

# Spatio-Temporal Dynamics of Resident and Immigrating Populations of *Carcinops pumilio* (Coleoptera: Histeridae) in High-Rise Poultry Facilities

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**ABSTRACT** The histerid beetle *Carcinops pumilio* (Erichson) is an important natural predator of the house fly, *Musca domestica* L., in accumulated poultry house manure. We examined the spatio-temporal dynamics of establishing adult *C. pumilio* in high-rise poultry facilities using conventional and geostatistical approaches. The growth curves of resident and immigrating populations followed logistic and exponential equations, respectively, and their rates of establishment were statistically the same. Frequency distributions for both populations were strongly positively skewed, and  $\approx 53\%$  of sampling intervals were significantly modeled by the negative binomial. Taylor's power law indicated both populations to be aggregated, and gave excellent least squares regression fits to both populations. Correlograms, a geostatistical tool, suggested little local spatial structure (e.g., 2nd order effects) for either population. The resident population was 'randomly' aggregated: beetles were clustered around randomly distributed aggregations of house fly immatures. The immigrating population exhibited significant spatial trends (e.g., 1st order effects) consistently seen at all sampling intervals. *C. pumilio* spatial structure was represented primarily by this spatial trend; thus, immigration of *C. pumilio* may have been either a singular event in time, or initiating at 1 or multiple times from a singular location.

**KEY WORDS** *Carcinops pumilio*, Histeridae, spatial and temporal dynamics, geostatistics

*Carcinops pumilio* (ERICHSON) is a naturally occurring predator of house fly, *Musca domestica* L., eggs and early instars in confined high-rise poultry house manure. Its association with poultry manure was first described by Peck (1969) and Peck and Anderson (1969). Since then, much work has focused on its value as a biological control agent of house flies, which breed rapidly in poultry house manure. Geden and Axtell (1988) and Geden et al. (1988) examined the predatory capacity of *C. pumilio* at varying densities of both predator and prey, and reported that at low predator densities (e.g., 5 adults per 250 cm<sup>3</sup> medium), up to 54 fly immatures were destroyed per beetle per day. Geden and Stoffolano (1988) studied dispersion patterns of *C. pumilio* in accumulated manure and reported that *C. pumilio* adults were most common at the crest of the manure mound relative to any other location. Geden et al. (1987) and Geden (1990) also suggested a mechanism for poultry facility-to-facility dispersal by demonstrating that adults were positively phototactic and engaged in flight when food sources were depleted because of, for example, overcrowding.

Efforts to commercially produce *C. pumilio* have been unsuccessful, and deliberate introduction of adults from other facilities is not practical because adults have been observed to serve as a reservoir for *Salmonella enteritidis* (Gaertner) (Eubacteriales: Enterobacteriaceae) under laboratory conditions (Gray

et al. 1999). Because of the effectiveness of *C. pumilio* as a biological control agent, successful and economical house fly control is greatly enhanced by an insight into both the rate of *C. pumilio* establishment and the spatial pattern of this establishment.

Temporal and spatial patterns of observed insect densities have been modeled with conventional approaches (nonlinear modeling of mean densities, fitting of frequency distributions, and estimation of dispersion indices) and geostatistics, the latter of which are receiving more attention among ecologists (Robertson 1987, Legendre and Fortin 1989, Rossi et al. 1992, Williams et al. 1992, Real and McElhany 1996, Sharov et al. 1996). The theoretical basis for geostatistics was developed by mining engineers to estimate locations of rich gold deposits from known quantities derived from samples separated by a given distance and direction in a vector. The theory is based on the notion that the degree of correlation among samples can be described as a function of distance, so that 2 data that are close to each other in space are more likely to have similar values than 2 data that are farther apart (Isaaks and Srivastava 1989). In geostatistics, actual spatial coordinates are considered so that spatial distributions are explicitly analyzed, whereas conventional approaches, such as frequency distribution analyses and dispersion indices, rely on mean-to-variance relationships and do not consider the location in

space of the sample estimates (Williams et al. 1992). We investigated the spatial distribution of resident and immigrating populations of adult *C. pumilio* using both conventional approaches, such as frequency distribution analyses and dispersion indices, and geostatistical approaches. We also present empirical models on the temporal dynamics of both populations.

### Materials and Methods

**Sampling Regime.** Two high-rise poultry facilities in central Pennsylvania were chosen for this study. Both were 2-storied, with the top story containing egg-laying hens, and the bottom story, or the pit, containing accumulating hen manure. Manure accumulated in 6 rows running lengthwise, and each row was separated by 0.5–1.5 m walkways. The 1st facility (e.g., house 1) was 79.2 m long by 13.9 m wide and contained  $\approx 60,000$  HyLine W36 hens. The 2nd facility (e.g., house 2) was 159.4 by 16.6 m and contained  $\approx 108,000$  HyLine W36 hens. Both facilities were closed, and indoor temperatures (20–24°C) were regulated by fans located at evenly spaced intervals on both lengths of the facility. The fans were especially important because they were the primary ports of entry and egress for *C. pumilio*. The pit of house 1 was divided into 9 quadrats (106.3 m<sup>2</sup> each), and in house 2, the pit was divided into 9 quadrats (275.6 m<sup>2</sup> each).

At house 1, samples were taken weekly for the first 8 wk, and biweekly for the next 10 wk. Twelve samples from each quadrat were extracted at each sampling interval ( $N = 108$ ). Sampling points were arranged in a systematic square grid within the quadrat, and were spatially referenced with respect to one corner of the facility. Sampling began 5 d after manure clean-out, although clean-out was not complete and  $\approx 5\%$  of the manure volume, accumulated over  $\approx 10$  mo, was left in the facility. Sampling began on 25 November 1996, when outside weather conditions in central Pennsylvania, where monthly mean temperatures (November 1996 to March 1997) were consistently  $< 5^\circ\text{C}$  (National Weather Service 1998), negated immigration. Because of the extent of the manure clean-out and weather conditions, *C. pumilio* in house 1 was considered a resident population.

At house 2, samples were taken weekly for 10 wk, with 18 samples extracted from each quadrat at each interval ( $N = 162$ ). Sampling points were likewise spatially referenced but were hexagonally arranged within each quadrat. Sampling began 90 d after manure clean-out on 3 April 1997, and the manure was not only completely removed, but the pit was chemically sterilized after clean-out to reduce the risk of flock-to-flock disease transmission. Mean monthly temperatures for central Pennsylvania during April, May, and June 1997 were 10.6, 15.3, and 21.9°C, respectively (National Weather Service 1998). Because of the extent of the manure clean-out, *C. pumilio* in house 2 was deemed an immigrating population.

Manure samples were collected at sampling points with a trowel, placed into self-sealing plastic bags, and sealed. Samples were weighed, and generally ranged

from 100 to 200 g. Adult *C. pumilio* were separated from manure solids using a sucrose flotation method (Tobin and Pitts 1999). Moisture subsamples were taken from manure samples, and water content was measured by the oven-dry method (Tobin 1997). Counts of *C. pumilio* were expressed as numbers of adult beetles per 200 g of dry manure matter. To gain an understanding of their relative density with respect to the house fly population, 3rd-instar house flies were also extracted from each manure sample through flotation, counted, and expressed as larvae per 200 g of dry manure matter.

**Temporal Dynamics of *C. pumilio*.** The respective mean densities of both resident and immigrating *C. pumilio* per sampling interval were modeled using nonlinear regression (PROC NLIN, SAS Institute 1990). Scatterplots of the data suggested the appropriateness of 2 models: logistic and exponential. The former is

$$N_t = \frac{K}{\left(1 + \frac{(K - N_o)}{N_o e^{rt}}\right)}, \quad [1]$$

where  $N_t$  is an estimate of the density at time  $t$  (d),  $K$  is the carrying capacity,  $N_o$  is the initial density,  $r$  is a growth parameter or intrinsic rate of increase (Hastings 1997), and  $t$  is the time since manure clean-out. The exponential model is

$$N_t = N_o e^{rt}. \quad [2]$$

To compare growth rates during the log phase of exponential growth, we subset the data by removing sampling intervals with a mean of 0 ( $N = 5$  in house 1 and 1 in house 2). The remaining means ( $N = 8$  in house 1 and 9 in house 2) were transformed using  $\log_{10}$  to linearize the response (Sokal and Rohlf 1995), and tested, using type III sum of squares, for intercept and slope homogeneity between the 2 populations using time, population (resident or immigrating), and a time  $\times$  population interaction as independent variables (PROC GLM, SAS Institute 1990).

**Spatial Dynamics of *C. pumilio*.** The negative binomial distribution (Anscombe 1949) was used to model the frequency distribution, and Taylor's power law (Taylor 1961) to model the variance-to-mean relationship of *C. pumilio*. These were viewed as conventional approaches to infer spatial aggregation of adult beetles, and developed to provide estimates for sampling plans. The means and variances from each population and sampling interval were used to calculate moment estimates of  $k$  of the negative binomial distribution,

$$k = \frac{m^2}{(s^2 - m)}, \quad [3]$$

in which  $s^2$  and  $m$  are respective estimates of the variance and mean. Estimates of  $k$  from equation 3 were used as reference values in maximum-likelihood equations (Elliott 1977). The range of counts for each sampling interval was divided into 20 discrete categories, and agreement with the negative binomial dis-

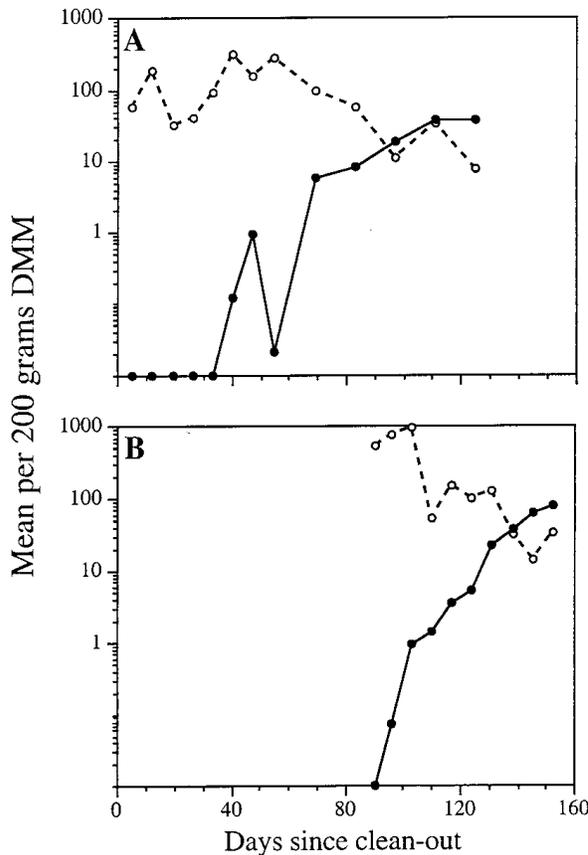


Fig. 1. Temporal dynamics of *C. pumilio* adults (solid circles and line) with respect to 3rd-instar house flies (open circle and dashed line) in resident (A) and immigrating (B) populations: mean number per 200 g dry manure matter (DMM) on a logarithmic scale ( $N = 108$  and  $162$  for [A] and [B], respectively).

tribution was analyzed using the chi-square statistic (Elliott 1977).

Taylor's power law is described by

$$\log s^2 = a + b \log m, \quad [4]$$

where  $a$  and  $b$  are regression parameters (Taylor 1961). Means and variances for each of the 9 quadrats at each sampling interval were pooled, transformed using  $\log_{10}(Z+1)$ , and analyzed by a least squares regression of the  $\log_{10}$  of the sample variance on the  $\log_{10}$  of the sample mean (PROC GLM, SAS Institute 1990). The parameters  $a$  and  $b$  were estimated by the intercept and slope coefficients, respectively, from the regression equation (Elliott 1977).

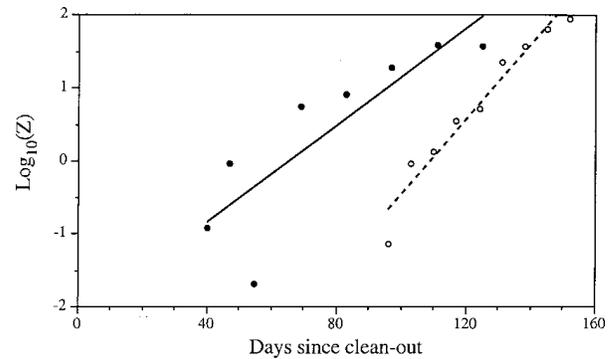


Fig. 2. Test of slope homogeneity between the rate of *C. pumilio* adult establishment for resident (solid circles and line) and immigrating (open circles and dashed line) populations. Slopes of both regression lines are statistically the same ( $F = 2.54$ ,  $P = 0.1347$ ).

For geostatistical analyses, the distributions of *C. pumilio* were log-normal, and thus sample densities were transformed using  $\log_{10}(Z+1)$  (Sokal and Rohlf 1995). We subjected data from the last 5 sampling intervals for each population to omnidirectional spatial analyses using  $S^+$  (Mathsoft 1996). Other sampling intervals were not analyzed because of the low number of adult *C. pumilio* present. The correlation function, or correlogram ( $\rho_h$ ), which measures the relationship between the density of pairs of samples at each distance,  $h$ , separating samples (Isaaks and Srivastava 1989), was used to investigate *C. pumilio* spatial structure. It is expressed as

$$\rho_h = \frac{C_h}{s_{-h} + s_{+h}}, \quad [5]$$

in which  $s_{-h}$  and  $s_{+h}$  are the respective standard deviations of the tail and head values of the vector  $h$ . The covariance function,  $C_h$ , is

$$C_h = \frac{1}{N_{(h)}} \sum_{(i,j) | h_{ij}=h}^{N_{(h)}} (v_i v_j - m_{-h} m_{+h}), \quad [6]$$

where  $N_{(h)}$  is the number of pairs in the vector  $h$ ,  $v_i$  is a value at location  $i$ ,  $v_j$  is a value  $h$  distance from  $v_i$ , and  $m_{-h}$  and  $m_{+h}$  are the respective means of the tail and head values of the vector  $h$ . (Isaaks and Srivastava 1989, Sharov et al. 1996). The correlogram was used as a measure of 1st and 2nd order effects in the spatial structure of resident and immigrating *C. pumilio*. First order effects refer to variations in the mean value of a spatial process, such as global or large-scale trends.

Table 1. Nonlinear regression models and parameter estimates of the growth curves for resident and immigrating *C. pumilio* populations

Population	Model	Parameter estimates (SE)			$R^2$
		$A$	$N_0$	$r$	
Resident	L	42.115 (2.931)*	0.001 (0.003)NS	0.107 (0.020)*	0.98
Resident	E	—	0.707 (0.411)NS	0.033 (0.005)*	0.91
Immigrating	E	—	0.002 (0.002)NS	0.071 (0.001)*	0.98

NS, Not significant; \*,  $P < 0.05$ ;  $H_0$ : parameter = 0. L, logistic (equation 1); E, exponential (equation 2).

**Table 2.** Ranges of the aggregation index,  $k$ , for *C. pumilio* adults for each population and the percent acceptance under the negative binomial distribution

Population	Range of $k^a$	% acceptance of $H_0$
Resident	0.12–5.23	62.5
Immigrating	0.04–1.88	44.4

$H_0$ : negative binomial distribution is appropriate. Percent acceptance was calculated by the percentage of sampling intervals in which  $\chi^{2*} \leq \chi^{2_{0.05}(N-3)}$ .

<sup>a</sup> Values of  $k$  were determined by the proportion of 2 reference values calculated by maximum likelihood equations (Elliott 1977).

Spatial trends can be represented by linear, nonhorizontal correlogram behavior (Rossi et al. 1992). Second order effects result from local spatial correlation structure, such as the tendency for deviations in values from the mean to be similar to those deviations in neighboring sites (Bailey and Gatrell 1995). These effects are represented by nonlinear correlogram behavior, in which correlogram values approach an asymptote over increasing lag distance.

In all spatial analyses, we used a 4 m lag separation distance with a 2 m tolerance. Resulting correlogram values were modeled with either a nonlinear exponential model (using PROC NLIN) or linear model (using PROC GLM) in SAS (SAS Institute 1990). The former was defined by

$$\rho_h = C e^{(-3h/A)}, \quad [7]$$

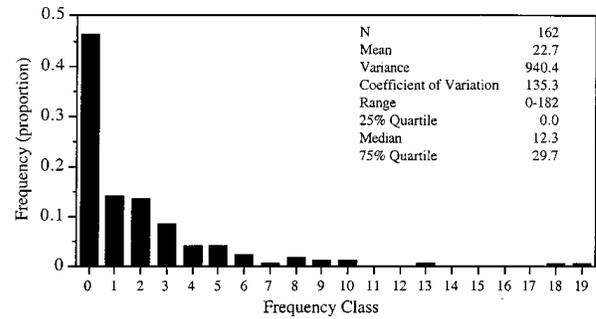
where  $C$  is an estimate of the correlation between samples separated by small distances and  $A$  is an estimate of the range of spatial continuity (e.g., the lag distance,  $h$ , at which the correlogram is 95% of the asymptote). The linear model was defined by

$$\rho_h = \beta_0 + \beta_1 h, \quad [8]$$

where  $\beta_0$  and  $\beta_1$  are estimates of the intercept and slope, respectively. When the analyses suggested the presence of spatial trends in the data (e.g., linear, nonhorizontal correlogram values over increasing lag distance [Rossi et al. 1992]), the trend was removed by fitting the  $\log_{10}(Z+1)$ -transformed counts with the multifactor polynomial model,

$$\log_{10}(Z_i+1) = \beta_0 + \beta_1 X_i + \beta_2 Y_i + \beta_3 X_i Y_i + \beta_4 X_i^2 + \beta_5 Y_i^2, \quad [9]$$

where  $X$  and  $Y$  are the  $x$  and  $y$  coordinates (m), respectively. Stepwise regression was used to maximize  $R^2$  (PROC REG, SAS Institute 1990), and regression residuals were obtained from each trend model and resubjected to omnidirectional spatial analyses to assess spatial structure in the detrended data (Sharov et al. 1996). The trend itself was modeled for appropriate sampling intervals by fitting polynomial regression models to the means of the  $\log_{10}(Z+1)$ -transformed counts per quadrat (PROC GLM, SAS Institute 1990). Voucher specimens for this project have been deposited in the Frost Entomological Museum, The Pennsylvania State University, University Park, PA.

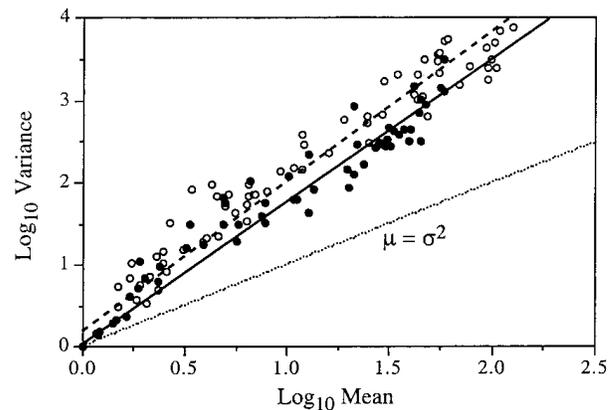


**Fig. 3.** Example frequency histogram and summary statistics for an immigrating population of *C. pumilio* at day 131. Distribution yielded a value of the negative binomial  $k$  of 0.56 and a  $\chi^{2*}$  of 13.82 (compared with  $\chi^{2}_{0.05,9} = 16.92$ ).

## Results

Temporal dynamics of *C. pumilio* with respect to 3rd-instar house flies for both populations are shown in Fig. 1, and this temporal relationship is typical of house fly-*C. pumilio* interactions in poultry house manure (Wilhoit et al. 1991). The logistic model gave a higher  $R^2$  than the exponential model for the resident population (0.98–0.91), and the exponential model was strongly applicable to the immigrating population (Table 1). The last 5 sampling intervals from each facility are somewhat consistent with each other in terms of *C. pumilio* density. For these intervals, mean numbers of resident and immigrating *C. pumilio* per 200 g of dry manure matter ranged from 5.8 to 38.9 and 5.3 to 82.4, respectively. Population growth curve rates, estimated by  $r$  (equations 1 and 2), for resident and immigrating *C. pumilio* ranged from 0.07 to 0.11 (Table 1).

We are confident in labeling the *C. pumilio* population in house 2 as immigrating because no beetles



**Fig. 4.** Taylor's power law calculation for number of *C. pumilio* adults per 200 g dry manure matter. Resident population is represented by solid circles and line, immigrating by open circles and dashed line. The finely dashed line shows the variance equal to the mean (i.e., random dispersion). Resident:  $\log_{10} \text{variance} = 0.05 (\pm 0.02) + 1.74 (\pm 0.03) \cdot \log_{10} \text{mean}$ ;  $N = 117$ ,  $R^2 = 0.97$ . Immigrating:  $\log_{10} \text{variance} = 0.19 (\pm 0.04) + 1.83 (\pm 0.04) \cdot \log_{10} \text{mean}$ ;  $N = 90$ ,  $R^2 = 0.96$ .

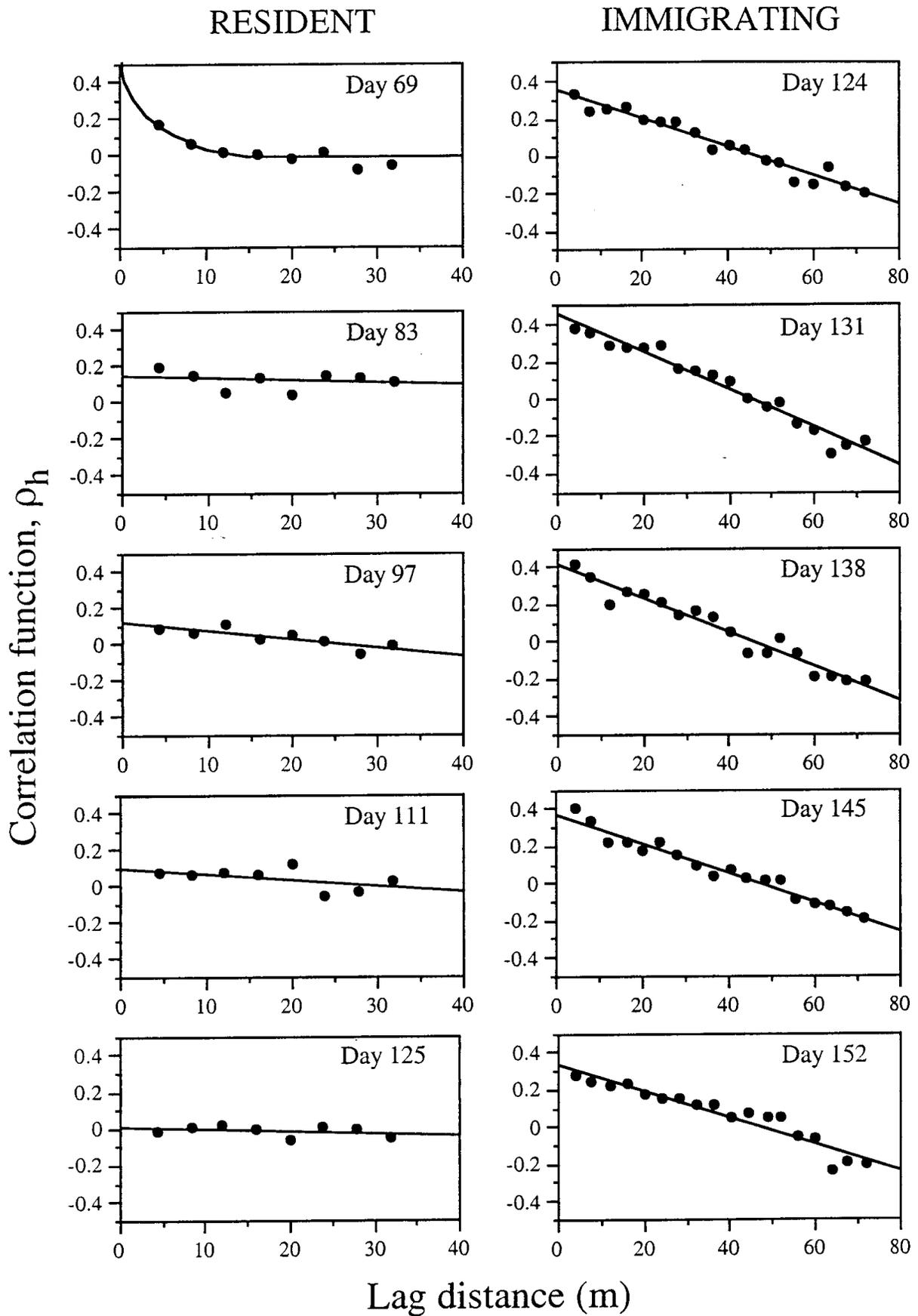


Fig. 5. Plots of the correlogram,  $\rho_h$ , for resident and immigrating populations of *C. pumilio*.

**Table 3.** Correlogram models, parameters, and  $R^2$  values for resident and immigrating populations of *C. pumilio*

Population	Day <sup>a</sup>	Model	Parameter estimates (SE)		$R^2$
			$\beta_0$ or $C$	$\beta_1$ or $A$	
Resident	69	E	0.555 (0.446)*	10.670 (6.089)*	0.74
	83	L	0.140 (0.041)*	-0.001 (0.002)NS	0.05
	97	L	0.118 (0.026)*	-0.005 (0.001)*	0.69
	111	L	0.102 (0.040)*	-0.003 (0.002)NS	0.33
	125	L	0.008 (0.023)NS	-0.001 (0.001)NS	0.15
Immigrating	124	L	0.352 (0.018)**	-0.008 (0.001)**	0.95
	131	L	0.458 (0.022)**	-0.010 (0.001)**	0.96
	138	L	0.415 (0.023)**	-0.009 (0.001)**	0.95
	145	L	0.372 (0.017)**	-0.008 (0.001)**	0.96
	152	L	0.336 (0.024)**	-0.007 (0.001)**	0.91

NS, not significant; \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ;  $H_0$ : parameter = 0. E, exponential (equation 7); L, linear (equation 8).

<sup>a</sup> Days since manure cleanout.

were recovered from 162 samples at day 90 (e.g., 90 d after clean-out; 4 April 1997), and that only 5 adults were recovered at day 96. The appearance of *C. pumilio* in house 2 corresponded well with warmer outdoor temperatures that allowed immigration. In contrast, in house 1, where  $\approx 5\%$  of the manure was left after clean-out and outdoor winter temperatures negated immigration, *C. pumilio* adults were first recovered at day 40 (30 December 1996). By day 97, the population of *C. pumilio* adults had exceeded that of the 3rd-instar house flies in house 1 (Fig. 1).

The GLM model testing intercept and slope homogeneity of *C. pumilio* establishment between the 2 populations showed significant differences in intercepts ( $F = 7.04$ ,  $P = 0.0199$ ), but not in slopes ( $F = 2.54$ ,  $P = 0.1347$ ) (Fig. 2). The respective estimates ( $\pm$ SE) of the intercept for resident and immigrating populations were  $-2.16 (\pm 0.71)$  and  $-5.57 (\pm 0.59)$ , whereas the estimate of the common slope was  $0.024 (\pm 0.006)$ .

The negative binomial frequency distribution was appropriate for  $\approx 53\%$  of all sampling intervals (Table 2). Five of 8 (62.5%) sampling intervals from the resident population were significantly modeled by the negative binomial, and 4 of 9 (44.4%) sampling intervals from the immigrating population were significantly modeled ( $P < 0.05$ ). All histograms were strongly positively skewed, and almost all frequency distributions contained some proportion, usually small, of observed values in higher frequency classes (Fig. 3).

Taylor's power law provided a good least squares regression fit to the data from each population (Fig. 4). Variances were consistently greater than the means, implying that *C. pumilio* adults were aggregated in their spatial distribution on a quadrat level. The respective estimates ( $\pm$ SE) of Taylor's  $b$  (equation 4) for the resident and immigrating population were  $1.74 (\pm 0.03)$  and  $1.83 (\pm 0.04)$ .

Plots of the behavior of the correlogram,  $\rho_h$ , over increasing lag distance,  $h$ , for the last 5 sampling intervals of each population are shown in Fig. 5. Some degree of spatial structure was observed in the resident population at day 69, and the correlogram was modeled with an exponential model (equation 7). All other correlograms for both populations were mod-

eled with the linear model (equation 8), and estimates of each model's parameters and resulting  $R^2$  values are listed in Table 3.

In the resident population, while 4 of 5 correlograms were modeled with a linear model, only 1 of these yielded a significant estimate of the slope ( $P < 0.05$ ;  $H_0$ : parameter estimate = 0; Table 3). In contrast, all 5 correlograms from the immigrating population were modeled with a linear model, and all intercept and slope estimates were highly significant ( $P < 0.01$ ; Table 3). Thus, the data from these 5 were detrended and resubjected to omnidirectional spatial analysis.

The plots of correlogram behavior for the immigrating *C. pumilio* population after removing the spatial trend are shown in Fig. 6. All plots were represented by a linear, horizontal correlogram behavior, and none of their respective intercept or slope estimates was significantly different from 0 ( $P > 0.05$ ).

The spatial trend model of immigrating *C. pumilio* is represented in Fig. 7 and is shown only as a function of the length of the facility (e.g., the  $x$  coordinate). This is a result of the geometry of a poultry house, which is only 16.6 m wide yet 159.8 m long, and of the fact that manure rows were continuous lengthwise in the facility, whereas in the  $y$  plane, manure rows were separated by concrete walkways. Also, when decomposing the sum of squares from equation 9, the majority (64–72%) of variation for each sampling interval was partitioned to the  $x$  coordinate. In contrast, 20–30% was partitioned to the  $y$  coordinate, and 4–15% to the  $xy$  interaction. For each of these sampling intervals, a 3rd order polynomial model provided the best fit based on  $R^2$ , the values of which ranged from 0.91 to 0.96 (Fig. 7). The trend models showed a consistently high concentration of *C. pumilio* in 1 section of the manure pit, with a gradual leveling off of the polynomial curves over time as the overall *C. pumilio* density increased. Further analyses of the trend also revealed an edge effect, in that higher densities in the  $y$  plane were observed near one of the outer walls.

## Discussion

This research provides a basis for understanding the spatio-temporal dynamics of establishing *C. pumilio*.

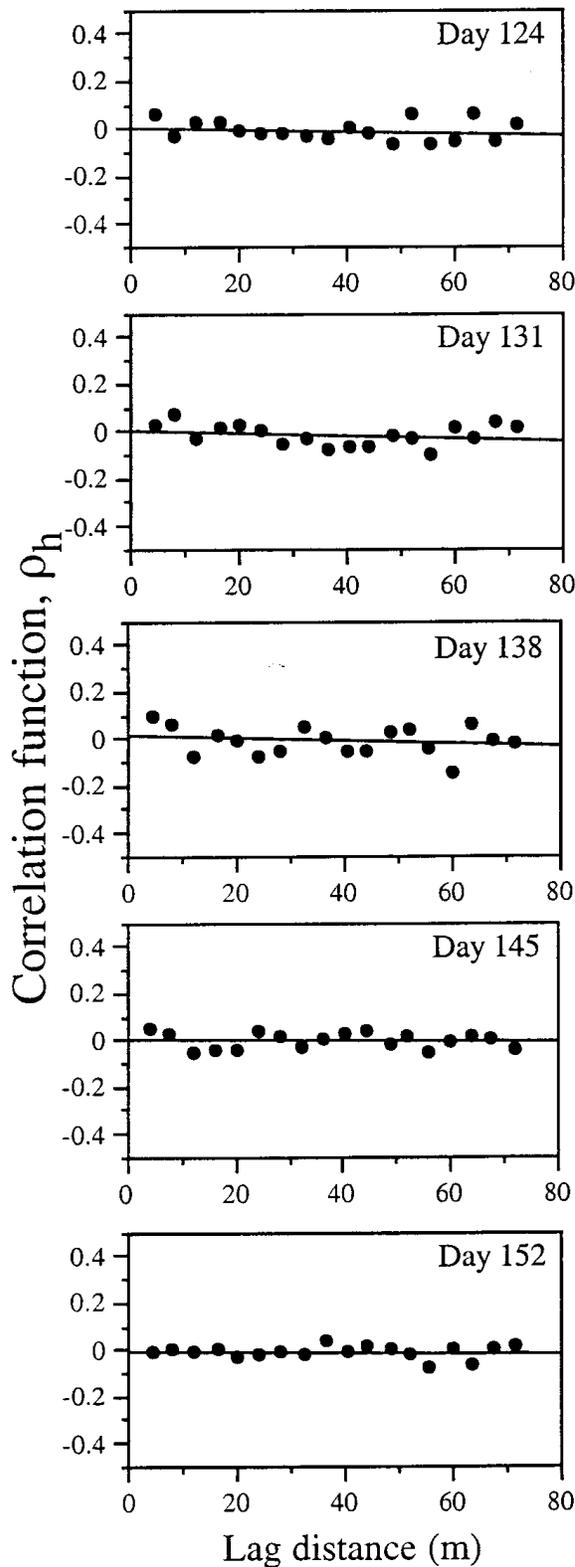


Fig. 6. Plots of the correlogram,  $\rho_h$ , for immigrating *C. pumilio* after detrending the data (equation 8; Sharov et al. 1996).

Both populations of *C. pumilio* exhibited exponential growth (Fig. 1; Table 1), suggesting that, despite differences in resource availability (e.g., house fly eggs and immatures), prey population was not a limiting factor in the establishment of *C. pumilio*. This is reinforced by the lack of a significant difference in the rate of establishment (e.g., slopes in Fig. 2) between resident and immigrating *C. pumilio* populations. Temperatures within poultry facilities are usually maintained at a constant 20–24°C to optimize hen egg production, suggesting that population growth models can be reasonably extrapolated to other facilities given that other conditions remain similar as well. Our data suggest population growth rates of 0.03–0.10 (Table 1). This rate, if it can be effectively modeled, can provide poultry producers with the ability to predict the increase of this valuable biological control agent, providing that scouting efforts are made to identify initial concentrations of *C. pumilio*.

The negative binomial frequency distribution is fairly robust and was useful in modeling  $\approx 53\%$  of the histograms of both *C. pumilio* populations (Table 2). Histograms were always strongly positively skewed in a manner typically modeled well with a negative binomial (Fig. 3), suggesting aggregation within the manure pit. Data from sampling intervals in which the negative binomial was not appropriate were often bimodally distributed, especially after pooling counts in the right tail. One biological explanation of these fairly high proportions in the tail of frequency distributions is environmental heterogeneity. Although poultry facilities in Pennsylvania are closed environments, manure habitats are still subjected to structural variation, such as water leaks from hen water hoses and the location of fans used in ventilation. Avian diseases, such as various types of enteritis, can be a cause of environmental variation, and the close confinement among hens ( $\approx 27$  hens/m<sup>3</sup>; Wilhoit et al. 1991) facilitates bird-to-bird transmission. Water leaks, fan distribution, and avian diseases affect manure moisture, consequently influencing the manure community. Although *C. pumilio* adults are not significantly positively correlated with manure moisture, *C. pumilio* larvae are (Geden and Stoffolano 1988). Also, Stafford and Bay (1987) reported that the majority of house fly larvae were recovered from a poultry manure moisture range of 70–79%, whereas very few were recovered from moisture levels  $< 40\%$ .

Taylor's power law provided a sound least squares regression fit for both populations of *C. pumilio* (Fig. 4). Taylor's  $b$ , although influenced by quadrat size (Elliott 1977, Sawyer 1989), is less sensitive to environmental heterogeneity than the negative binomial because means and variances of a quadrat are considered rather than individual counts from a sampling point. The estimates of Taylor's  $b$  are useful in determining optimal sample sizes and can be exploited in future studies, as suggested by Stafford and Bay (1994) with respect to 3rd-instar house flies. However, because Taylor's power law considers the spatial process at a quadrat level, individual, high density clumps of *C. pumilio* resulting from environmental heterogeneity

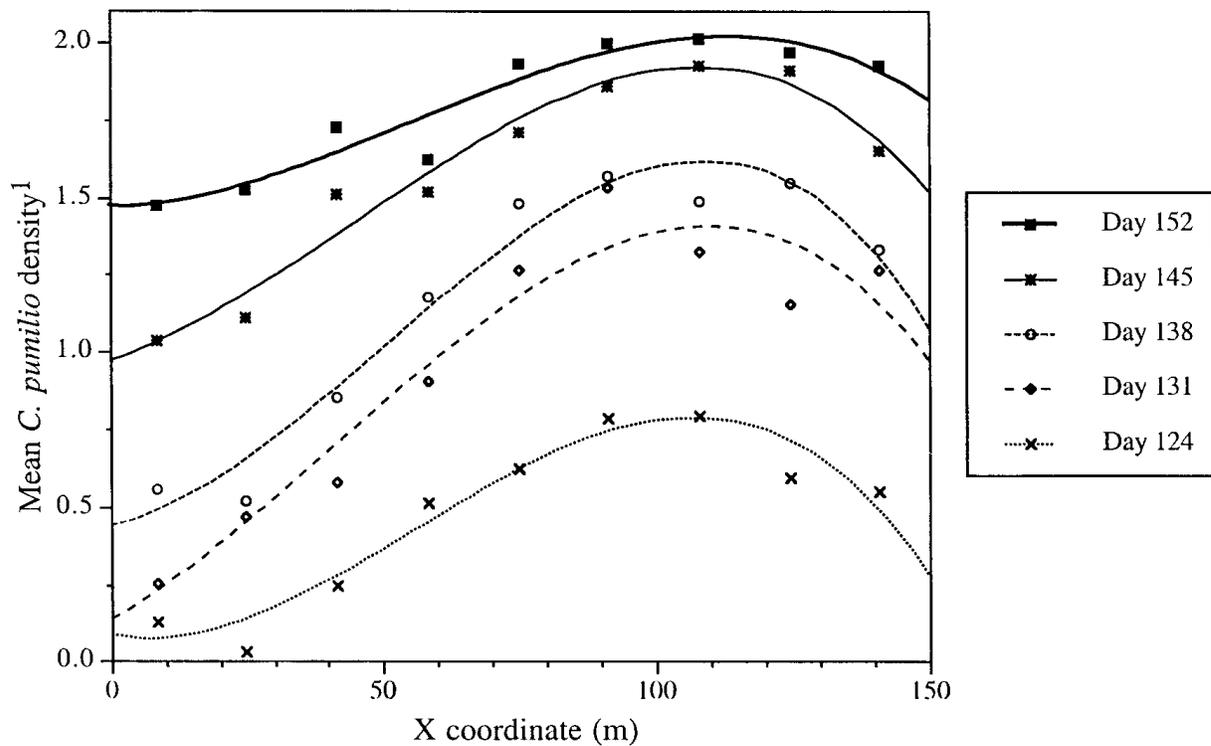


Fig. 7. Spatial trend models of immigrating *C. pumilio*. The X coordinate is the midpoint of respective quadrats. <sup>1</sup>Mean of the  $\text{Log}_{10}(Z+1)$  counts per quadrat ( $N = 18$ ).

are not recognized in any form other than large variance-to-mean ratios. Large aggregations of *C. pumilio* observed from frequency distribution analyses, are ecologically interesting, especially in investigations of stochastic processes inherent to spatio-temporal dynamics of phenomena. Geostatistics, such as correlogram estimation, allow the opportunity to examine spatial processes at finer scales.

Correlograms indicated a lack of spatial structure, either in the form of 1st order or 2nd order effects, in the distribution of resident *C. pumilio* in house 1 (Fig. 5). At day 69, we observed some 2nd order effects represented by nonlinear correlogram values and a significant estimate of the range of spatial continuity. This suggests that samples separated by small distances were statistically correlated, so that biologically there was some degree of clustering of *C. pumilio* between sampling points. However, the range, or spatial scale in which statistical correlation was observed, was limited and only observed at 1 sampling interval. The lack of any substantial spatial structure is somewhat expected, because at the time of the last manure clean-out, *C. pumilio* had already become well established. Leaving  $\approx 5\%$  of the manure during clean-out is a common management practice, because it permits natural enemies of house flies to reestablish themselves. This is especially critical during winter seasons when immigration is not a factor.

The degree of aggregation in the *C. pumilio* population on a quadrat level is largely attributable to the aggregated house fly population, the mechanisms behind which were elegantly discussed by Stafford and

Bay (1994). *C. pumilio* adults, which are effective predators of house fly eggs and 1st–2nd instars, generally forage for aggregations of house fly immatures. Given that house flies remain in the egg and larval stages for  $\approx 8$  d at  $26^{\circ}\text{C}$ , of which 3–4 are spent as 3rd instars (Lysyk and Axtell 1987), fly immatures are vulnerable to predation by *C. pumilio* for only 4–5 d. Therefore, it is expected that adult beetles would be found in clumps and in the vicinity of fly egg masses and developing immatures.

We therefore propose that after clean-out, resident *C. pumilio* reestablished and redistributed itself in response to the location of its prey. These aggregations of *C. pumilio*, which, according to Taylor's power law were present at a quadrat level, were spatially random with respect to individual sampling points. Other localized variables, such as manure moisture, are important, and more work is needed to assess their influence on redistribution of resident *C. pumilio*.

First order spatial effects were strongly evident in the immigrating *C. pumilio* population in house 2. Counts from samples separated by small distances were positively correlated, those separated by larger distances were negatively correlated, and this relationship was strongly linear (Fig. 5). After detrending the data, we observed no evidence of spatial structure (Fig. 6); therefore, the degree of spatial continuity of immigrating *C. pumilio* was defined by the spatial trend. This trend was consistently observed to proceed in the same direction at each sampling interval (Fig. 7), illustrating stability of spatial pattern. Thus, the spatial process of immigrating *C. pumilio* pro-

ceeded along a gradient over all time intervals, with the process emanating from 1 section of the house.

Although entry ports (i.e., ventilation fans) were located at evenly spaced intervals along both lengths of the facility, our statistical analyses strongly suggest that *C. pumilio* adults were 1st recovered in 1 section of the house, and this section remained the area of highest concentration throughout the study. Thus, the behavior of the spatial trend (Fig. 7) suggests that the initial immigration of *C. pumilio* appeared in only 1 region of the pit at 1 or multiple time intervals, that subsequent immigrations of adults in other regions of the facility were either nonexistent or negligible, and that redistribution from areas of initial immigration (particularly during the log phase of exponential growth), were primarily responsible for the eventual colonization of the entire house.

We propose 3 hypotheses to explain the singular in space immigration event in house 2, all of which require future research. First, *C. pumilio* immigration may have occurred at multiple locations within the manure pit, but successful establishment, perhaps because of prey availability and habitat quality, may have occurred in only 1 section. Second, adjacent land cover and particularly the location of nearby poultry facilities with existing *C. pumilio* populations, undoubtedly plays a role in the spatial pattern of *C. pumilio* immigration. Finally, chemically mediated immigration, such as through manure volatiles, kairomones released by *M. domestica* and perhaps other prey species, and pheromones released by establishing *C. pumilio*, and the direction of prevailing winds which carry exiting volatiles, may also play a role. Detection and release of chemical cues by *C. pumilio* have not been investigated, and future work should address their role on immigration.

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