responsible for a large, although unknown, proportion of mortality of house fly immatures and are an essential component of such programs (Axtell 1970, 1981, Legner 1971, Legner et al. 1973, 1975a, Axtell & Rutz 1986). The use of predators in house fly IPM programs by conservation or augmentation requires an understanding of predator population dynamics and the environmental and biotic factors that influence their effectiveness. Predators of house flies and other filth flies have been surveyed in different types of poultry housing in various regions of the United States, especially North Carolina (Axtell 1970, Pfeiffer & Axtell 1980), California (Peck & Anderson 1969, Legner et al. 1975b), and Massachusetts (Geden & Stoffolano 1987). These studies generally have indicated that the most abundant filth fly predators in poultry manure are the histerid beetle *Carcinops pumilio* (Erichson), the macrochelid mite *Macrocheles muscaedomesticae* (Sco-

poli), the uropodid mite *Fuscuropoda vegetans* (DeGeer), and parasitid mites of the genus *Poecilochirus*.

Rates of predation by *M. muscaedomesticae* (reviewed by Axtell [1969]) and *F. vegetans* (O'Donnell & Axtell 1965, Willis & Axtell 1968) have been studied extensively under a variety of experimental conditions, with variable results. Comparatively few data are available on predation by *C. pumilio* (Peck 1969, Morgan et al. 1983) and other members of the manure-inhabiting predator community. The objectives of the present study were to use uniform experimental conditions to determine predation rates at varying predator-prey densities for the histerids *C. pumilio* and *Dendrophilus xavieri* Marseul, the macrochelid mites *M. muscaedomesticae* and *Glyptolapsis confusa* (Foá), larvae of the muscid fly *Ophyra aenescens* (Weidemann), and a parasitid mite of the genus *Poecilochirus* (Wise et al. in press); to determine the effects of starvation and interspecific competition on fly destruction by *C. pumilio*, *M. muscaedomesticae*, and *Poecilochirus* sp.; and to obtain estimates of predation rates in poultry houses for comparison with results observed in the laboratory.

Materials and Methods

Sources of Predators. Beetle and mite predators were collected in 1986 from poultry houses in Wake

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and Chatham Counties, N.C., and maintained in screen-topped 4-liter plastic pails (17 cm high by 20.5 cm diameter) filled to a depth of 10 cm with a 1:1 mixture of fresh poultry manure and prepared fly rearing medium (Ralston-Purina, St. Louis, Mo.). The moisture content of this mixture ranged from 65 to 75%. Frozen house fly eggs were added to the cultures every 2 d, and predators were transferred to fresh medium every 1–3 wk. Live rhabditid nematodes in rearing medium were also added to the mite cultures every 4 d. *Ophyra aenescens* adults were collected from a poultry house in Wake County, N.C., and were maintained in screen cages on a diet of milk and granulated sucrose. Eggs were collected from tissue paper in the milk dishes and placed in 2-liter screen-topped plastic containers with 1,000 cm³ of the substrate described above. All predator cultures were held in rearing rooms maintained at about 27°C with a photoperiod of 12:12 (L:D).

Predation Rates at Varying Predator Densities.

Predators were removed from cultures and transferred to screen-topped plastic cups (10.7 cm high; 360 ml capacity) containing 250 cm³ of 1:1 poultry manure/fly rearing medium (8 cm deep). Three to six predator density treatments were evaluated for each of the following species and life stages: *C. pumilio* females, males, and second instars (there are only two instars for this species), unsexed *D. xavieri* adults, *M. muscaedomesticae* females, *G. confusa* females, and *Poecilochirus* sp. deutonymphs and females. The precise age of the predators at the time of the experiments was not known. Predators were held without prey for 24 h, then 400–500 fresh (<4 h old) house fly eggs in about 0.7 ml water were pipetted onto the surface of the medium in each cup. In tests with *Ophyra* larvae, predator density was held constant at 10 third instars per cup and tested with four different fly egg densities: 460, 930, 1,400, and 1,800 eggs per cup. Egg numbers were estimated volumetrically, and the actual number dispensed in a given test was assumed to be the mean of five samples that were pipetted into empty plastic dishes and counted at the same time that the assay cups received eggs. Cups containing medium and fly eggs without predators were used as controls.

Cups were held for 14–20 d at 27°C, after which the adult flies were counted, and fly mortality in each cup was calculated by: $(a - b)/a$, where a is the mean number of eggs introduced and b is the number of flies that emerged. Corrected mortality (Abbott 1925) in each cup containing predators was multiplied by the mean number of eggs introduced to yield the number of flies destroyed by predators for each cup, then this fly destruction was divided by the number of predators present and by the number of days that the house fly immatures were vulnerable to predation, to yield the predation rate (fly immatures destroyed per predator per day). Based on our observations, the prey vulnerability period was about 1 d for the beetle and mite pred-

ators (only eggs and first instars are preyed upon) and 5 d for *Ophyra* larvae (all larval instars are preyed upon) under our rearing conditions. Tests were rejected and repeated when control mortality exceeded 30%.

Each test was conducted twice (at least 1 wk apart) using five cups per predator (or prey) density per test, for a total of 10 observations per treatment, plus controls. Predation rates were analyzed by two-way analysis of variance, using treatment, replication (tests 1 and 2), and treatment $\times$ replication as the grouping variables (Proc ANOVA, Statistical Analysis System [SAS Institute 1982]).

Influence of Feeding History on Predation. The influence of predator feeding history on predation rates was evaluated by extracting predators from cultures, transferring them to fresh manure-rearing medium in cups, and subjecting them to the following six feeding treatments: fed on house fly eggs for 5, 3, or 1 d in succession, or deprived of prey (starved) for 1, 3, or 5 d in succession. Beetles were preconditioned before placement on feeding-starvation treatments by either starving them for 3 d (beetles placed on feeding treatments) or feeding them for 3 d (beetles placed on starvation treatments). Predators were then transferred to assay cups (10 *C. pumilio* adults and *Poecilochirus* sp. deutonymphs and females per cup; 20 *M. muscaedomesticae* females per cup), and house fly eggs were added. Between 400 and 500 eggs were added to each cup in the mite tests. In the beetle tests, more eggs were added to each cup in the starved (starved 1 d, $\bar{x}$ = 708 eggs; 3 d, $\bar{x}$ = 968; 5 d, $\bar{x}$ = 1,189) than in the fed treatment groups ($\bar{x}$ = 514 eggs) because initial tests demonstrated that starved beetles destroyed substantially more fly immatures than fed beetles. The low egg dosage of 514 eggs per cup was used in the controls. Cups were held at 27°C (two test replications of five cups per treatment, plus controls) until the flies emerged. Predation rates were calculated as described in the previous section and analyzed by two-way ANOVA (feeding treatment, replication, treatment $\times$ replication).

Interspecific Interference. Possible competition and interference between predator species was evaluated by comparing fly destruction by *C. pumilio* adults, *M. muscaedomesticae* females, and *Poecilochirus* sp. deutonymphs alone and in various combinations. Experiments were conducted by simultaneously testing the total corrected fly destruction (corrected mortality $\times$ eggs introduced) by particular predator treatments both separately and together. Fly destructions observed in the separate predator treatments were added and compared with fly destruction by the same numbers of predators tested together. Total fly destruction was used as the unit of measurement and analysis in these experiments because the predation rate (daily fly destruction per predator) varied depending on the relative proportion of each predator in tests with mixed species. However, predation rates

were calculated as well and are presented to allow comparison with the other experiments.

The following *C. pumilio*/*M. muscaedomesticae* combinations were evaluated: 7:38 (about equal fly destruction), 20:20 (equal numbers, fly destruction by *C. pumilio* favored), and 5:147 (fly destruction by *M. muscaedomesticae* favored). Because fly destruction by *Poecilochirus* sp. deutonymphs was relatively low and predation rates decreased with increasing mite density, it was impossible to evaluate mixed-species combinations that greatly favored fly destruction by this mite without using unacceptably low numbers of the other species in the tests. For *M. muscaedomesticae*/*Poecilochirus* sp. interactions, *M. muscaedomesticae* were held constant at 20 mites per cup and tested in combinations with 10, 20, and 80 *Poecilochirus* sp. For *C. pumilio*/*Poecilochirus* sp. interactions, the following combinations were used: 5:60 (about equal fly destruction), 10:10 (equal numbers), and 5:120.

Predators were placed in assay cups as before (two test replications of five cups per treatment, plus controls) and starved for 1 d. Fresh house fly eggs then were added at dosages that were appropriate for the particular predator densities used in the tests, and cups were held at 27°C until the flies emerged. Differences between expected and observed fly destruction were analyzed using the Kruskal-Wallis test (Kruskal & Wallis 1952), a non-parametric analysis (Proc NPARIWAY of SAS [SAS Institute 1982]).

Predation Rates Under Field Conditions. An experiment was conducted in an open-sided caged-layer house in Wake County, N.C., to determine the predation rates of naturally occurring predators in poultry manure. The manure in the house had accumulated for about 2 mo and was known to contain high densities of *C. pumilio* adults and larvae, *M. muscaedomesticae* females, and lower levels of *Ophyra* sp. larvae. Manure samples (250 cm³) were scooped from the manure rows and placed in plastic dishes (6.0 cm high, 9.3 cm top diameter, 5.6 cm bottom diameter) at 0800 hours (EST). The dishes (24 on each of two test dates, 27 May and 16 June) then were returned to the same locations in the manure by pressing them back into the depressions formed when the samples were collected. About 3,000 ($\bar{x}$ = 2,960) fresh house fly eggs were added to each dish 4 h later (1200 hours [EST]). Five dishes containing an equal volume of manure that had been frozen and thawed to kill existing arthropods were used as controls on both test dates and were held inside a screen cage in the house. Dishes were left in place for 24 h, then transferred to 2.5-liter screen-topped plastic pails to exclude additional predators and prevent emigration of developing fly larvae. The manure samples were extracted through Tullgren funnels into 80% ethanol 2 d later, and the arthropods (house fly larvae and predators) present in the samples were counted. The number of flies destroyed in

each sample was calculated after adjusting for control mortality (Abbott 1925). Predator abundance and fly destruction data from the two sampling dates were pooled and subjected to multiple linear regression analysis (Proc REG of SAS [SAS Institute 1982]) using the model $Y = b_1X_1 + b_2X_2 + b_3X_3 + b_4X_4$, where Y is the number of flies destroyed and X_1 through X_4 are the numbers of *C. pumilio* adults and larvae, *M. muscaedomesticae* females, and *Ophyra* sp. larvae recovered per sample, respectively. The estimated slope parameters b_1 through b_4 therefore represent the contribution to fly destruction by the four predators, yielding field-derived daily predation rate estimates for *C. pumilio* and *M. muscaedomesticae*. For *Ophyra*, the predation rate was determined by dividing the slope estimate b_4 by three to account for the 3 d of prey vulnerability in this experiment.

Results

Predation Rates at Varying Predator Densities.

Predator density had a significant effect ($P < 0.05$) on predation rates of all predators tested (Table 1). Both males and females of *C. pumilio* destroyed 48–49 fly immatures per beetle per day at the lowest beetle density of five predators per container, and predation rates decreased to about 21 as beetle densities increased to 20. Larvae (second instars) of *C. pumilio* destroyed significantly fewer prey per predator with increasing predator density, and the predation rate was twice as high at five larvae per container (26 fly immatures destroyed per larva per day) as at 20 predator larvae per container (13). Adults of *D. xavieri* destroyed 13 flies per beetle per day at the lowest predator density (five beetles per container), and fewer (4–5) at higher densities. Females of *M. muscaedomesticae* destroyed about twice as many flies (21 fly immatures per mite per day) at the lowest density of 10 mites per container as at the higher mite densities of 30 and 40 predators per container (12 and 10, respectively). *Glyptolapsis confusa* destroyed 30–50% as many flies (4–10) as *M. muscaedomesticae* at the three mite densities that were evaluated for this species. Predation rates of *Poecilochirus* sp. deutonymphs declined from 4.8 to 1.6 over the range of densities tested (10–40). Female *Poecilochirus* destroyed about twice as many fly immatures as the deutonymphs, and predation rates were four times higher (9.8 fly immatures destroyed per mite per day) at the lowest predator density (10) than at the highest density (40 mites per container, 2.5 fly immatures per mite per day).

Ophyra larvae (not presented in a table), which were evaluated at a constant density (10 larvae) with varying prey numbers, destroyed 17.6 ± 5.3 ($n = 10$) fly immatures per predator per day when prey were abundant (1,400 and 1,800 eggs per container). At lower prey densities (460 and 930 eggs per container), predation rates were 7.1 ± 2.2

Table 1. Rates of predation on house fly immatures at varying densities of *C. pumilio*, *D. xavieri*, *M. muscaedomesticae*, *G. confusa*, and *Poecilochirus* sp.

Predator species and stage	Predator density (no. per assay cup)								F ^a	df
	0	5	10	15	20	25	30	40		
<i>C. pumilio</i> adult females										
$\bar{x}$ (SE) no. flies emerged	395.5 (16.94)	165.6 (23.21)	75.9 (19.14)	56.1 (12.28)	17.4 (4.35)	—	—	—	17.65**	3, 32
$\bar{x}$ (SE) % mortality ^b	—	55.5 (5.67)	79.9 (5.17)	84.3 (3.62)	95.3 (1.24)	—	—	—		
$\bar{x}$ (SE) predation rate ^c	—	48.8 (5.09)	35.2 (2.18)	25.0 (1.55)	21.1 (0.68)	—	—	—		
<i>C. pumilio</i> adult males										
$\bar{x}$ (SE) no. flies emerged	369.5 (16.94)	167.7 (14.63)	62.8 (15.46)	50.3 (16.31)	19.6 (3.31)	—	—	—	34.92**	3, 32
$\bar{x}$ (SE) % mortality	—	54.4 (4.19)	82.1 (4.62)	85.3 (5.00)	94.6 (0.90)	—	—	—		
$\bar{x}$ (SE) predation rate	—	48.3 (4.15)	36.7 (2.89)	25.5 (2.06)	20.9 (0.74)	—	—	—		
<i>C. pumilio</i> second-instar larvae ^d										
$\bar{x}$ (SE) no. flies emerged	379.8 (10.29)	269.0 (12.41)	200.1 (14.44)	182.6 (25.50)	158.3 (26.08)	—	—	—	9.59**	3, 32
$\bar{x}$ (SE) % mortality	—	29.2 (3.14)	47.8 (3.47)	52.5 (6.27)	59.0 (6.33)	—	—	—		
$\bar{x}$ (SE) predation rate	—	25.5 (2.74)	20.6 (1.42)	15.0 (1.63)	12.7 (1.17)	—	—	—		
<i>D. xavieri</i> adults (mixed sexes)										
$\bar{x}$ (SE) no. flies emerged	345.1 (11.50)	295.4 (11.03)	257.4 (20.54)	297.3 (14.41)	244.7 (19.19)	—	—	—	4.38**	3, 32
$\bar{x}$ (SE) % mortality	—	14.4 (2.62)	25.2 (5.78)	14.1 (2.94)	29.6 (4.56)	—	—	—		
$\bar{x}$ (SE) predation rate	—	12.6 (2.21)	11.1 (2.76)	4.0 (0.83)	5.0 (0.43)	—	—	—		
<i>M. muscaedomesticae</i> adult females										
$\bar{x}$ (SE) no. flies emerged	397.1 (19.62)	—	227.8 (26.64)	189.1 (21.95)	153.3 (33.37)	118.4 (26.12)	114.4 (25.03)	78.4 (27.51)	28.03**	5, 48
$\bar{x}$ (SE) % mortality	—	—	44.2 (4.51)	50.6 (4.75)	63.8 (6.95)	69.9 (6.17)	73.0 (5.24)	82.3 (6.11)		
$\bar{x}$ (SE) predation rate	—	—	21.3 (10.43)	16.2 (1.38)	15.4 (1.42)	13.3 (1.01)	11.8 (0.63)	10.0 (0.59)		
<i>G. confusa</i> adult females										
$\bar{x}$ (SE) no. flies emerged	316.6 (16.14)	—	240.6 (15.47)	—	246.4 (10.98)	—	225.1 (12.68)	—	7.46**	2, 24
$\bar{x}$ (SE) % mortality	—	—	23.9 (4.68)	—	21.8 (3.42)	—	28.1 (5.01)	—		
$\bar{x}$ (SE) predation rate	—	—	9.9 (1.85)	—	4.6 (0.84)	—	4.0 (0.77)	—		
<i>Poecilochirus</i> sp. deutonymphs										
$\bar{x}$ (SE) no. flies emerged	359.4 (14.58)	—	316.5 (12.42)	—	319.3 (16.43)	—	308.4 (19.31)	301.9 (18.42)	3.75*	3, 32
$\bar{x}$ (SE) % mortality	—	—	11.9 (2.72)	—	11.4 (3.07)	—	16.1 (4.45)	14.8 (3.42)		
$\bar{x}$ (SE) predation rate	—	—	4.8 (1.10)	—	2.3 (0.62)	—	2.0 (0.46)	1.6 (0.45)		
<i>Poecilochirus</i> sp. adult females										
$\bar{x}$ (SE) no. flies emerged	341.2 (12.61)	—	258.1 (8.69)	—	257.0 (8.06)	—	251.5 (7.82)	255.5 (9.98)	24.92**	3, 32
$\bar{x}$ (SE) % mortality	—	—	24.2 (2.68)	—	24.6 (2.48)	—	26.2 (2.07)	25.0 (2.89)		
$\bar{x}$ (SE) predation rate	—	—	9.8 (1.09)	—	5.0 (0.53)	—	3.6 (0.28)	2.5 (0.29)		

^a F values represent the contribution to two-way analysis of variance that can be attributed to predator density. Other terms in the ANOVA (replication and replication $\times$ predator density) were not significant and are not presented. NS, $P > 0.05$; *, $P \leq 0.05$; **, $P < 0.01$.

^b Corrected for control mortality (range, 11–23%) by Abbott's (1925) formula.

^c Number of house fly immatures destroyed per individual predator; calculated by multiplying corrected mortality by the number of fly eggs used in the tests (range, 400–500 eggs), then dividing this product by the number of predators present in the treatment.

Table 2. Influence of previous feeding history on rates of predation by *C. pumilio*, *M. muscaedomesticae*, and *Poecilochirus* sp. on house fly immatures

Predator species and stage	Predator feeding treatment							<i>F</i> ^a
	Control (no predators)	Fed 5 d	Fed 3 d	Fed 1 d	Starved 1 d	Starved 3 d	Starved 5 d	
<i>C. pumilio</i> adult (mixed sex, 10 per cup)								
$\bar{x}$ (SE) no. flies emerged	368.4 (29.33)	181.4 (22.38)	147.9 (18.95)	62.2 (15.43)	124.2 (23.83)	180.3 (26.70)	102.7 (24.80)	149.8**
$\bar{x}$ (SE) % mortality ^b	—	50.0 (3.68)	59.8 (2.65)	83.7 (3.14)	75.3 (4.30)	74.1 (2.99)	88.2 (2.37)	
$\bar{x}$ (SE) predation rate ^c	—	25.4 (2.57)	30.2 (2.13)	42.5 (3.31)	53.0 (3.03)	70.9 (4.30)	104.2 (6.03)	
<i>M. muscaedomesticae</i> adult females (20 per cup)								
$\bar{x}$ (SE) no. flies emerged	360.2 (19.13)	172.0 (23.04)	168.4 (18.60)	160.2 (14.53)	164.9 (26.82)	159.9 (20.18)	154.7 (14.53)	0.35NS
$\bar{x}$ (SE) % mortality	—	54.0 (4.07)	54.5 (2.86)	55.9 (2.65)	56.3 (5.26)	56.9 (3.73)	57.5 (3.39)	
$\bar{x}$ (SE) predation rate	—	12.2 (0.68)	12.4 (0.41)	12.8 (0.61)	12.7 (0.97)	13.0 (0.63)	13.2 (0.72)	
<i>Poecilochirus</i> sp. deutonymphs (10 per cup)								
$\bar{x}$ (SE) no. flies emerged	388.8 (21.16)	344.3 (11.23)	324.7 (9.41)	352.6 (12.79)	347.0 (10.60)	343.8 (16.67)	345.0 (8.55)	0.67NS
$\bar{x}$ (SE) % mortality	—	11.4 (2.89)	16.5 (2.42)	9.3 (3.29)	10.8 (2.73)	11.6 (4.29)	11.3 (2.20)	
$\bar{x}$ (SE) predation rate	—	4.7 (1.20)	6.8 (1.00)	3.8 (1.36)	4.4 (1.13)	4.8 (1.78)	4.7 (0.91)	
<i>Poecilochirus</i> sp. adult females (10 per cup)								
$\bar{x}$ (SE) no. flies emerged	371.5 (13.43)	295.0 (11.61)	297.0 (15.98)	290.3 (15.81)	291.0 (11.59)	280.3 (15.69)	288.5 (19.05)	0.29NS
$\bar{x}$ (SE) % mortality	—	20.5 (1.74)	20.1 (2.67)	21.8 (3.48)	21.3 (2.80)	24.7 (2.62)	22.6 (3.96)	
$\bar{x}$ (SE) predation rate	—	8.9 (0.82)	8.6 (1.08)	9.4 (1.51)	9.3 (1.33)	10.6 (1.17)	9.7 (1.60)	

^a *F* values represent the contribution to two-way analysis of variance that can be attributed to feeding treatment (df = 5, 48). Other terms in the ANOVA (replication and replication × predator density) are not presented. NS, *P* > 0.05; **, *P* < 0.01.

^b Corrected for control mortality (range, 6–30%) by Abbott's (1925) formula.

^c Number of house fly immatures destroyed per individual predator; calculated by multiplying corrected mortality by the number of fly eggs used in the test (see text for egg dosages used).

Table 3. Predation by *C. pumilio* adults, *M. muscaedomesticae* females, and *Poecilochirus* sp. deutonymphs on house fly immatures when predators were tested separately and together in different combinations

Ratio (actual nos.) predator 1/ predator 2 used per cup	Predator 1 tested separately (A)	Predator 2 tested separately (B)	A + B	Predators tested together (C)	χ^2 A + B vs C ^a
<i>C. pumilio</i> (predator 1) with <i>M. muscaedomesticae</i> (predator 2)					
7:38					
$\bar{x}$ (SE) no. flies destroyed ^b	400.1 (36.11)	449.3 (41.33)	849.4 (65.60)	777.5 (34.23)	0.98NS
$\bar{x}$ (SE) predation rate	57.2 (5.16)	11.8 (1.09)	18.9 (1.46)	17.2 (0.77)	—
20:20					
$\bar{x}$ (SE) no. flies destroyed	1,010.5 (45.34)	298.7 (21.75)	1,309.2 (60.75)	1,181.5 (69.60)	0.94NS
$\bar{x}$ (SE) predation rate	50.5 (2.27)	14.9 (1.09)	32.7 (1.52)	29.5 (1.74)	—
5:147					
$\bar{x}$ (SE) no. flies destroyed	359.4 (30.55)	1,478.9 (127.61)	1,838.3 (139.22)	1,491.5 (83.31)	4.22*
$\bar{x}$ (SE) predation rate	71.9 (6.11)	10.1 (0.87)	[12.1 (0.92)]	9.8 (0.54)	—
<i>M. muscaedomesticae</i> (predator 1) with <i>Poecilochirus</i> sp. (predator 2)					
20:10					
$\bar{x}$ (SE) no. flies destroyed	247.7 (19.88)	67.9 (12.77)	315.6 (30.21)	279.3 (17.84)	0.72NS
$\bar{x}$ (SE) predation rate	12.4 (0.99)	6.8 (1.28)	10.5 (1.01)	9.3 (0.26)	—
20:20					
$\bar{x}$ (SE) no. flies destroyed	224.4 (19.77)	75.1 (17.51)	297.5 (32.61)	285.1 (11.52)	0.10NS
$\bar{x}$ (SE) predation rate	11.1 (0.99)	3.8 (0.88)	7.4 (0.81)	7.1 (0.29)	—
20:80					
$\bar{x}$ (SE) no. flies destroyed	241.5 (22.78)	93.7 (10.94)	335.2 (24.11)	257.4 (14.01)	5.01*
$\bar{x}$ (SE) predation rate	12.1 (1.14)	1.2 (0.14)	3.4 (0.24)	2.6 (0.14)	—
<i>C. pumilio</i> (predator 1) with <i>Poecilochirus</i> sp. (predator 2)					
5:60					
$\bar{x}$ (SE) no. flies destroyed	201.6 (16.01)	180.8 (17.75)	382.4 (24.16)	210.6 (23.98)	10.32**
$\bar{x}$ (SE) predation rate	40.3 (3.20)	3.0 (0.29)	5.9 (0.37)	3.2 (0.37)	—
10:10					
$\bar{x}$ (SE) no. flies destroyed	416.8 (14.32)	67.9 (13.33)	484.7 (21.36)	322.1 (34.46)	8.87**
$\bar{x}$ (SE) predation rate	41.7 (1.43)	6.8 (1.33)	24.2 (1.07)	16.1 (1.72)	—
5:120					
$\bar{x}$ (SE) no. flies destroyed	202.9 (17.53)	98.0 (23.87)	300.9 (32.50)	152.7 (12.72)	10.45**
$\bar{x}$ (SE) predation rate	40.6 (3.51)	0.8 (0.19)	2.4 (0.26)	1.2 (0.01)	—

^a df = 1. NS, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$; Kruskal-Wallis test.^b Calculated by multiplying corrected (Abbott 1925) mortality (control mortality range, 12–25%) by the number of eggs used in the test.

and 13.1 ± 3.8 fly immatures destroyed per larva per day, respectively, although 90 and 220 flies, respectively, emerged from these low-prey-density containers (overall $\bar{x} = 13.8$).

Influence of Feeding History on Predation. Adults of *C. pumilio* destroyed significantly ($P < 0.01$) greater numbers of house fly immatures after periods of starvation than after periods of feeding (Table 2). Predation rates ranged from 25 fly immatures destroyed per predator per day among beetles fed for 5 d before testing to 104 among beetles starved for 5 d.

In contrast, no significant feeding treatment effects ($P > 0.05$) were observed for *M. muscaedomesticae* females. Predation rates after all feeding and starvation treatments fell within a narrow range (12–13 fly immatures destroyed per mite per day). Similar results were observed with *Poecilochirus* sp.; neither the deutonymphs nor the females destroyed significantly different numbers of fly immatures in response to feeding or starvation treatments.

Interspecific Interference. Results of predator interaction tests are presented in Table 3. Although fly destruction was used in the analyses, predation rates also are presented in the table to allow comparison with previous experiments. No significant interference was observed between *C. pumilio* and *M. muscaedomesticae* when there were either fewer mites than beetles or equal numbers of both, but when five beetles were tested with 147 mites, the predators together destroyed significantly ($P < 0.05$) fewer fly immatures than expected based on the sum of flies destroyed by predators tested separately. Similar results were obtained with combinations of *M. muscaedomesticae* and *Poecilochirus* sp.; significant interference was observed only when substantially more *Poecilochirus* sp. deutonymphs were present than *M. muscaedomesticae*.

Predation by combinations of *C. pumilio* with *Poecilochirus* sp. was significantly lower ($P < 0.01$) than expected in all three combinations of the beetles and mites. Observed fly destruction was 45, 34,

and 50% lower than expected in the 5:60, 10:10, and 5:120 combinations, respectively.

Visual observations of predator behavior also were made in the assay cups. Both *C. pumilio* and *M. muscaedomesticae* were relatively slow in their movements and often spent up to a minute handling an individual fly egg before destroying it, whereas *Poecilochirus* sp. deutonymphs moved very rapidly over the prey and other predators in the containers and were rarely observed feeding. When *C. pumilio* and *M. muscaedomesticae* were held together, the predators generally moved away from each other slightly after making initial contact, but this did not appear to affect substantially the foraging behavior of either. In contrast, the *Poecilochirus* sp. deutonymphs, because of their rapid and persistent movements, often caused the *C. pumilio* to drop the egg they were handling, forcing them to begin handling a new one. This effect was not observed in combinations of *Poecilochirus* sp. with *M. muscaedomesticae*.

Predation Rates Under Field Conditions. When 48 250-cm³ samples of manure under caged laying hens were inoculated with ca. 3,000 fly eggs, an average of 1,301 larvae were recovered. After correcting for control mortality (18.9%), about 1,700 fly immatures were destroyed per sample (Table 4). These samples contained an average of 22 *C. pumilio* adults, 11 *C. pumilio* larvae, 27 *M. muscaedomesticae* females, and 4 *Ophyra* third instars (mostly *O. aenescens*). No *Poecilochirus* sp., *G. confusa*, or *D. xavieri* were recovered. Estimates of field-derived daily predation rates were 37.1 fly immatures destroyed per *C. pumilio* adult, 16.9 per *C. pumilio* larva, 7.5 per *M. muscaedomesticae* female, and 25.0 per *Ophyra* sp. third-instar larva.

Discussion

The predation rates of *C. pumilio* adults in this study are in general agreement with the results of Peck (1969) and Toyama & Ikeda (1976). Morgan et al. (1983) conducted a 48-d experiment in which beetles were presented with an abundance of prey daily (150 eggs per beetle), and found that both male and female beetles consumed only about 13 fly eggs per day. This figure is somewhat lower than our lowest observed predation rate, and this may be due to the use of frozen rather than live fly eggs in their study, which eliminated the contribution to fly destruction by beetles feeding on newly hatched fly larvae.

The sexes of *C. pumilio* did not differ significantly in their predation rates. Males may require high levels of nutritional input to maintain spermatophore production (Geden 1984).

The predation rates of adult *C. pumilio* varied with changes in feeding history, with rates ranging from 25 fly immatures destroyed per predator per day among beetles fed for 5 d in succession, to 104 among beetles starved for 5 d. It is unlikely that

Table 4. Density of naturally occurring predators of house fly immatures recovered from 250-cm³ manure samples, and predation rates estimated by multiple linear regression analysis. Model $Y = b_1x_1 + b_2x_2 + b_3x_3 + b_4x_4$, where Y is the corrected fly destruction by combined predators

	$\bar{x}$ no. (SE) per 250-cm ³ sample (x_1 - x_4)	Predation rate (SE) (estimates of b_1 - b_4)
<i>C. pumilio</i> adults	21.6 (3.19) ^a	37.1 (5.54)
<i>C. pumilio</i> larvae	10.9 (2.48)	16.9 (9.90)
<i>M. muscaedomesticae</i> females	26.9 (4.05)	7.5 (5.28)
<i>Ophyra</i> sp. third instars	4.1 (1.03)	25.0 (7.06) ^b
$R^2 = 0.85, P < 0.001$		

^a $n = 24$ samples on each of two occasions. Corrected fly destruction $Y = 1,689.4 \pm 138.87$ fly immatures per sample out of 2,960.6 $\pm$ 96.78 eggs introduced. Control mortality, 18.9%.

^b *Ophyra* slope estimate was divided by three to account for the three days that house fly immatures were vulnerable to predation by these predators.

beetles in the field are sufficiently sated for such low predation rates to prevail very often, and our field experiments indicate that a rate in the low to middle range of predation potential, about 37, is a closer approximation of natural feeding. The highest rate of 104 after 5 d of starvation is also unlikely to occur in the field, because of the presence of alternative dipteran and acarine prey (Geden & Stoffolano 1987), and because beetles that are completely deprived of prey disperse from the local environment after 3-4 d of starvation (Geden et al. 1987).

There is very little information on predation by *C. pumilio* larvae. Peck (1969) observed a second instar predation rate of 27.0 (32.8 when corrected for control mortality) at five predators per container, which is close to our observed rate of 25.5 fly immatures destroyed per larva per day at this predator density. In the field experiment, where beetle larvae were present at 11 predators per 250 cm³ of manure (the same volume as in laboratory tests), a predation rate of 17 was estimated, which agrees with the laboratory-derived rate of 15 at this approximate density. Larval *C. pumilio* densities are commonly in the range of 15 to 20 per 250 cm³ in manure after long accumulation times (Geden & Stoffolano 1987), and predation at these densities is presumably lower.

Predation rates of *M. muscaedomesticae* ranged from 10 to 21 fly immatures destroyed per mite per day throughout all laboratory experiments and treatments and appeared to be most sensitive to changes in predator density. No significant predation effects attributable to feeding history were observed. Rodriguez & Wade (1961) found no consistent trend among mites subjected to two different starvation treatments on a variety of substrates. Published reports of predation rates by *M. muscaedomesticae* vary widely (reviewed by Axtell [1969]) and range from 2.3 (Singh et al. 1966) to

34.1 (Rodriguez & Wade 1961) fly immatures destroyed per mite per day. Higher rates (>10) generally have been observed in animal manure and fly rearing medium (Rodriguez & Wade 1961, Wallwork & Rodriguez 1963, Willis & Axtell 1968, Peck 1969) than on absorbent cotton and paper substrates (Axtell 1961, O'Donnell & Axtell 1965, Kinn 1966, Toyama & Ikeda 1976). There is also considerable variation depending on the type of manure or medium that is used as a substrate (Rodriguez & Wade 1961), and this may be related to the presence of chemical stimuli that elicit higher rates of prey destruction (Wallwork & Rodriguez 1963).

Estimated *M. muscaedomesticae* predation rates under field conditions were lower (7.5) than expected based on laboratory results (13.3) at comparable mite densities. Lower rates of fly destruction in simulated field settings have been reported by others (Axtell 1963a, Singh et al. 1966, Rodriguez et al. 1970); they may be caused by the presence of alternative prey. Saprophytic nematodes in animal manure are suitable prey for this mite; their presence may deflect some predation from house fly immatures (Rodriguez et al. 1962, Filipponi & di Delupis 1963, Ito 1971, 1973, 1977).

Predation by *G. confusa* ranged from 4 to 10 fly immatures per mite per day, and these rates were similar to those obtained by Axtell (1961) and Peck (1969), who observed rates of 9.9 and 7.3, respectively. Because this species is more common in horse and cow manure than in poultry manure and generally is most abundant in manure of very long accumulation times (Axtell 1963b, Rodriguez et al. 1970), it is probably of minor importance in regulating house fly populations in most caged-layer houses.

Deutonymphs of *Poecilochirus* sp. were relatively inefficient predators; their predation rate fell to barely detectable levels with increasing mite densities. Parasitids are most abundant in fresh manure and are most commonly collected in the weeks after manure cleanout (Axtell 1970). Because parasitids appear to prey mainly on newly hatched fly larvae (Wise & Axtell 1969, Ito 1971, 1977), they may complement the predatory activity of *C. pumilio* and *M. muscaedomesticae*, which primarily attack eggs (Peck 1969, Toyama & Ikeda 1976). However, our data suggest that in spite of their predatory nature, the contribution of *Poecilochirus* sp. to fly control is probably modest. Indeed, data presented in Table 3 indicate that their presence may result in a net loss of fly destruction because of interference with other predators. These mites also may have a negative impact on the population dynamics of more beneficial predators by preying on the immatures of the latter, as occurs in mixed populations of *Parasitus coleoptorum* (L.) and *Macrocheles glaber* (Müller) (Ignatowicz 1974).

Third instars of *Ophyra aenescens* destroyed between 7 and 18 house fly immatures per predator per day in the laboratory, and the field-derived

estimate of 25 is not far out of this range. Peck (1969) observed that *O. leucostoma* larvae destroyed 30.6 fly immatures per predator (about six per day) using methods similar to ours; however, this is undoubtedly an underestimate because almost no flies (0.1) emerged from the predator-treated containers in that experiment. Other reported daily predation rates of *Ophyra* are 4–7 for *O. capensis* (Olckers & Hulley 1984) and 2–20 for *O. leucostoma* (Anderson & Poorbaugh 1964).

Ophyra spp. often are very abundant in poultry houses and sometimes are the dominant muscoid fly species present (Nolan & Kissam 1985, Lysyk & Axtell 1986). Although some have proposed mass-rearing and releasing these flies for house fly control (Nolan & Kissam 1985), it remains to be established that *Ophyra* do not pose substantial public health or nuisance problems.

The arthropod community structure in poultry manure is complex, and it is difficult to make a priori judgments of fly control potential simply by counting and cataloging predator abundance. Natural rates of predation are likely to vary with temperature, house fly density, maturity and stability of the manure habitat, and with the presence and relative acceptability of alternative dipteran, acarine, and nematode prey (Geden & Axtell in press). Our laboratory and field results indicate that reasonable estimates of daily fly destruction by key predators are 30–50 and 10–20 fly immatures per *C. pumilio* adult and larva, respectively, 5–15 per *M. muscaedomesticae* female, and 10–25 per *Ophyra* sp. third instar. Our results also demonstrate that laboratory-derived rates of predation can resemble rates occurring under field conditions and can provide baseline data for future investigations into other factors that impinge on the effectiveness of predators in regulating house fly populations.

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