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POPULATION ENERGETICS OF BACTERIAL-FEEDING NEMATODES: STAGE-SPECIFIC DEVELOPMENT AND FECUNDITY RATES

H. FERRIS,* M. EYRE, R. C. VENETTE and S. S. LAU
Department of Nematology, University of California, Davis, CA 95616, U.S.A.

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Summary—By grazing on bacteria, bacterial-feeding nematodes participate in decomposition food webs and N mineralization to an extent determined by metabolic and behavioral attributes and by life history. We determined the stage-specific development and fecundity rates for seven species on a physiological time scale to allow time and temperature-varying predictions of population progressions. Development from egg to adult of four species in the Rhabditidae (*Bursilla labiata*, *Caenorhabditis elegans*, *Cruznema tripartitum* and *Rhabditis cucumeris*) was faster than that for three species in the Cephalobidae (*Acrobeloides bodenheimeri*, *A. buetschlii* and *Cephalobus persegnis*) on a Julian time (calendar) basis at 20°C. Development in the Rhabditidae was generally faster on a physiological (degree–day) time scale as well, but those times are not directly comparable as the basal threshold for degree–day (DD) accumulation differed among the species. The fecundity period for females of the seven species varied between 55 and 75% of the total duration of the life course, during which they produced between 125 eggs (*B. labiata*) and 567 eggs (*C. tripartitum*). Simulated population growth under favorable temperature conditions, using parameter values determined in these studies, indicated rapid population growth in the large-bodied, highly-fecund rhabditid species (*R. cucumeris* and *C. tripartitum*). Population growth was intermediate in the small-bodied, less-fecund rhabditids with short egg-production periods (*B. labiata*), slower in the cephalobids (*A. bodenheimeri* and *A. buetschlii*) and slowest in *C. persegnis*. *R. cucumeris* spent a greater proportion of its development time in the egg stage than did any of the other species.

INTRODUCTION

In soil, bacteria are primary decomposers in detritivore food webs. They are grazed upon primarily by bacterial-feeding nematodes and protozoa. In these and other trophic interchanges in the food web, some ingested molecules are not assimilated; some are used as sources of energy; some are incorporated into body structure; some are stored as reserves; and, those in excess of needs are excreted as waste to preserve osmoregulatory integrity. Each organism in the web, and its excretions, are potential sources of food and energy for other organisms. Population size, individual and population growth rates, and metabolic activities of individuals determine the extent to which species contribute to, and participate in, energy and nutrient flow in an ecosystem.

Studies of metabolic and respiratory energetics of soil-inhabiting nematodes indicate a range of activity across species (De Cuyper and Vanfleteren, 1982; Ferris *et al.*, 1995a; Klekowski *et al.*, 1972, 1974; Nicholas, 1975; Schiemer, 1982, 1983). However, due to the time required for genus and species identification, bacterial-feeding nematodes are often categorized at the trophic group level in soil ecosystem studies (Freckman and Mankau, 1986; Niblack, 1989; Parmelee and Alston, 1986). Although descriptively useful, aggregating nematode species with different biology into a single trophic group may mask the importance of individual species (Ferris, 1982, 1993). Estimates of contributions of bacterial-feeding nematodes to energy flow and nutrient dynamics based on trophic level groupings may have quantitative and temporal biases resulting from differing population age structures and dynamics of individual species.

A useful alternative to aggregating species into trophic groups may be the grouping species of like biology into "trophic species" (Cohen, 1989), with the attendant requirement of acquiring greater knowledge of the biology, metabolic rates and life-table characteristics of the organisms. Bongers (1990) provided a useful framework for trophic species groupings of free-living nematodes. He categorized free-living nematodes at the family level into five classes along a continuum from "colonizers" to "persisters" based upon known and assumed behavioral, metabolic and life-table attributes of species in each family. Of the common bacterial-feeding nematodes in the soil, those in the family Rhabditidae are assigned to Class 1, enrichment opportunists with a suite of "r" characteristics; those in the Cephalobidae are assigned to Class 2,

*Author for correspondence.

stress-tolerant species that are somewhat less opportunistic than those in Class 1. Nematodes in classes 3 to 5 are successional species and are most common in stable ecosystems. Validation of this scheme will be enhanced by filling the void of knowledge on the energetics and food preferences of the various species, genera and families categorized in each class.

Life course duration, fecundity and survivorship data have been developed for a few species of bacteria-feeding nematodes (e.g. Sohlenius, 1968, 1973; Yeates, 1970), but there is little information on stage specific rates of development. Usually development and fecundity data have been measured at one or a few temperatures and rates are not generalized in physiological time to allow assessment of the effects of varying temperatures.

Our objectives were to: (i) determine the life-table parameters (stage-specific development, fecundity and survivorship) of bacterial-feeding nematodes species; and (ii) examine the commonalities of life-table characteristics of species in nematode families representing two colonizer/persister classes.

MATERIALS AND METHODS

The nematode species studied are representatives of two families of the order Rhabditida: *Acrobeloides bodenheimeri*, *A. buetschlii* and *Cephalobus persegnis* (family Cephalobidae); *Bursilla labiata*, *Caenorhabditis elegans*, *Cruznema tripartitum* and *Rhabditis cucumeris* (family Rhabditidae). Voucher specimens of the nematodes used in these experiments are deposited in the U.C. Davis Nematode Collection with the following accession numbers: *A. bodenheimeri*—UCDNC 2908 and 2909; *A. buetschlii*—UCDNC 3030; *B.labiata*—UCDNC 3028 and 3029; *C. elegans*—UCDNC 3032; *C. persegnis*—UCDNC 3031; *C. tripartitum*—UCDNC 2910 and 2911; and *R. cucumeris*—UCDNC 3033. The *C. elegans* population was a laboratory culture included as a comparative standard. All other species were endemic in the field site of a long-term Sustainable Agriculture Farming Systems (SAFS) project at the University of California Davis campus (Temple *et al.*, 1994).

Nematodes were extracted from soil samples by elutriation and sugar-centrifugation (Byrd *et al.*, 1976; Barker, 1985). Individual species were hand-picked based on visual similarities, and placed on water agar. After about 1 week, single gravid females were removed from the water agar and transferred to individual Petri dishes of nematode growth medium (NGM) (Sulston and Hodgkin, 1988). Bacteria associated with the nematodes flourished and provided food. For some isolations, we transferred the nematodes and associated bacteria to Petri dishes with a lawn of *Escherichia coli* strain OP50 on NGM agar (Sulston and Hodgkin, 1988) in an attempt to standardize food sources.

Fecundity

Egg production and development rates were determined by establishing 10 or more Petri dishes of 0.1-strength nutrient agar plus cholesterol (Venette and Ferris, 1996). A patch of *E. coli* was established in the center of each dish. A single fourth-stage juvenile (J4), and a single male in the case of sexually-reproducing species, were placed on each Petri dish. The dishes were incubated at constant temperature (usually at 20 $\pm$ 1°C, but at 23 $\pm$ 1°C in some different experiments). In each case the incubation temperature was within the range over which the relationship between development rate and temperature approximates linearity (Venette and Ferris, 1996) and below any upper thermal threshold (Baskerville and Emin, 1969) for the individual species. Petri dishes were monitored at least daily and up to eight times in 24 h depending on the observed development and fecundity rates. For dishes in which the J4 developed into an adult female, the total numbers of eggs and individuals in each life stage were determined at each observation. All the individuals observed on a Petri dish through time were the offspring of the founder female. As offspring approached adulthood, the founder female (and male) were transferred to new Petri dishes seeded with bacterial substrate. The process was continued until no further egg production occurred. Cumulative egg production was calculated for each founder female.

The egg production data were used to calculate the total number of eggs per female and time for egg development. The fecundity period was determined by observation of the period over which individual females produced eggs. A degree–day (DD) time scale as a measure of "physiological time" was developed using basal threshold temperatures for each species determined in other studies (Venette and Ferris, 1996). Egg production rates, as eggs female^{-1} DD^{-1}, were determined by linear regression of cumulative numbers of offspring per female over time. We also examined the data to determine any relationships between fecundity parameters and anatomical characteristics of females.

Development

We estimated size ranges for the life stages of each species based on size classes of individuals in a process similar to that used by Anderson and Kirchner (1982). The body lengths of 300–500 individuals were arranged in rank order in a Lotus 1-2-3 spreadsheet, and graphed as a frequency distribution. Adults were distinguished by anatomical characters and their body lengths measured. Other life stages were distinguished by peaks in the frequency distribution of the body length data set. The smallest nematodes were considered to be first- and second-stage juveniles (J1 and J2). The size range for each life stage was determined as the length of

individuals at the intersection points of frequency curves fitted empirically to the body length data for each putative life stage. The coincidence between body size and life stage is only inferred, since except for adults, it was not confirmed by observation of molting (Ferris *et al.*, 1995a).

To determine the physiological time required for completion of each life stage, two procedures were used. In one, a "single-stage" cohort of 100 juveniles (J2 / J3) was hand-picked based on size and placed on each of five Petri dishes of NGM agar; in the other, the populations remaining in the fecundity experiment after removal of the founder female (and male) were used. The Petri dishes were kept at the same temperatures as for the fecundity observations. They were observed from once to several times daily, depending on the observed development rates, to ensure that the frequency of observations was at intervals less than the mean development time for a life stage. Observations were discontinued at the time that eggs of the second generation began to hatch. By that time the agar surface of the culture plate was disrupted by bacterial growth and nematode movement tracks so that eggs and small juvenile stages were difficult to see. Observations were also discontinued when it was evident that the dish contaminated by bacteria was having deleterious effects on the nematode population. The ratio of males to females for each species was estimated from the total number of males and females across all replicates for that species. Development rates were determined in two experiments for each species.

The data were subjected to the parameter-estimation procedure developed by Schneider and Ferris (1986) for an age-structured, distributed-delay population model. The model has a box-car format in which each life stage is advanced in development through a series of time steps. Graduation from one life stage to the next is distributed about a mean developmental time based upon the variability of individuals in that life stage. The probability function governing graduation from one stage to the next is the asymmetric, positively-skewed, Erlang distribution (Manetsch, 1976; Schneider and Ferris, 1986). Stage-specific mortality is distributed across a life stage, with the proportion of organisms dying in each of the k time steps being the kth root of the total mortality for that stage. Essentially the simulation model is provided with a range of possible values for each parameter to be estimated and set into an iterative mode. The parameter values that provide the best fit of the model to the data are the accepted estimates.

Life-stage parameter values were estimated from the observations in each replicate separately. Parameter values determined experimentally were used where possible. Those included male-to-female ratio, rate of egg production per female, and length of the egg-production period. Initially, trial stage development times (in DD base 10°C) were selected to widely bracket the expected time for each stage; the standard deviation for development times was set at 50% of the mean; and stage-specific survivorship at 100%. An iterative process ensued: (1) best-fit development times within the selected range were determined for fixed levels of the other parameters; (2) best-fit standard deviations were determined with other parameters fixed; (3) best-fit survivorship values were selected with other parameters fixed. The process was repeated until the best least-squares estimate of all values was obtained. Stage developmental times were again determined with the new values of the other parameters to ensure that the best fit selected was not a local least-squares phenomenon (Schneider and Ferris, 1986).

Our algorithm for calculating stage-specific development times, standard deviations of those times and stage-specific survivorship can require many millions of iterations to simulate population datasets and compare them to the observations from each experimental microcosm. When searches were made for the best-fit solution of all three parameters for each life stage simultaneously, it was easy to generate at least a week of computation time for a DOS-compatible personal computer with a 486-50 microprocessor, even when the possible range of each value was restricted. Consequently we used the step-wise approach of screening for best-fit solutions for each parameter separately. We considered that level of control over the progression of the analyses to be preferable to simultaneous solution for all unknowns, since it allowed monitoring of the biological likelihood of each solution as it was achieved.

A chi-square test was conducted of the goodness-of-fit of the replicate parameter values to the observed data. Due to the lack of reliability of second generation egg counts, the eggs female^{-1} DD^{-1} parameter of the algorithm was set to zero, and the observed and predicted number of eggs were omitted from the goodness-of-fit calculations. Egg development, variance and survivorship values were selected based on the best fit of the model to the data for all other life stages. If chi-square values of goodness-of-fit indicated that the population data simulated with the estimated life-stage parameters differed from the observed population data ($P < 0.05$), the parameters were re-estimated. If there was still discordance between observed and expected population values, the parameter estimates from that Petri dish microcosm were omitted from further consideration. That occurred for fewer than 5% of the microcosms.

The final stage in refinement of the life-stage parameters was to calculate global values for stage-specific development times and their standard deviations. The global parameters for development times and standard deviations were the means of those values across all replicates. The global values were then used with the Schneider and Ferris (1986) algorithm for selected replicates of each nematode,

Table 1. Anatomical characteristics, sex ratios, and family of seven species of bacterial-feeding nematodes at 20°C (Body weight data from Ferris *et al.*, 1995a)

	Male-to-Female ratio	Number of ovaries	Body weight (μg / Female)	Family
Abod	0.76	1	1.271	Cephalobidae
Abut	0.0	1	0.643	Cephalobidae
Burs	0.15	1	0.478	Rhabditidae
Cele	0.0	2	0.622	Rhabditidae
Ceph	0.0	1	0.475	Cephalobidae
Cruz	0.42	1	7.708	Rhabditidae
Rhab	0.14	2	4.273	Rhabditidae

Abod, *Acrobeloides bodenheimeri*; Abut, *A. buetschlii*; Burs, *Bursilla labiata*; Cele, *Caenorhabditis elegans*; Ceph = *Cephalobus persegnis*; Cruz = *Cruznema tripartitum*; Rhab, *Rhabditis cucumeris*.

along with the best-fit survivorship values determined for that replicate in the previous analyses. This process recognized that each Petri dish microcosm was a potentially unique environment, and that survivorship often varied among microcosms. A chi-square test of goodness-of-fit of the global parameters and replicate survivorship values was conducted to ensure that the goodness-of-fit was reasonable. If the chi-square test suggested that the individual Petri dish observations differed from the dataset simulated with global parameters ($P < 0.1$), the analyses for each Petri dish were repeated.

The experimentally-determined basal threshold values used for the fecundity analyses were also applied to development (Venette and Ferris, 1996). Stage-specific development times and fecundity, and their standard deviations, were recalculated based on the measured thresholds. Since all incubations were conducted above the basal thresholds, we also calculated development times and rates in Julian time at 20°C.

Simulated nematode population growth

The same distributed-delay simulation model used to estimate species- and stage-specific lifetable parameters (Schneider and Ferris, 1986) was used to predict population growth of each nematode species over a 60 d period using a soil temperature profile for April 10 to June 10, 1993 from the SAFS project. Stage-specific development times and their standard deviations (in DDs above the respective basal threshold) were those measured in these experiments. Since field survivorship levels for each life stage of each species are unknown, survivorship values for each life stage were selected arbitrarily as 0.25, 0.20, 0.30, 0.35 and 0.40 for eggs, J2, J3, J4 and adults, respectively, and standardized across all species. Resources were assumed to be unlimited.

RESULTS

Males were absent in three of the nematode species, two in the family Rhabditidae and one in the Cephalobidae. Sex ratios ranged from 0.0 to 0.76 males per female in the other species. There were no obvious associations between sex ratio and family (Table 1). Two of the species, both in the Rhabditidae, have females with two ovaries, the others have females with a single ovary. Body weights of individual females (Ferris *et al.*, 1995a) ranged from 0.47 to 7.71 g, without obvious association with either number of ovaries, sex ratios or higher taxonomic classification.

Fecundity

Egg production rates at 20°C ranged from 12.5 eggs d^{-1} for *C. persegnis* to 65.7 eggs d^{-1} for *R. cucumeris*. When calculated in DDs relative to the respective basal thresholds of the individual species, production rates ranged from 0.62 eggs $female^{-1}$ $DD_{0.0}^{-1}$ for *C. persegnis* to 5.74 eggs $female^{-1}$ $DD_{10.0}^{-1}$ for *C. tripartitum* (Table 2). The total period of egg production ranged from 5.5 d for *C. elegans* to 21.4 d for *C. persegnis*. The species in the Rhabditidae had egg production periods ranging from 5.5 to 9.9 d, while those in the Cephalobidae ranged from 10.6 to 21.4 d (Fig. 1). In physiological time, the range was from 59.7 $DD_{10.6}$ for *B. labiata* to 427.1 $DD_{0.0}$ for *C. persegnis* (Table 2). Total eggs per female throughout the duration of the fecundity period

Table 2. Duration and rate of egg production in seven species of bacterial-feeding nematodes, and duration of total life course, measured at 20°C

		Production period			Eggs $female^{-1}$			Total life course	
Species	Basal threshold (T)	DD_T	SD	D^{-1}	SD	DD_T^{-1}	SD	Ds	DD_T
Abod	13.8	65.6	19.0	20.6	11.8	3.32	1.90	19.3	119.6
Abut	14.8	68.7	20.6	12.9	1.3	2.48	0.25	21.6	112.4
Burs	10.6	59.7	9.5	19.6	5.0	2.09	0.53	10.1	94.2
Cele	5.0	82.6	20.1	58.0	10.8	3.88	0.72	7.6	113.7
Ceph	0.0	427.1	39.2	12.5	1.7	0.62	0.09	30.0	599.6
Cruz	10.0	98.8	9.0	57.4	12.4	5.74	1.24	15.4	153.8
Rhab	1.4	140.7	25.5	65.7	20.7	3.53	1.11	11.6	215.8

Abod, *Acrobeloides bodenheimeri*; Abut, *A. buetschlii*; Burs, *Bursilla labiata*; Cele, *Caenorhabditis elegans*; Ceph, *Cephalobus persegnis*; Cruz, *Cruznema tripartitum*; Rhab, *Rhabditis cucumeris*; DD_T, degree-days above a basal temperature threshold (T); SD, standard deviation.

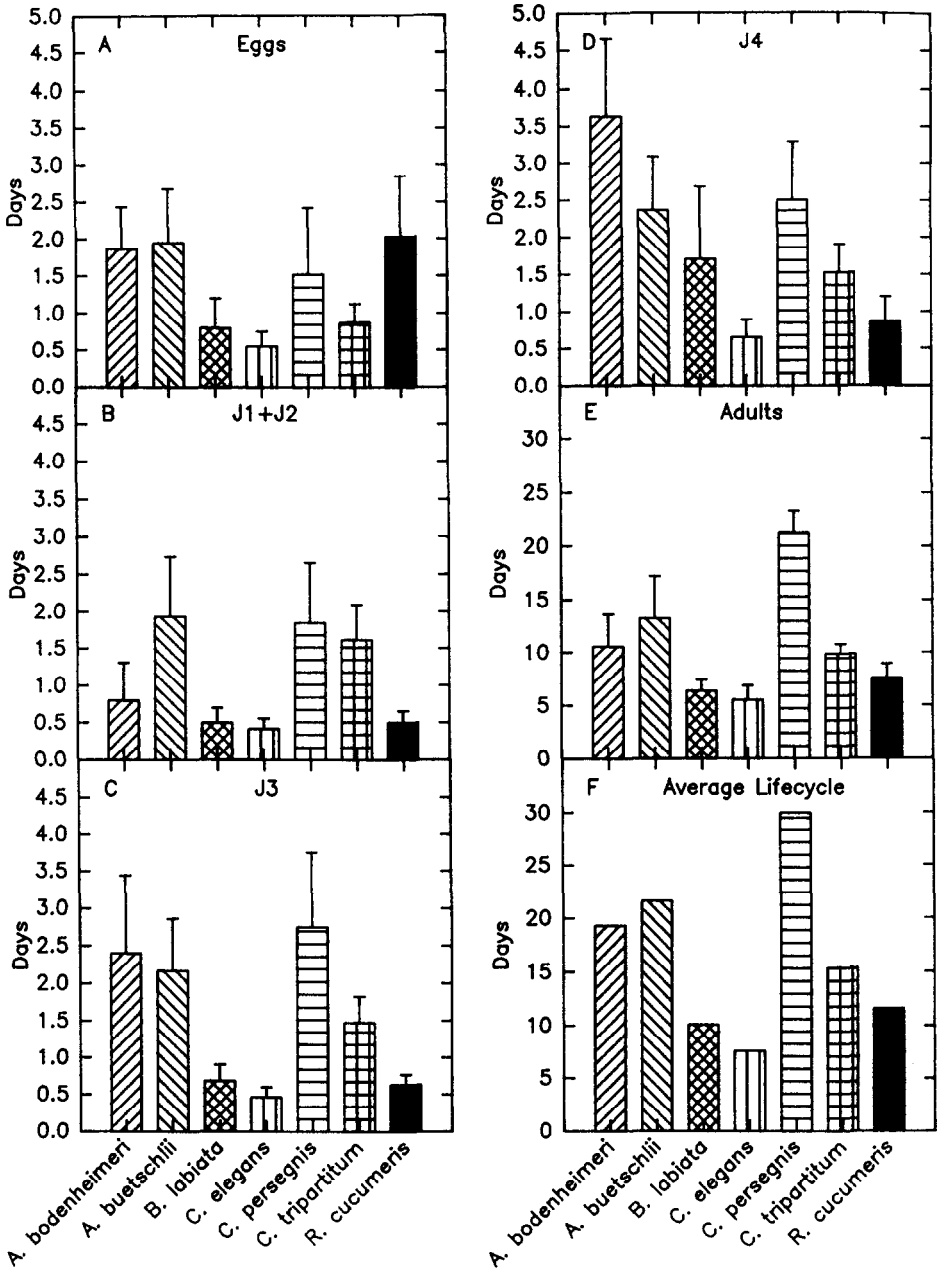

Fig. 1. Stage-specific development times at 20°C, and their standard deviations, for seven species of bacterial-feeding nematodes in the families Cephalobidae and Rhabditidae. (A) Eggs; (B) second-stage juveniles (and first-stage if not completed in egg); (C) third-stage juveniles; (D) fourth-stage juveniles; (E) adults; and (F) average length of the total life course from egg to completion of the adult stage.

ranged from 125 for *B. labiata* to 567 for *C. tripartitum*. The proportion of the total life course committed to egg production was remarkably similar, ranging from 0.55 to 0.73, with no clear trends among genera or families (Tables 2 and 3).

Total egg production was greatest in the large (*C. tripartitum* and *R. cucumeris*) nematodes, but there was no clear relationship of egg number to body size in the smaller nematodes (Tables 1 and 3). Similarly there was no relationship between egg number and number of ovaries (Tables 1 and 3). The rate of egg production ovary^{-1} d^{-1} was somewhat greater in the larger nematodes, and greater in the Rhabditidae than the Cephalobidae (Tables 1 and 3). The rate of egg production per unit weight of female nematode varied within families. It was greatest in *C. elegans* and least in *C. tripartitum* (both Rhabditidae). The body weight of the first juvenile stage to emerge from the egg (Ferris *et al.*, 1995a) was used as an estimator of egg weight since nematode eggs have no yolk and display total cleavage. The weight of eggs produced^{-1} d^{-1} per unit weight of female

Table 3. Egg productivity ratios for seven species of bacterial-feeding nematodes measured at 20°C

Species	Total eggs	Eggs ovary^{-1} d^{-1}	Eggs μg^{-1} μg^{-1}-female d^{-1}	μg Eggs μg^{-1}-female d^{-1}	Fecundity period as propn. of life course
Abod	218	20.6	16.2	0.50	0.55
Abut	170	12.9	20.0	0.68	0.61
Burs	125	19.6	33.9	0.71	0.63
Cele	320	29.0	93.3	2.24	0.73
Ceph	266	12.5	26.2	0.87	0.71
Cruz	567	57.4	7.5	0.78	0.64
Rhab	497	32.9	15.4	0.62	0.65

Abod, *Acrobeloides bodenheimeri*; Abut, *A. buetschlii*; Burs, *Bursilla labiata*; Cele, *Caenorhabditis elegans*; Ceph, *Cephalobus persegnis*; Cruz, *Cruznema tripartitum*; Rhab, *Rhabditis cucumeris*.

nematode was fairly similar for all species from the field site. It was approximately three times greater in the laboratory-maintained and selected *C. elegans* (Table 3).

Development

The portion of the total life course committed to individual development and growth is that time prior to the onset of egg production. As a proportion of the total life course duration, it varied from 0.27 in *C. elegans* to 0.45 in *A. bodenheimeri*. Of the nematodes isolated from the SAFS site, the smallest proportion of total longevity committed to development and growth was 0.29 in *C. persegnis* (Table 3). Of course, these proportions represent different stage-specific physiological development times (Table 4). The nematodes species differed in the proportion of the life course spent in the egg stage. For the two *Acrobeloides* spp, *B. labiata* and *C. elegans* between 21 and 26% of the development time was spent in the egg stage. For *C. persegnis* and *C. tripartitum* the proportion of development time spent in the egg stage was around 16%, but for *R. cucumeris* it was 50%. The Julian time spent in the egg stage was about twice as long in the species in the Cephalobidae as those in the Rhabditidae, with the exception of *R. cucumeris* [Fig. 1(A)].

The Julian time equivalents of the physiological development times indicate that for all life stages other than eggs of *R. cucumeris*, development [Fig. 1(A–D)] or longevity [Fig. 1(E–F)] is greater in the representatives of the Cephalobidae than in those of the Rhabditidae. Once feeding has commenced, the Rhabditidae are very similar in their development characteristics, with *C. elegans* being somewhat more rapid than the others. Observed differences in physiological development time result from varying adaptation to metabolic activity at lower temperatures, as exhibited by the range of basal thresholds (Table 4).

We found that stage-specific survivorship rates often varied among microcosms. If survival in a microcosm was abnormally low or there was obvious contamination, those data were not used in the lifetable analyses. Since the survivorship values are essentially curve-fitting constants for individual microcosms and are not representative of soil conditions, they are not presented here.

Simulated nematode population growth

The 60 d population growth curves indicated rapid population increase of shorter life course species. *R. cucumeris* and *C. tripartitum* increased rapidly, followed by *B. labiata*. The species in the Cephalobidae increased less rapidly (Fig. 2).

DISCUSSION

There were two distinct classes of egg production rate exhibited by these nematode species at 20°C, one in the 10–20 eggs female^{-1} d^{-1} range and one in the >50 eggs female^{-1} d^{-1} range (Table 2). We explored the relationship of these rates to the anatomical configuration of female reproductive structures, sex ratio, body size and higher classification. The simple notion that females with two ovaries should be able to produce eggs at twice the rate of those with one ovary held up for all species except *C. tripartitum*, which produced eggs at the higher rate despite having a single ovary. We also

Table 4. Mean stage-specific development times in degree–days (DD_T) above a basal threshold (T) and their standard deviations (SD) for seven species of bacterial-feeding nematodes measured at 20°C

		Eggs		J1 / J2		J3		J4	
Species	Basal threshold (T)	DD_T	SD	DD_T	SD	DD_T	SD	DD_T	SD
Abod	13.8	11.6	3.6	5.0	3.1	14.9	6.5	22.5	6.3
Abut	14.8	10.1	3.8	10.0	4.2	11.2	3.6	12.3	3.7
Burs	10.6	7.5	3.7	4.7	1.9	6.4	2.1	15.9	9.1
Cele	5.0	8.2	3.0	6.2	2.1	7.0	2.0	9.7	3.6
Ceph	0.0	30.5	17.9	37.0	16.1	55.0	20.1	50.0	15.8
Cruz	10.0	8.8	2.5	16.2	4.8	14.8	3.5	15.2	3.8
Rhab	1.4	37.9	15.1	9.3	2.9	11.8	2.6	16.1	6.2

Abod, *Acrobeloides bodenheimeri*; Abut, *A. buetschlii*; Burs, *Bursilla labiata*; Cele, *Caenorhabditis elegans*; Ceph, *Cephalobus persegnis*; Cruz, *Cruznema tripartitum*; Rhab, *Rhabditis cucumeris*.

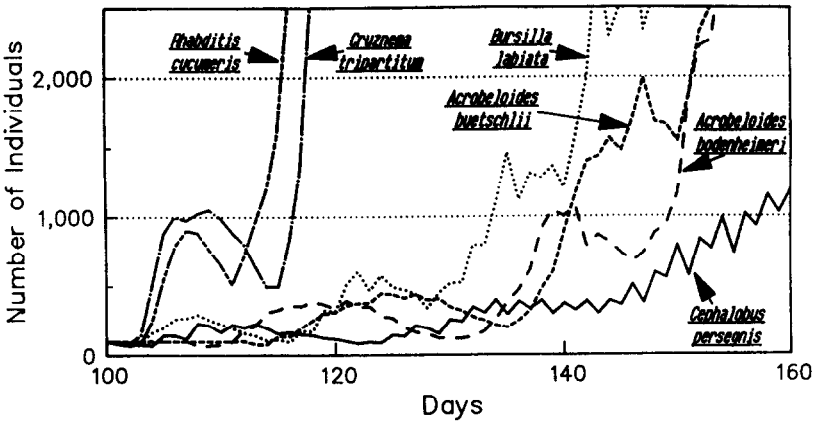

Fig. 2. Simulated total population levels of six species of bacterial-feeding nematodes during a 60 d period under varying temperature conditions. Temperatures measured at 15 cm-depth between 10 April and 10 June 1993 in the field from which the nematodes were obtained.

examined the total number of eggs produced per female. Generally females with a single ovary produced fewer eggs than those with two ovaries. Again, *C. tripartitum* was the exception. Strategies for partitioning resources between body weight and egg production varied among species, with the long-lived *C. persegnis* producing as many eggs per unit of body weight as the short-lived *B. labiata*. However the short-lived *C. tripartitum* clearly produced fewer eggs per unit of body mass, and presumably food intake, than the other species. When egg production was expressed in terms of weight, the proportional partitioning of resources between body mass and egg production of the soil nematodes was quite similar and about one-third of that in *C. elegans* (Table 3).

The rate of egg production in the presence of abundant food by *R. cucumeris* in these studies was about 3-fold that observed for similar-sized *R. terricola* in xenic culture at 20°C (Sohlenius, 1968). Similarly, egg production rates for the two *Acrobeloides* spp were at least double those observed for *A. nanus* at 21°C (Sohlenius, 1973). Our measurements of the productivity of individual *C. persegnis* females (12.5 eggs d^{-1} for 21.3 d, yielding 266 eggs) were comparable to previous results at 21°C of 10–19 eggs d^{-1} for 26.5 d, yielding 299 eggs (Popovici, 1972).

R. cucumeris completed 50% of its development time in the egg stage while other species spent a considerably smaller proportion of their development in that stage. We assume that, as observed with related species (Skiba and Schierenberg, 1992), although the sequence of cell divisions may vary, the number of cell divisions completed in the egg stage is similar to that observed in *C. elegans* (Sulston *et al.*, 1983; Wood, 1988). About 65% all cell divisions in these nematodes occur while in the egg and food reserves available for development are not obtained by feeding but are maternal contributions to the ovum. There must be a tradeoff in benefits of protection by the egg shell offset by depletion of resources. In fact, the period of egg development in all these species range from 0.5 to 2 d at 20°C (Fig. 1), apparently unrelated to adult or juvenile size and comparable to ranges measured in other studies (Skiba and Schierenberg, 1992). The variation in proportion of development life course spent in the egg stage is determined by the variability in the time of development from egg to adulthood. *R. cucumeris* adults are 9 times heavier than those of *B. labiata*, another rhabditid species. However, at 20°C *R. cucumeris* grows from hatched egg to maturity in 1.9 d while *B. labiata* requires 2.8 d. *C. tripartitum* appears to grow in body mass at a similar rate to *R. cucumeris*. Clearly both are voracious feeders; assessing the integral contribution of the three species to energy flow and nutrient cycling in soil based on numbers of individuals is inadequate. Consideration of individual size and trophic biomass would be an improvement.

Shaffer (1983) determined the relationship of standard deviation (SD) to the mean (x) of stage-specific development times for published information on 113 species of insects and mites. He determined that the relationship $SD = 0.209x^{0.73}$ ($r^2 = 0.69$). Because such relationships are very useful in developing stochastic models of the development of poikilothermic organisms at varying temperature, we conducted similar analyses with our more limited data set. The relationship between standard deviation and mean of stage-specific development time for the five life stages of the seven species of bacterial-feeding nematodes studied is $SD = 0.64x^{0.755}$ ($r^2 = 0.85$). Interestingly, the exponent of this relationship, obtained as the slope of the linear relationship between the log of the standard deviations and the log of the developmental means, is remarkably similar to that for insects. When slopes are similar, as in this case, the constant essentially serves as a scaling factor that matches the line with the dataset (Fig. 3). The larger constant for these nematode data than for the insect data implies that stage-specific development

times are somewhat more variable for nematodes, as measured by our algorithm for seven species, than those reported for insects. However, the increase in variability with increase in development time is similar in both cases.

The simulated population growth curves are of interest in that they reveal the effect of different life-table strategies on population growth. The physiological time for egg development in *R. cucumeris* is 4-fold that of *C. tripartitum* (Table 4), but since it has a lower basal threshold, DDs are accumulated more rapidly, resulting in only a 2-fold difference in Julian time for egg development (Fig. 1). The net effect of more rapid post-embryo growth and similar egg production rates results in rapid population increase of both species (Fig. 2). *B. labiata* also has a higher threshold than *R. cucumeris* and a lower rate of egg production than both *R. cucumeris* and *C. tripartitum* (Table 2). Consequently, it lags in population development over the soil temperature range between 10 April and 10 June 1993 in the SAFS project (Fig. 2). The *Acrobeloides* spp have relatively short physiological developmental time in each life stage, but accumulate DD slowly because of their high basal thresholds (Table 4), resulting in slower population increase than any of the species in the Rhabditidae (Fig. 2). *Cephalobus persegnis* has the longest stage-specific physiological development times of all nematodes tested; it completes its development in a slower but comparable Julian time than the other species due to the very low basal threshold and rapid accumulation of physiological time (Table 4). The dynamics of population increase of *C. persegnis* were slower than any of the other species over the temperature range simulated (Fig. 2).

Unfortunately it is impossible to validate the simulated data from field observations because of the unknown stage-specific survivorship in the field, and the complication of unknown extraction efficiency in measuring numbers of each life stage from the field. Also, it is not possible to assay egg numbers in the field. The simulations therefore are unlikely to provide field-realistic predictions, but do allow study of the effects of the life-table partitioning strategies on population development. Also, the temperature conditions used to drive the simulation model occur only around and at the same depth as the temperature sensor in field soil. Assessment of field nematode populations is accomplished by removing cores of soil that span a range of soil depths encompassing a spectrum of dynamic environmental conditions, including temperature, moisture and food availability. While corrections might be applied for some of these variables, the availability of food at microsites, and the effects of reduced food availability, is unknown (Sohlenius, 1973). As in many such studies, the choice of observational units of appropriate scale presents a dilemma.

The relationship between developmental rates and temperature approximates linearity across a range of temperatures, which is the basis for using DDs as a measure of temperature-independent physiological time. However, those approaches require accommodation for the effect of temperatures below or above the limits of linearity of this relationship. We have expressed species- and stage-specific development periods and productivity in DDs above species-specific basal thresholds (Venette and Ferris, 1996). Our measurements of development rates were conducted at temperatures within the favorable range for each of the nematode species. However, we recognize from other studies that these species have upper thermal thresholds which may limit metabolic rates, development, productivity and survivorship

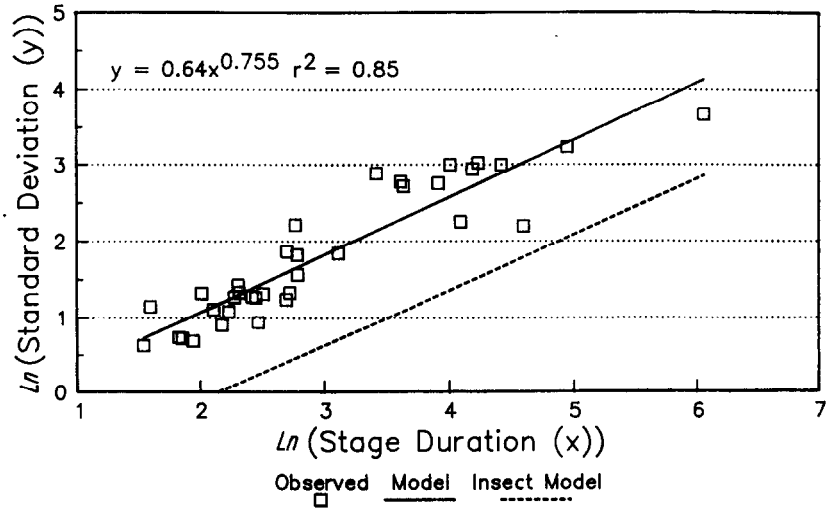

Fig. 3. The relationship between standard deviation of the time to complete a life stage and the mean duration of that life stage for all life stages of seven species of bacterial-feeding nematodes. The relationship ($y = 0.64x^{0.755}$) is compared to a similar relationship determined for data for insect and mite species by Shaffer (1983) (SD = $0.209x^{0.73}$).

(Baskerville and Emin, 1969; Ferris *et al.*, 1995a; Venette and Ferris, 1996). Those upper thresholds should be integrated into heat-unit accumulations and survivorship values for simulations conducted later into the summer and would adversely affect population development of some of these species. For example, *R. cucumeris* has a lower upper developmental threshold (24.6°C) than the other species (Venette and Ferris, 1996). While its population increases rapidly in the simulations using soil temperatures experienced between April and June (Fig. 2), it would decline in simulations using July soil temperatures as observed in our field data (Ferris *et al.*, 1995b).

Clearly the existence of lower and upper thermal thresholds which differ among species of bacterial-feeding nematodes in the same family, along with different development and productivity rates, underscores the complexity of niche-dimension of the individual species in relation to soil depth and time (Venette and Ferris, 1996). That complexity has implications in the contribution of different species to decomposition processes, energy flow, nutrient cycling and soil fertility at different times during the year and at different depths in the soil. We have observed the effects of these factors on the temporal prevalence of different species during the tomato-growing season (Ferris *et al.*, 1995b).

Nematode species in the Rhabditidae and Cephalobidae differ in their life-table characteristics and strategies, which impacts their population dynamics and influence on ecosystem flows. The reduction in usage of broad-spectrum biocides for management of plant-parasitic nematodes in agriculture provides opportunities for capitalizing on the contributions of bacterial-feeding nematodes in soil fertility (Ferris, 1992, 1993). The more information that we have on individual species, the better we will fine-tune our assessments of their roles and formulate strategies for their management. We note with interest that the differences measured in these studies, when integrated through a simulation model, predicted population dynamics for the species in two nematode families that align with expectations resulting from the classification proposed by Bongers (1990), which we equate with the beginnings of a trophic species (Cohen, 1989) classification.

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