Predation by *Carcinops pumilio* (Coleoptera: Histeridae) and *Macrocheles muscaedomesticae* (Acarina: Macrochelidae) on the House Fly (Diptera: Muscidae): Functional Response, Effects of Temperature, and Availability of Alternative Prey

C. J. GEDEN AND R. C. AXTELL

Department of Entomology, North Carolina State University, Raleigh, North Carolina 27695

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ABSTRACT Rates of house fly, *Musca domestica* L., destruction by *Carcinops pumilio* (Erichson) adults and *Macrocheles muscaedomesticae* (Scopoli) females at two densities in a poultry manure substrate were determined at 27°C as a function of prey availability, and models based on the disk equation of Holling fit the observed data closely ($R^2 > 0.92$). Asymptotic predation rates were 54 fly immatures destroyed per predator per day for *C. pumilio* and 17 and 11 for *M. muscaedomesticae* at 5 and 20 mites per assay container, respectively. At 15 and 33°C, predation rates of *C. pumilio* were 12.3 and 82.7 per day, respectively, and those of *M. muscaedomesticae* were 5.0 and 36.3 per day, respectively. *C. pumilio* destroyed significantly fewer house flies when acarid mites (*Caloglyphus* sp.) were present as an alternative prey than when only fly immatures were present; there were no reductions in predation on the house fly in the presence of nematodes (*Diplogasteroides* sp.) or sphaerocerid (*Coproica hirtula* Rondani) immatures. *M. muscaedomesticae* destroyed significantly fewer house flies when nematodes and sphaerocerids were present than when only fly immatures were present; there was no reduction in predation on the house fly in the presence of acarid mites.

KEY WORDS Arachnida, Insecta, house fly, *Carcinops pumilio*, *Macrocheles muscaedomesticae*

ARTHROPOD PREDATORS in poultry manure can have a substantial effect in regulating populations of filth flies, and predator conservation is one of the principal goals of integrated pest management programs for house fly, *Musca domestica* L., in poultry production systems (Axtell 1986a,b). The two most important predators of house fly immatures in the United States, and probably worldwide, are the histerid beetle, *Carcinops pumilio* (Erichson), and the macrochelid mite, *Macrocheles muscaedomesticae* (Scopoli) (Axtell 1969, 1970; Peck 1969; Legner et al. 1975; Axtell 1981; Geden & Stoffolano 1987, 1988; Geden et al. 1987, 1988).

Carcinops pumilio adults and *M. muscaedomesticae* females are capable of destroying 104 and 21 house fly immatures per day, respectively, under experimental conditions where prey are not limiting; these rates are lower under conditions of predator crowding (*M. muscaedomesticae*), prior feeding (*C. pumilio*), and when other predator species are present in assay containers (Geden et al. 1988). Predation rates under field conditions are somewhat lower than in laboratory tests; this may be related to limited prey availability, abiotic factors such as temperature, and the presence of alternative prey in natural manure accumulations (Geden et al. 1988).

The objectives of the present study were to determine the relationship between house fly prey density and rates of fly destruction by *C. pumilio* adults and *M. muscaedomesticae* females (the functional response); develop models of temperature-dependent predation rates; and determine whether the presence of abundant alternative nematode, dipteran, and acarine prey reduces predation on house fly immatures.

Materials and Methods

Functional Response. The functional responses of *C. pumilio* adults (unsexed) and *M. muscaedomesticae* adult females were examined at two predator densities. The precise age of the predators could not be determined by the methods used. Predators (5 and 20 per assay cup) were transferred from stock cultures (Geden et al. 1988) to plastic cups topped with fine-mesh screen (10.7 cm high, 360-ml capacity) containing 125 cm^3 (5 cm deep, 28.3-cm^2 surface area) of a medium consisting of a 1:1 mixture of fresh poultry manure and prepared CSMA fly larva rearing medium (Ralston-Purina, St. Louis, Mo.). Predators were held in the assay cups without prey for 24 h at 27°C, then fresh (<3 h old) house fly eggs were counted and pipetted onto the medium surface in ca. 0.6 ml water; volumetric estimation methods were used to dispense eggs when more than 500 per assay cup were required (Geden

et al. 1988). Dosages used in *C. pumilio* tests were 1, 5, 10, 20, 30, 40, 50, 60, 80, and 100 eggs per beetle in tests with 20 beetles per assay cup; additional dosages of 120 and 140 eggs per beetle were used in tests with five beetles per assay cup. Dosages in *M. muscaedomesticae* tests were 1, 4, 8, 12, 16, 20, 25, 30, 40, and 60 eggs per mite. Cups containing medium and fly eggs without predators were used as controls. Additional fresh medium (175 cm^3) was added to each cup 2 d after egg introduction to promote fly larval development. Cups were then held at 27 ± 1°C for 14 to 20 d. Drying of the medium in the cups was minor because of the fine-mesh cloth tops and ca. 60% RH in the holding room. The number of flies in each cup was counted, and the predation rate (number of fly immatures destroyed per predator per day) was calculated for each cup containing predators by:

$$\text{predation rate} = \frac{E\left[\frac{(E - F)}{E} - M\right]}{(P)(T)(1 - M)} \quad (1)$$

where E is the number of fly eggs added to the assay cup, F is the number of fly adults emerged, M is the mean control mortality (as a decimal fraction) in corresponding cups with no predators, P is the number of predators present in the assay cup, and T is the effective search time (in days) of the predators, or the amount of time that house fly immatures are vulnerable to predation before larvae become too large for predators to destroy. Because both *C. pumilio* and *M. muscaedomesticae* feed on house fly eggs and newly hatched larvae, T is approximately 1 d at 27°C (Geden et al. 1988).

Tests were conducted on two separate days, at least three days apart, using five assay cups per predator density and egg dose for each predator species plus their respective controls. Data from the two assay dates were pooled, and functional response models were fit to mean predation rates using the NLIN Procedure of the Statistical Analysis System (SAS Institute 1982). For *C. pumilio* tests, parameter estimates were obtained for the disc equation of Holling (1959):

$$\frac{\text{no. fly immatures destroyed}}{} = \frac{(a')(N)(T)(P)}{[1 + (a')(Th)(N)]} \quad (2)$$

where a' is an estimate of the instantaneous attack rate, N is the number of fly eggs presented per predator, T is the fly vulnerablity period, P is the number of predators present (5 or 20), and Th is an estimate of handling time and satiation effects (Southwood 1978).

A similar model was used for *M. muscaedomesticae*, except it was necessary to adjust the model to account for predator density effects (interference). Best fit was achieved by dividing Equation 2 by P^x, where x is a coefficient of interference:

$$\frac{\text{no. fly immatures destroyed}}{} = \frac{(a')(N)(T)(P)}{[1 + (a')(Th)(N)](P^x)} \quad (3)$$

Goodness-of-fit for the models was determined by linear regression of observed with predicted predation rates by using the REG procedure of SAS (SAS Institute 1982).

Temperature-Dependent Predation Rates. *Carcinops pumilio* adults and *M. muscaedomesticae* females were placed in screen-topped assay cups (five predators per cup) containing medium as previously described, then placed in incubators maintained (±0.5°C) at 15, 21, 27, and 33°C (five cups per temperature plus five cups containing medium only). After 24 h, ca. 400 fresh house fly eggs in 0.6 ml water were pipetted onto the surface of the medium in each cup, and cups were transferred to a rearing room maintained at 27°C at the end of the fly vulnerability period, or effective predator search time (T, Equation 1–3). Assuming that $T = 1$ at 27°C, and that this represents a constant proportion of total development time at different temperatures, T at each of the four test temperatures was derived using house fly temperature-dependent development-rate data in Lysyk & Axtell (1987)—3.86, 1.89, 1.0, and 0.66 d at 15, 21, 27, and 33°C, respectively (Table 3). Cups were then held at 27°C until fly emergence, the flies in each cup were counted, and predation rates determined (Equation 1). Tests were replicated twice, at least 1 wk apart. Possible temperature effects independent of T were evaluated by calculating predation rates at $T = 1$ for all temperatures and analyzing data by two-way analysis of variance, using temperature, replication, and temperature × replication as the grouping variables (GLM procedure of SAS [SAS Institute 1982]).

Mean T-adjusted predation rates at the four temperatures were fit to the thermodynamic model of poikilotherm temperature-dependent processes of Sharpe & DeMichele (1977), using a Statistical Analysis System program designed to determine parameter estimates for the model (Wagner et al. 1984). Because no evidence was found for either high or low temperature inhibition at the temperatures tested, the two-parameter model was used:

$$\text{Predation rate at temperature } T \text{ (°C)} = \text{RH025}\frac{T + 273.15}{298.15} \cdot \exp\left[\frac{\text{HA}}{1.987}\left(\frac{1.0}{298.15} - \frac{1.0}{T + 273.15}\right)\right] \quad (4)$$

where RHO25 is the predation rate at 25°C and HA is a constant associated with a single rate-controlling enzyme (see Schoolfield et al. [1981] for a discussion of the biological significance of the parameters). Goodness-of-fit for the models was de-

Table 1. Mean (SE) predation rates (daily destruction of house fly immatures) of *C. pumilio* adults and *M. muscaedomesticae* females at different prey densities

C. pumilio			*M. muscaedomesticae*		
No. fly eggs presented per beetle	No. fly immatures destroyed per beetle at two densities		No. fly eggs presented per mite	No. fly immatures destroyed per beetle at two densities	
	5[a]	20		5	20
1	0.68 (0.103)	0.96 (0.022)	1	0.95 (0.033)	1.00 (0.000)
5	3.85 (0.305)	4.85 (0.035)	4	3.18 (0.310)	4.00 (0.005)
10	8.59 (0.434)	9.34 (0.258)	8	6.57 (0.697)	7.28 (0.175)
20	14.91 (1.403)	19.10 (0.252)	12	9.54 (0.346)	9.84 (0.401)
30	20.75 (1.925)	28.36 (1.089)	16	10.02 (0.724)	10.52 (0.491)
40	25.33 (2.193)	36.36 (1.045)	20	11.83 (0.748)	12.44 (0.776)
50	32.26 (3.890)	42.93 (2.497)	25	13.03 (1.036)	12.18 (0.905)
60	34.53 (3.127)	46.66 (3.840)	30	15.44 (0.792)	12.07 (0.711)
70	38.48 (6.978)	48.62 (3.452)	40	17.17 (0.990)	11.04 (1.570)
80	40.40 (4.154)	53.07 (3.592)	60	17.18 (2.389)	11.38 (1.687)
100	51.61 (4.871)	55.66 (3.873)			
120	56.32 (6.192)	—			
140	51.84 (4.969)	—			

[a] Number of predators per assay cup.

termined by linear regression of observed with predicted predation rates (REG procedure of SAS [SAS Institute 1982]).

Effect of Presence of Alternative Prey. Predation rates of *C. pumilio* and *M. muscaedomesticae* were determined when predators were tested with house fly eggs alone and house fly eggs plus representative nematode, dipteran, and acarine alternative prey. The prey used were a nematode in the genus *Diplogasteroides*, the sphaerocerid fly *Coproica hirtula* Rondani, and an acarid mite in the genus *Caloglyphus*. Cultures of all three prey items were established in 1986–1987 from poultry manure in Wake County, N.C. and were subsequently maintained in screen-topped plastic cups containing 250 cm^3 of the medium described previously. Nematodes were subcultured every 2–3 d by transferring ca. 10 cm^3 of nematode-rich medium from existing cultures containing 25,000–50,000 nematodes per cm^3 of medium to fresh medium. Acarid mites were subcultured weekly by transferring ca. 25 cm^3 of existing cultures containing 500–2,000 mites per cm^3 to fresh medium. Sphaerocerid flies were subcultured every 10–12 d by transferring 1,200–2,500 newly emerged adults to screen-topped 5-liter plastic pails containing 4 plastic drinking cups with 250 cm^3 of fresh medium per cup.

Predator tests were conducted by first placing predators in screen-topped plastic cups containing 125 cm^3 of medium (10 predators per cup). Predators were held in the assay cups for 24 h without prey, then house fly eggs (ca. 400 for *M. muscaedomesticae* tests, ca. 800 for *C. pumilio* tests) were added to all cups (10 cups containing predators for both predator species and 10 controls), and alternative prey were also added to half of the cups. For nematode and acarid tests, the prey inocula added were the same as those used in maintaining prey cultures (10 and 25 cm^3 of prey-rich medium, respectively). For sphaerocerid tests, 25 cm^3 of medium that had been exposed to ca. 500 adult flies for 4 d (therefore contained many larvae) was used as the alternative prey inoculum. Sample acarid and sphaerocerid inocula were extracted into alcohol using Berlese funnels and counted; these samples contained 16,314 ± 1,747 mites and 6,721 ± 1,452 sphaerocerid larvae, respectively (n = 15).

Assay cups were held at 27°C until the flies emerged, and predation rates in the presence and absence of alternative prey were calculated using the respective controls to correct for control mortality (M, Equation 1). Tests were replicated twice for a total of 10 observations per treatment (with and without alternative prey) for both predators, data from the two test replications were pooled, and differences between predation rates in the presence and absence of alternative prey were evaluated by the Kruskal-Wallis test (Kruskal & Wallis 1952), using the NPAR1WAY procedure of SAS (SAS Institute 1982).

Results and Discussion

Functional Response. No substantial predator density effects on predation were observed with *C. pumilio* adults (Table 1). Beetles destroyed 70–90% of the available fly immatures at prey/predator ratios of up to 60:1. The asymptotic predation rate (ca. 54 fly immatures destroyed per predator per day) was reached at prey/predator ratios in excess of 80:1 (Fig. 1). Parameter estimates a and Th for the disc equation model are presented in Table 2; linear regression indicated a high degree of correlation (R^2 = 0.988) between observed predation rates and those predicted by the model. *C. pumilio* predation rates have been observed to decrease with increasing predator densities (Geden et al. 1988); however this decrease was associated with declining prey/predator ratios. Predicted predation rates using the model presented here correlate well with observed rates in Geden et al. (1988).

Table 2. Parameter estimates (SE) for functional response (Equations 2 and 3) and temperature-dependent predation rate (Equation 4) models for *C. pumilio* and *M. muscaedomesticae*, and coefficients of determination (R^2) of observed predation rates vs rates predicted by the models

Model and parameter	Parameter estimate	
	C. pumilio	*M. muscaedomesticae*
Functional response		
a'	1.1729 (0.0947)	1.9727 (0.3365)
Th	0.0115 (0.0008)	0.0400 (0.0047)
x	—	0.1295 (0.0412)
R^2	0.9883	0.9236
Temp-dependent predation rates		
RHO25	35.5459 (0.6934)	14.8891 (0.4514)
HA	18,232.8653 (534.8968)	19,552.6998 (828.1046)
R^2	0.9887	0.9982

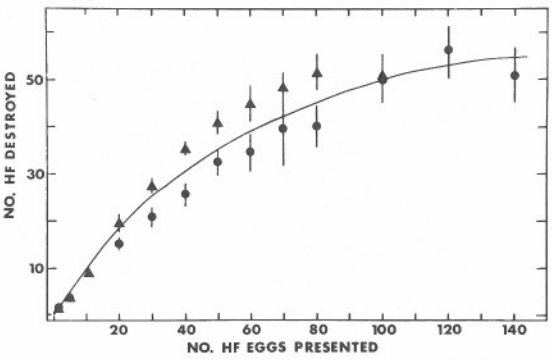

Fig. 1. Functional response of *Carcinops pumilio* adults. Model from Equation 2, parameters from Table 2; observed data (means ± SE) represented by circles (five beetles per assay cup) and triangles (20 beetles per assay cup).

Macrocheles muscaedomesticae predation rates were similar at the two mite densities tested (5 and 20 mites per assay cup) until prey/predator ratios exceeded 25:1 (Table 1). At five mites per assay cup, the asymptotic predation rate (ca. 17 fly immatures destroyed per mite per day) was not reached until prey/predator ratios exceeded 30:1; in contrast, mites at 20 per cup showed maximal predation rates (ca. 11) at prey/predator ratios greater than 12:1, indicating substantial predator interference at higher mite densities (Fig. 2). Parameter estimates of the modified disk equation for *M. muscaedomesticae* females show a high degree of correlation between observed predation rates and those predicted by the model (R^2 = 0.9236, Table 2). Interference at high mite densities was observed in a previous study, but interference effects level off above a mite density of 20 to 40 mites per assay cup; even at densities in excess of 100 per cup, the mites destroy about 10 house flies per predator per day (Geden et al. 1988). Mutual interference, in combination with mite responses to prey availability, may account for much of the variation in *M. muscaedomesticae* predation rates that have been reported (Axtell 1969). It is likely that mites in natural manure accumulations disperse into less populated regions of the habitat as mite densities approach those that result in interference with feeding behavior.

Both *C. pumilio* and *M. muscaedomesticae* exhibited the type II functional response typical of invertebrate predators and parasitoids (Holling 1959). Additional research is needed on the effects of search area on predation, especially at low prey densities, where predator confinement can obscure a sigmoid (type III) functional response (Hertlein & Thorarinsson 1987).

Temperature-Dependent Predation Rates. Fly destruction by *C. pumilio* and *M. muscaedomesticae*, independent of the duration of the fly vulnerability period (T), did not differ significantly at the four temperatures tested (Table 3). When temperature-dependent fly development rates were used to adjust T, *C. pumilio* predation rates increased from 12 to 83, and those of *M. muscaedomesticae* increased from 5 to 37 fly immatures destroyed per predator per day as temperatures increased from 15 to 33°C (Table 3). Parameter estimates for the Sharpe-DeMichele model (two-parameter) of temperature-dependent rates are presented in Table 2. The model fit the observed data well (Fig. 3) as indicated by R^2 values greater

Table 3. Mean (SE) predation by *C. pumilio* and *M. muscaedomesticae* at four constant temperatures

	Temperature (°C)			
	15	21	27	33
No. flies destroyed per predator				
C. pumilio	47.59 (6.27)	43.59 (2.50)	42.39 (4.39)	54.28 (6.88)NS[a]
M. muscaedomesticae	19.33 (2.50)	16.43 (3.03)	18.91 (2.59)	23.58 (5.20)NS
Fly development time in days[b]	50.07	24.46	12.96	8.51
Fly vulnerability period in days (T)	3.86	1.89	1.00	0.66
No. flies destroyed per predator per day (predation rate)				
C. pumilio	12.33 (3.19)	23.09 (3.39)	42.39 (4.39)	82.67 (10.47)
M. muscaedomesticae	5.01 (0.65)	8.71 (1.61)	18.91 (2.59)	36.31 (5.20)

[a] $P > 0.05$ ($F < 1.3$) for the temperature and temperature × replication (df = 3, 32) contribution to two-way ANOVA.
[b] From data in Lysyk & Axtell (1987).

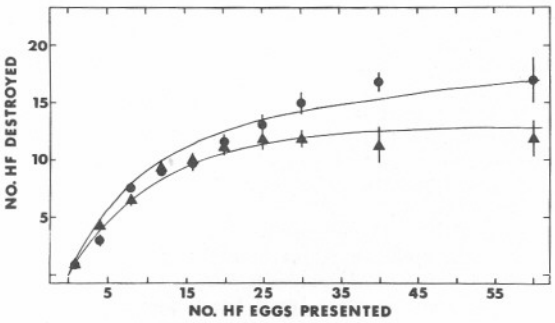

Fig. 2. Functional response of *Macrochles muscaedomesticae* females. Model from Equation 3, parameters from Table 2; observed data (means ± SE) represented by circles (five mites per assay cup) and triangles (20 mites per assay cup).

than 0.98 (observed versus predicted predation rates) for the models of both predator species.

The absence of temperature effects on net fly destruction indicates that for each incremental change in house fly development rates as a function of temperature, there was a corresponding change in predator activity, with the result that neither predator nor prey received substantial advantage over the range of temperatures normally experienced by arthropods in poultry manure.

Effect of Presence of Alternate Prey. Predation rates of *C. pumilio* were not altered significantly by the addition of high dosages of nematodes (*Diplogasteroides* sp.) or sphaerocerid (*Coproica hirtula*) larvae (Table 4). *Carcinops pumilio* adults are known to feed on *C. hirtula* immatures (Geden et al. 1987), and these results, in addition to those of Geden & Stoffolano (1988), suggest that beetles prefer house fly over sphaerocerid immatures. However, beetle predation rates were significantly lower (42.2) in the presence of acarid mites (*Caloglyphus* sp.) than when predators were tested with house fly eggs only (65.1), a reduction of 35%. *Carcinops pumilio* adults feed on acarids readily in the laboratory, and we have used starved beetles to eliminate acarids from cultures of other predators when they have become contaminated with the mites (unpublished data). Populations of acarids also are thought to be important in sustaining large predator populations in the field (Geden & Stoffolano 1987, 1988).

In contrast, predation rates of *M. muscaedomesticae* were unaffected by the presence of acarids but were 57 and 61% lower in the presence of nematodes and sphaerocerid larvae, respectively, than when mites were tested with house fly eggs alone (Table 4). Although adult female macrochelids prefer house fly eggs over nematodes (Rodriguez et al. 1962, Filipponi & Delupis 1963, Ito 1977), these results and those of Ito (1973) demonstrate that substantial predation pressure can be deflected from house fly immatures when large nematode populations are available to the mites.

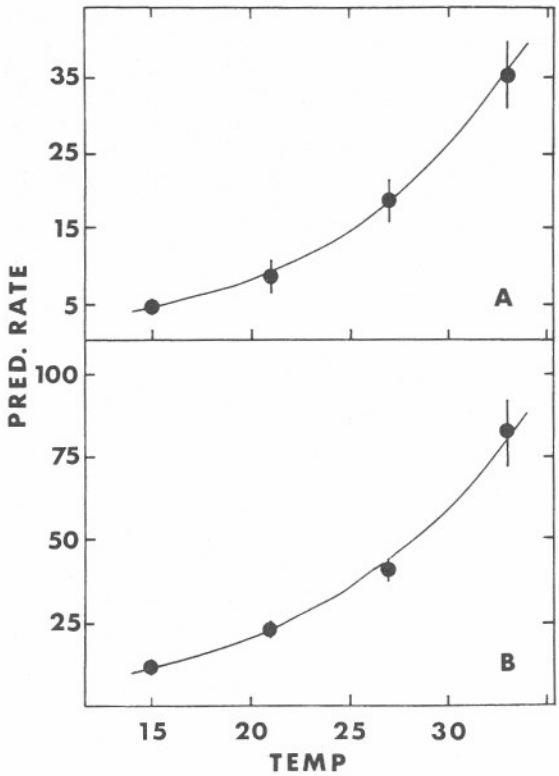

Fig. 3. Relationship between temperature and predation rates of *Macrocheles muscaedomesticae* females (A) and *Carcinops pumilio* adults (B). Model from Equation 4, parameters from Table 2; observed data (means ± SE) represented by circles.

In summary, rates of house fly destruction by *C. pumilio* and *M. muscaedomesticae* are tempered by house fly density, predator density (*M. muscaedomesticae*), and the presence and quality of alternative food items in the environment. On balance, the benefits for fly control provided by populations of alternative prey (arthropod community stability, promoting predator populations in the

Table 4. Mean (SE) predation rates of *C. pumilio* and *M. muscaedomesticae* tested in the presence and absence of alternative nematode (*Diplogasteroides* sp.), dipteran (*Coproica hirtula*) larvae, and acarine (*Caloglyphus* sp.) prey

Predator and alternative prey	Predation rate		Chi-square[a]
	With alt. prey	Without alt. prey	
C. pumilio &			
Nematodes	72.6 (4.36)	62.4 (2.49)	3.29NS
Sphaerocerids	49.9 (5.88)	48.3 (3.20)	1.85NS
Acarids	42.2 (4.76)	65.1 (7.74)	6.61*
M. muscaedomesticae &			
Nematodes	7.5 (3.38)	17.5 (2.33)	4.81*
Sphaerocerids	4.0 (3.12)	10.3 (1.47)	4.48*
Acarids	7.0 (1.50)	9.6 (1.14)	1.65NS

[a] *, $P < 0.05$; NS, $P > 0.05$ (Kruskal-Wallis test, df = 1).

absence of house fly) probably outweigh the reductions in rates of fly destruction by predators in the presence of these other food items.

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