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Species, Guilds, and Functional Groups: Taxonomy and Behavior in Nematophagous Arthropods[1]

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Abstract: Phylogenetic relationship is an indication of shared abilities, or at least of shared constraints, on morphology, physiology, and behavior; but is phylogenetic relationship a sufficient criterion for predicting ecological function? Ecologists have assumed that the function of invertebrates in soil systems can be predicted at a low level of taxonomic resolution, but our research indicates that critical functional parameters—e.g., feeding behavior, developmental rate, and reproductive mode—are rarely predictable above the generic level. Since morphology is more strongly conserved than behavior, feeding guilds or functional groups based on broad taxonomic relationship or untested assumptions about correlations between trophic morphology and feeding behavior have little meaning for nematophagous arthropods from grassland soils in Colorado.

Key words: arthropod, feeding guild, functional group, grassland soil, nematophagy, phylogenetic constraint.

Although terrestrial ecosystems literally rest on the foundation provided by the soil, little is known about the behavior and function of the invertebrate species that form the below-ground food web. In general, below-ground food webs are described as links between broadly defined taxonomic groups which are assumed to have consistent trophic behaviors. These links occur between "trophic species . . . collection(s) of organisms that feed on a common set of organisms" (3).

Most ecologists agree that aggregations based on similar resource use can be employed to analyze animal communities, and this approach has become firmly established in animal ecology as the guild concept (24) and in ecosystem ecology as functional groups (5). In practice, however, taxonomic identity is usually the first, and often the only, criterion for membership in a trophic species, guild, or functional group, and actual resource use is secondary or even tertiary (14,37). Because of the high diversity of poorly known taxa that compose the below-ground food web, soil ecologists have been especially dependent on using broad taxonomic relationships to infer function.

Nematophages are a functional group of special interest in grassland soils. In the western United States, most nematodes are found in the rhizosphere (13), nematode densities show a positive correlation to live root biomass (43), and nematodes strongly influence primary production (28). Nematodes affect primary production both negatively, when feeding on plant roots (28), and positively, when microbivores stimulate decomposition and mineralization (5,13).

Our objectives were to 1) determine the level of taxonomic resolution necessary to identify the nematophagous arthropod component in grassland soils; 2) present detailed studies of factors such as feeding rates, developmental times, and reproductive potential that influence the ability of mesostigmatic mites (Acari: Parasitiformes: Mesostigmata), the most numerous and diverse group of nematophagous arthropods in grassland soils, to regulate nematode populations; and 3) update and summarize the results of an extensive survey of nematophagous arthropods in grassland soils in Colorado and adjacent areas over the last 3 years.

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Materials and Methods

Tullgren funnels were used to extract live arthropods into jars with moistened plaster of paris floors, and nematodes were isolated from soil samples using Baermann funnels. Cultures of arthropods, nematodes, and fungi were established as described in Walter et al. (37). Arthropod cultures were periodically treated with captan to reduce growth of contaminants. Gut contents, prey choice experiments, and the ability to develop and reproduce on nematode prey were the criteria used to determine if an arthropod was nematophagous. Specific protocols are detailed in Walter et al. (37).

Collections: Fifty sites dominated by grasses or grass-like plants were sampled during 1985–88. In Colorado, 10 sites were semiarid shortgrass prairie dominated by C4 grasses; 2 sites were desert C4 bunchgrasses; 7 sites were low-elevation (1,500–2,000 m), canyon riparian zones surrounded by semiarid habitats; 15 sites were montane riparian meadows between 2,300 and 3,500 m in elevation; 8 sites were riparian cattle and horse pastures; and 4 sites were highly disturbed grasslands including a riparian zone, a lawn, an alfalfa field, and a dry abandoned pasture. Additional shortgrass prairie sites and fields of winter wheat and crested wheatgrass were sampled in Nebraska and Wyoming.

Feeding experiments: Feeding and rearing experiments for nematophages were conducted in 3.7-ml shell vials about one-third filled with charcoal and plaster of paris (1:10 by weight) that maintained a high humidity, provided a two-dimensional mimic of a soil habitat, and allowed for easy observation. Vials were sealed with parafilm and ventilated with a minuten pin to prevent condensation.

Feeding rates were obtained at constant temperature, relative humidity, prey size, prey density, predator life stage, and hunger level using adult female mites starved for 24 hours. Each female was then transferred to a 3.7-ml shell vial with 10 adult female nematodes, except for the large dorylaimids (1,500–2,000 μm long) and *Longidorus* sp. (ca. 5,000 μm long), where five nematodes were used, and *Steinernema feltiae* Filipjev (=*Neoaplectana carpocapsae* Weiser), where 10 infective juveniles were used. Predators consuming 10 nematode prey in less than 24 hours were transferred to new vials at 8–12-hour intervals. Consumption was scored after 24 hours at 25 C by rinsing containers with a stream of water and counting remaining prey. Feeding test results are presented as the mean ± the standard error of the mean (SE) for at least 10 replicate mites of each species (range 10–30). Choice tests were conducted in the same manner except that equal proportions (6:6 or 5:5) of two nematode species were used. Nematode consumption was determined during development of the mites in the same manner except that newly hatched (within 14 hours), unfed mite larvae were used instead of adult females. Developing mites were transferred periodically to prevent prey depletion, and temperature was maintained at 30 C.

Similar feeding-rate experiments were conducted with an arthropod prey, first instar-nymphs of *Tullbergia granulata* Mills (Collembola: Onychiuridae). Ten newly hatched collembolans were transferred to 3.7-ml vials with a fine brush, and an adult female mite was added as in nematode prey experiments. Choice experiments were conducted between equal numbers of collembolan and nematode prey (*Acrobeloides* sp.).

Control vials without mites were used to estimate extraction efficiency for each nematode species. Overall extraction of nematodes from control vials averaged 89% (SE = 12%, N = 131) but was significantly different among nematode species used in feeding experiments (ANOVA, $F = 6.99$, $P < 0.001$). Extraction efficiency corrections used for each prey species were 0.95 for *Acrobeloides* sp. (SE = 0.1, N = 61), 0.81 for *Steinernema feltiae* (SE = 0.4, N = 17), 0.84 for *Acrobeloides nanus* (de Man) (SE = 0.5, N = 7), 0.94 for *Chiloplacus propinquus* (de Man) (SE = 0.2, N = 13), 0.81 for *Deladenus durus* (Cobb) (SE = 0.4, N = 15),

0.82 for *Rhabditis terricola* Dujardin (SE = 0.4, N = 18), 0.90 for *Pelodera* sp. (N = 2), and 1.00 for the large *Longidorus* sp. and dorylaimids. *Pelodera* sp., *Longidorus* sp., and the dorylaimids (*Mesodorylaimus* sp., *Chrysonema aurum* Thorne and ?*Aporcelaimus* sp.) were from field-collected individuals and were not established in culture. Other nematodes readily fed upon by nematophagous mites, but not used in feeding experiments, included *Aphelenchus avenae* Bastian, *Aphelenchoides bicaudatus* (Imamura), *Panagrolaimus subelongatus* (Cobb), and *Longidorus* sp.

Life history studies: Developmental times and egg production rates were obtained at controlled temperature, relative humidity, and food availability and quality. Vial substrates were kept moist and held over a saturated salt solution that maintained 95% RH at 25 C in constant temperature incubators. Excess prey (defined as more *Acrobeloides* sp. than could be eaten between checks) was maintained in rearing vials so that mite development was never limited by lack of food.

Reproductive mode was determined by rearing individual animals and determining the sex of any offspring of virgin females. If eggs were produced only after mating, the reproductive mode was defined as obligate mating. If virgin females produced only male offspring, arrhenotoky (haplo-diploidy) was assumed to be the reproductive mode. If virgin females produced only female offspring and no males were obtained from cultures or field collections, obligate thelytoky was assumed to be the reproductive mode. An exception occurred with *Gamasellodes bicolor* (Berlese) where many field collections included males, but a colony initiated from along the White River in Colorado was thelytokous.

Dry weights for eight mite species removed from cultures and dried in an oven at 60 C for 24 hours were obtained on a Cahn electrobalance using at least 20 adult female mites. A stage-calibrated ocular micrometer was used to measure the length of the dorsal shields(s) along the midline for cultured adult female mites. A cubed length regression ($R^2 = 0.995$), dry weight (μg) = 0.13029 + (42.9481 * length (mm)^3), derived from five species in the small-pore nematophagous mite guild, was used to estimate biomass for unweighed guild members. Dry mass ranged from 43 to 47% in the larger mesostigmatic mites, similar to the 40.3 to 43.0% reported by Edwards (7).

The body weights of nematodes were determined using length and width measurements of 120 randomly selected adult females. Measurements were converted to wet weight using Andràssy's formula (1). Dry weights were assumed to be 25% of wet weights (42). Wet weight to dry weight ratios calculated for adult nematodes used in feeding experiments were 0.818/0.205 μg for *Acrobeloides* sp., 0.137/0.034 μg for *Acrobeloides nanus,* and 0.611/0.153 μg for *Chiloplacus propinquus.*

The BMDP software package was used to perform statistical analyses (6). Significant differences among means in ANOVA analyses were determined using the Newman-Keuls method with n for unequal samples based on the geometric mean (40).

Mites were prepared for the scanning electron microscope by removing live mites from cultures and boiling them in 50% ethanol to extrude the chelicerae. Mites were fixed in 3% glutaraldehyde, dehydrated through increasing concentrations of ethanol and then acetone, sputter-coated with gold, and observed using the Philip's 505 SEM.

Results

Nematophagous arthropods from grassland soils: More than 150 species of soil arthropods from more than 40 grassland sites were tested for nematophagy over a 3-year period. Above-ground arthropod foragers (i.e., ants, spiders, surface hunting insects, plant-inhabiting mites) were not investigated. In the dry grasslands representing much of the area sampled, there is little accumulation of surface litter that would provide habitats for the larger hemiedaphic arthropods, an important component of the soil fauna in forests. As a result, most

grassland soil arthropods are less than 1 mm long (microarthropods). The dominant predatory arthropod fauna is composed of prostigmatic mites (Acari: Acariformes: Prostigmata), mesostigmatic mites (Acari: Parasitiformes: Mesostigmata), diplurans (Insecta: Diplura: Campodeidae, Japygidae), small centipedes (Centipeda), symphylans (Symphyla), pseudoscorpions (Arachnida: Pseudoscorpionida), and—in montane meadows, some low elevation riparian zones, and pastures—beetle larvae (Insecta: Coleoptera: Carabidae, Staphylinidae) and fly larvae (Insecta: Diptera: Cecidiomyiidae, Asilidae, et al.). None of the pseudoscorpions, japygids, and fly larvae (Cecidiomyiidae) tested were observed to feed on nematodes. One centipede (montane) and one campodeid (prairie) were observed to contain nematode prey in their gut contents. An unidentified carabid beetle larva (montane) and an omnivorous staphylinid (*Anotylus* sp.) (prairie) were observed to feed on nematodes in the laboratory. Omnivorous springtails (Collembola), and prostigmatic, astigmatic (Acari: Acariformes: Astigmata), and oribatid (Acari: Acariformes: Oribatida) mites also commonly fed on nematodes (8,29,35). Symphylans (*Symphylella* sp.) (prairie and low elevation montane) often contained nematode prey in gut contents, along with a variety of arthropod body parts. Up to seven large dorylaimid nematodes were observed in a single symphylan gut (38).

The most diverse and abundant nematophagus taxa were mesostigmatic and prostigmatic mites (31–34,36,37). A clear result of the laboratory feeding studies was that most predatory prostigmatic mites from grassland soils (Rhagidiidae, Bdellidae, Cunaxidae, Adamystidae, Raphignathoidea, Erythraeidae) are specialized predators of arthropods and are not important predators of nematodes (37). An exception is an early derivative group of prostigmatic mites, the Endeostigmata, which includes avid nematophages in the families Alicorhagiidae and Alycidae (8,33). These mites are commonly encountered in desert, prairie, riparian, and montane grasslands, but are rarely abundant.

In buried litter in the Chihuahuan desert, a group of prostigmatic mites, the Tydeidae, are considered important predators of free-living nematodes (26,27). Tydeid mites are often the most abundant arthropod in the shortgrass prairie, with densities often approaching 40,000/m² (17). In spite of numerous attempts, however, with nematode prey to establish cultures of tydeid mites, no development, egg production, or definite feeding on nematodes could be confirmed. In agroecosystems, leaf vagrant tydeids are known to feed on a variety of foods, including small arthropods and their eggs, pollen, and fungi (10), and it is possible that they are more important in regulating nematode numbers in Colorado grasslands than we have concluded from our studies.

Mesostigmatic mites appear to be the most important group of nematophagous arthropods in grassland soils in Colorado. Of the 63 species of mesostigmatic mites tested, only six did not readily feed on nematode prey. These included two of three phytoseiid mites (*Amblyseius* spp.), predators of grass-feeding spider mites; a veigaiid mite (*Veigaiia pusilla* (Berlese)), a predator of springtails; an ameroseiid mite (*Ameroseius* sp.), a fungal feeder; and a halolaelapid (*?Halodarcia* sp.) and uropodid mite (*Trachyuropoda* sp.) of unknown feeding habits. Approximately 85% of the mesostigmatic mite species tested (54 species) readily produced eggs and developed to adults with only nematode prey available. Typically, 10–25 species of mesostigmatic mites are present at a grassland site. Density estimates range from about 4,000/m² in a high elevation meadow (3,075 m) (8) to 5,000–12,000/m² in the shortgrass prairie (17) and are probably much higher in pasture soils (15). Adult female mesostigmatic mites range from 240 to > 1,000 μm in length and include many of the larger mites present in grassland soils.

Feeding rate and prey choice by nematophagous Mesostigmata: Feeding rates for 14 different species of mesostigmatic mites were obtained using *Acrobeloides* sp. (extraction efficiency = 95%). Consistency of results was tested by comparing two replicate

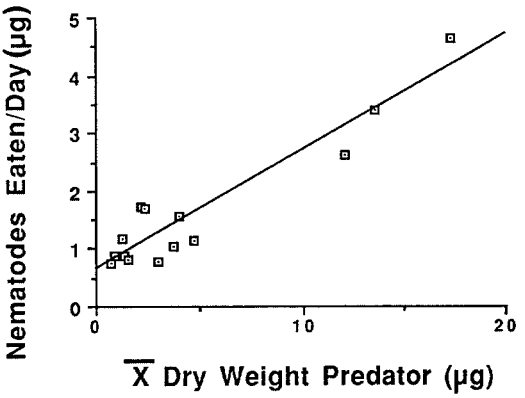

FIG. 1. Regression of average mite body mass (µg) by average biomass of nematodes (*Acrobeloides* sp.) eaten per day for 14 species of mesostigmatic mites from grassland soils in Colorado.

feeding experiments (N = 10 mites each) using the digamasellid mites, *Dendrolaelaps zwoelferi* Hirschmann, *D.* nr. *strenzkei* H., and *D.* nr. *procornutus* H. There were no significant differences among replicates for the three species, indicating that the feeding rate comparisons among mite species using *Acrobeloides* sp. (Fig. 1, Table 1) are reasonable. Three replicate feeding experiments (N = 10 mites each) using the ascid mite *Gamasellodes vermivorax* Walter and a nematode with a low extraction efficiency (*Rhabditis terricola* = 82%) were significantly different, however, indicating that caution should be used when comparing feeding rates on different nematode species (Table 2).

Consumptions of nine species of nematodes were determined for *G. vermivorax* (Table 2). Fewer than two of the large dorylaimids were eaten each day. The smaller rhabditid and tylenchid nematodes were consumed at rates of from four or five per day for *R. terricola* and *S. feltiae* to seven or eight per day for *D. durus* and *C. propinquus*. Overall, *G. vermivorax*, one of the smallest mites tested (1.29 µg), consumed an average of 4.8 nematodes (SE = 0.25, N = 132) each day. When mites were given a choice between equal proportions of nematode prey with different individual consumption rates, approximately equal numbers of both prey were eaten with no

TABLE 1. Size, daily consumption of nematodes (*Acrobeloides* sp.), developmental time, and reproductive mode for a guild of nematophagous mites from grassland soils in Colorado.

Nematode species	Mite size		Nematode consumption		Developmental time†	Reproductive mode‡
	Length (µm)	Dry wt. (µg)	Number	Dry wt. (µg)		
Rhodacaridae						
Rhodacarellus silesiacus	309	1.37	4.4 (± 0.8)	0.90 (± 0.16)	23.8 (± 0.5)	T
Rhodacarus denticulatus	283	1.10	—	—	—	MF
Ascidae						
Protogamasellus hibernicus	253	0.93	4.3 (± 0.6)	0.88 (± 0.37)	15.7 (± 0.2)	T
Protogamasellus mica	243	0.70	3.7 (± 0.5)	0.76 (± 0.11)	9.2 (± 0.1)	T
Gamasellodes vermivorax	304	1.29	5.7 (± 0.9)	1.17 (± 0.18)	6.7 (± 0.2)	A
Gamasellodes bicolor	346	1.91	—	—	8.7 (± 0.03)	T, (?A)
Gamasellodes n. sp.	363	2.19	8.4 (± 0.3)	1.74 (± 0.07)	7.5 (± 0.1)	A
Arctoseius cetratus	320	1.54	4.0 (± 0.09)	0.83 (± 0.19)	5.4 (± 0.1)	OM
Digamasellidae						
Dendrolaelaps zwoelferi	405	3.00	3.8 (± 0.7)	0.78 (± 0.14)	8.6 (± 0.1)	OM
Dendrolaelaps nr. *latior*	439	3.76	5.1 (± 1.4)	1.05 (± 0.28)	9.0 (± 0.3)	OM
Dendrolaelaps nr. *strenzkei*	372	2.34	8.3 (± 0.4)	1.70 (± 0.08)	8.7 (± 0.2)	OM
Dendrolaelaps nr. *procornutus*	449	4.02	7.7 (± 0.67)	1.58 (± 0.12)	8.3 (± 0.2)	OM

Mean (± standard error), – = not done.
† Days at 25 C from egg to adult.
‡ T = thelytoky; A = arrhenotoky; (?A) = some populations with males probably arrhenotokous; OM = bisexual, obligate mating; MF = bisexual, mode unknown.

TABLE 2. Daily consumption of nine species of nematodes by adult female *Gamasellodes vermivorax*.

Nematode species	Mean consumption†	(± SE)	N
DORYLAMIDA			
Aporcelaimidae			
?Aporcelaimus sp.	1.2 a	(± 0.49)	9
Dorylaimidae			
Mesodorylaimus sp.	1.6 a	(± 0.42)	8
RHABDITIDA			
Cephalobidae			
Chiloplacus propinquus	8.2 d	(± 0.40)	10
Acrobeloides nanus	5.8 bcd	(± 0.77)	10
Acrobeloides sp.	5.7 bcd	(± 0.87)	15
Rhabditidae			
Pelodera sp.	5.0 bc	(± 0.77)	10
Rhabditis terricola	3.8 b	(± 0.44)	30
Steinernematidae			
Steinernema feltiae	4.7 b	(± 0.45)	24
TYLENCHIDA			
Neotylenchidae			
Deladenus durus	7.1 cd	(± 0.58)	16

There are significant differences in numbers of different nematode species consumed (ANOVA, $F = 10.23$, $P < 0.00001$). Entries followed by the same letter are not significantly different at the 5% level (Newman-Keuls test).

† Mean consumption is the amount consumed in 24 hours at 25 C.

significant indication of preference (Table 3).

Consumption of *Acrobeloides* sp. during development from larva to adult was measured for 26 *G. vermivorax* at 30 C (at which temperature post-egg development takes less than 3 days). On average, 13.7 (± 1.0, N = 19) nematodes were consumed in the development from larva (0.13 μg) to adult female (1.29 μg), or 2.8 μg of nematode biomass to produce (1.29 − 0.13 =) 1.16 μg of mite biomass (41.5% yield). The smaller males consumed 23% fewer nematodes, averaging 10.6 (± 1.8, N = 7) nematodes or 2.2 μg of nematode biomass.

When mite body mass is regressed against feeding rate, a strong linear relationship is apparent (Fig. 1), with 89% of the variance in consumption explained by body weight of the predator. If the three largest species are removed from the regression, the R^2 falls to 0.69. It is possible that more data for larger predators might produce a line that would better fit a power function. Most of the variation in consumption rates occurs among the smaller species (Fig. 1, Table 1), and consumption as a function of body mass declines with increasing size. For example, the smallest mite, *Protogamasellus mica* (Athias), consumes about 1.09 μg nematodes/μg body weight daily, but *Rhodacarellus silesiacus* Willmann, which is about twice the mass of *P. mica*, consumes only 0.65 μg nematodes/μg body mass daily. The three largest mite species tested—*Lasioseius* sp. (female = 12.1 μg), *Lasioseius berlesei* (Oudemans) (female = 13.5 μg), and *Geolaelaps* sp. (39) (female = 17.3 μg)—consumed 2–5 times as many nematodes per day as the smaller mites, but in pro-

TABLE 3. Mean (± SE) number of nematodes eaten by predatory mites when offered in equal proportions over a 24-hour period (12 hours for *Lasioseius* sp.) at 25 C.

Predator	Mean no. nematodes eaten		N	
	Acrobeloides sp.	Other spp.		
		Deladenus durus		
Gamasellodes vermivorax	3.0 (± 0.49)	2.3 (± 0.28)	12	NS
Lasioseius sp.	1.6 (± 0.42)	2.3 (± 0.29)	9	NS
		Steinernema feltiae		
Gamasellodes vermivorax	3.4 (± 0.49)	2.9 (± 0.30)	20	NS
Dendrolaelaps zwoelferi	1.8 (± 0.32)	1.6 (± 0.28)	20	NS
		Chrysonema sp.		
Gamasellodes vermivorax	1.8 (± 0.86)	2.0 (± 0.00)	5	NS

NS = not significant.

portion to their respective body sizes this represented only 0.218, 0.255, and 0.272 μg nematodes/μg body mass daily. Mesostigmatic mites that are 2–3 times the body mass of *Geolaelaps* sp. are commonly found in the more mesic grassland habitats in Colorado. The large body size of these animals probably restricts their access to soil-inhabiting nematode prey, and we suspect that arthropod and annelid prey are more important resources to these predators.

The small-pore nematophagous mite guild: The species near the base of the regression line in Figure 1 are members of a closely related complex in the families Rhodacaridae, Digamasellidae, and Ascidae. The Rhodacaridae are the best known members of this complex, and in our experience the superficially similar digamasellid and ascid mites are often misidentified as rhodacarids. Rhodacarid mites are strongly euedaphic (25) and are characteristic of the deeper layers of mineral soil and interstitial spaces down to ground water (16). In the shortgrass prairie, rhodacarid mites reached their peak biomass levels at depths of 15 to 30 cm (17). The ascid mites *G. vermivorax* and *P. mica* can be found more than 8 m below the surface in association with mesquite roots in the Chihuahuan desert (D. W. Freckman, pers. comm.).

We consider this group of species to represent a guild (24) (hereafter the SPNM guild) characterized by 1) an ability to produce continuous cultures on nematode prey, 2) having similar chelicerae with alternating rows of large and small teeth (Type 4 below) (Fig. 2G, H) suggested as an adaptation for feeding on arthropods and nematodes (15), and 3) a convergent body plan allowing these animals access to small pore spaces and the prey that occur there. Morphological adaptations allowing access to these small pore spaces in the soil include a small body size (< 450 μm in length), narrow shape (width ½ length or less), and divided dorsal shield, usually with hypertrophied attachments (scleronoduli) for muscles that allow flexion of the body around soil particles (Rhodacaridae, Digamasellidae, and *P. mica* in the Ascidae).

Rhodocarellus silesiacus and *Arctoseius cetratus* (Sellnick), the most eurytopic members of the guild, occur in lawns, pastures, shortgrass prairie, low elevation riparian grasslands, montane meadows, and desert grasslands. An undescribed species of *Rhodacarellus* from the periphery of the study area is very rare in the Sidney, NE prairie samples. *A. cetratus* is replaced by a complex of larger species of *Arctoseius* at high elevations. *Rhodacarus denticulatus* Berlese and *P. mica* are broadly distributed in grassland habitats below 2,100 m. An undescribed species of *Gamasellodes* and *G. vermivorax* are found in association with C4 grasses and are replaced by *G. bicolor* in low elevation pastures and montane grasslands dominated by C3 grasses. *D.* nr. *strenzkei* and *D.* nr. *procornutus* are also found in association with C4 grasses and are replaced by *D. zwoelferi* and *D.* nr. *latior* (Leitner) in pastures dominated by C3 grasses. *Protogamasellus hibernicus* Evans and *Gamasellodes* sp. are the only members of the guild that were restricted to a few sites. About 12 species in this guild occur in grassland soils in Colorado (Table 1), and up to six species are often collected at a single grassland site.

Although the species in the SPNM guild are closely related and share similar prey, microhabitats, and macrohabitats, there are significant differences in most of the physiological parameters that were tested. All three of the reproductive modes found in the Acari (23) occur within the guild and the family Ascidae (Table 1). Reproductive mode is moderately consistent at the generic level, although thelytoky appears to have arisen independently in different genera. The reproductive period and lifetime egg production were measured for six members of the guild and showed significant differences (Table 4).

Developmental rates on nematode prey are variable among the guild members (Table 1), although many of the differences are minor. Most guild members take 7–9 days to develop from egg to adult at 25 C; however, *P. hibernicus* takes about twice and *R. silesiacus* about three times as long (on

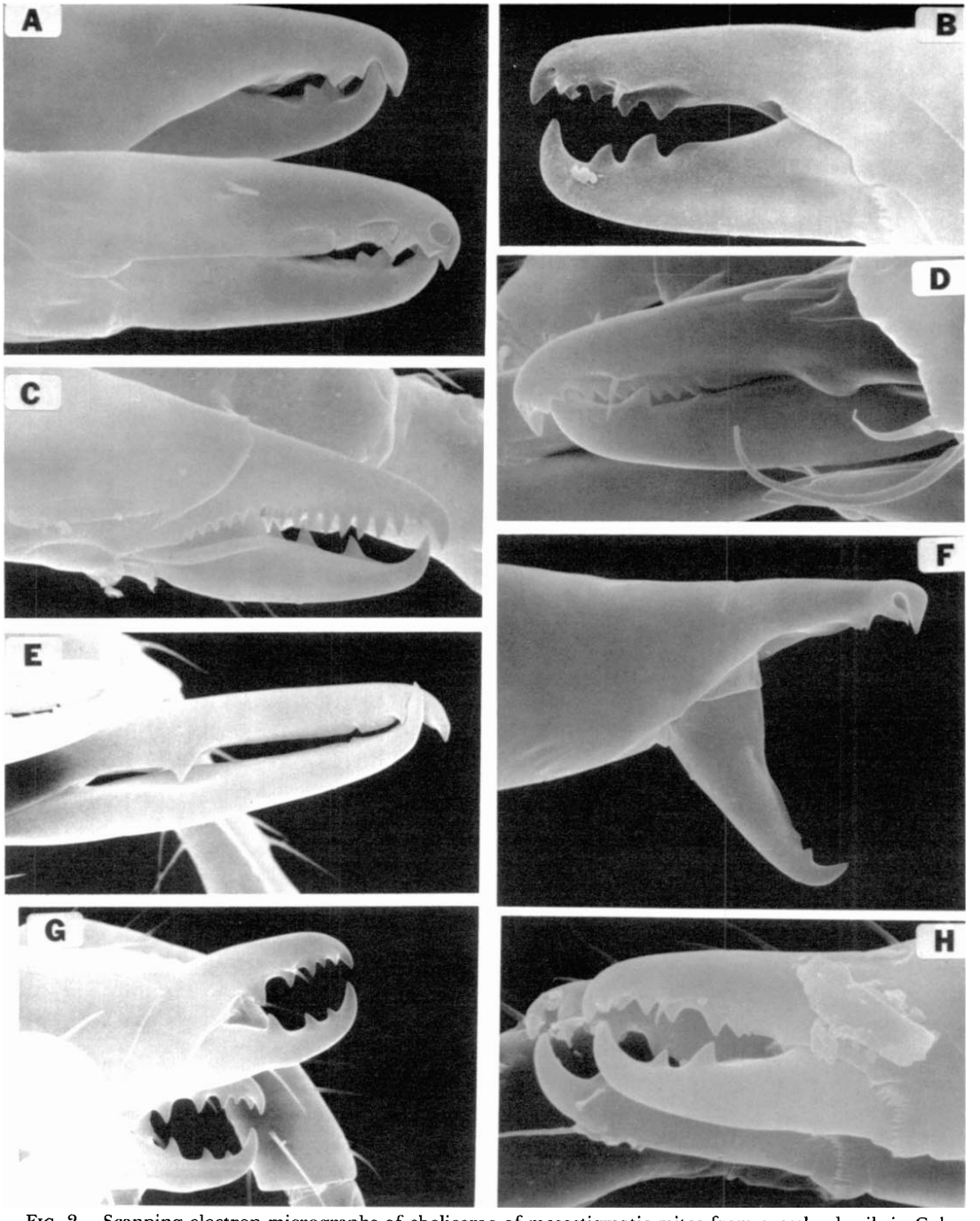

FIG. 2. Scanning electron micrographs of chelicerae of mesostigmatic mites from grassland soils in Colorado. A) Type I *Zygoseius furciger*, nematophage 2,720×. B) Type 1, *Asca nesoica*, nematode-arthropod predator 3,540×. C) Type 2, *Lasioseius berlesei*, omnivore 1,620×. D) Type 2, *Cheiroseius* nr. *mutilis*, nematophage 1,490×. E) Type 3, *Veigaia pusilla*, arthropod predator 1,150×. F) Type 3, *Cheiroseius* sp., nematophage 1,550×. G) Type 4, *Rhodacarellus silesiacus*, nematode-arthropod predator 1,310×. H) Type 4, *Protogamasellus hibernicus*, nematode-arthropod predator 2,890×.

arthropod prey, developmental times are even longer). We have limited data indicating that developmental times of other Rhodacaridae are also relatively long. Rhodacarid mites reared at room temperature (23 C) on a mixed diet of nematodes and arthropods took about 1 month to develop from egg to adult. At room temperature,

TABLE 4. Mean (± SE) reproductive period in days and total number of eggs laid by some members of a guild of nematophagous mesostigmatic mites from grassland soils in Colorado feeding on a rhabditid nematode (*Acrobeloides* sp.) at 25 C.

Nematode species	Reproductive period	Total eggs	Eggs/day
Rhodacaridae			
Rhodacarellus silesaicus	53.8 (± 5.7) c	67.2 (± 5.4) a	1.2
Ascidae			
Gamasellodes vermivorax	40.2 (± 10.3) bc	67.5 (± 5.2) a	1.7
Protogamasellus mica	16.5 (± 10.3) ab	32.7 (± 5.2) b	2.0
Digamasellidae			
Dendrolaelaps zwoelferi	20.0 (± 1.4) ab	94.4 (± 4.0) c	4.7
Dendrolaelaps strenzkei	14.0 (± 1.3) a	54.3 (± 4.0) a	3.9
Dendrolaelaps procornutus	15.8 (± 2.7) a	66.0 (± 9.2) a	4.2

Within a column, entries followed by the same letter are not significantly different ($P < 0.05$, Newman-Keuls test on significantly different ANOVA).

egg developmental times were 8.8 days (± 0.3, N = 9) for *R. denticulatus,* 7.0 days (± 1.0, N = 2) for *Rhodacarellus* sp., and 5.9 days (± 0.6, N = 9) for *R. silesiacus,* whereas for other guild members egg developmental time ranged from 3 to 5 days.

Morphological specializations for nematophagy in the Mesostigmata: Karg (15) has suggested that family and generic level taxa of mesostigmatic mites have become specialized feeders and these feeding specializations are reflected in the structure of the mouthparts. The chelicerae of 30 species of mesostigmatic mites whose feeding behaviors had been determined were examined using the scanning electron microscope (SEM). The chelicerae of an additional 10 species were examined using phase contrast microscopy. Cheliceral structure is often diagnostic at the generic level, but major differences in structure can exist among congeners (compare Fig. 2D with 2F) (11,19).

According to Karg (15), mesostigmatic mites that have become specialized nematophages have stout cheliceral digits with either a few large, offset teeth (Type 1) (Fig. 2A, B) meant to hold and crush the smooth, elongate nematode body as in the Eviphidoidea (Eviphididae, Macrochelidae, Pachylaelapidae), a few large, offset teeth opposed by a saw-like edge of sharp teeth (Type 2) (Fig. 2C, D) as in *Lasioseius* (Ascidae), or a tweezer-like arrangement of distal teeth opposed by a small saw-like area as in some species of *Cheiroseius* (Type 3) (Fig. 2E, F). General predators of nematodes and arthropods have more slender chelicerae with alternating rows of large and small teeth (Type 4) (Fig. 2G, H) as in the SPNM guild.

As has been the experience with Phytoseiidae in agroecosystems (19), correlating specific cheliceral morphologies with feeding on particular prey types was usually possible only a posteriori. For example, for three species with Type 1 chelicerae, *Zygoseius furciger* Berlese (Pachylaelapidae) (Fig. 2A) is entirely nematophagous, as would be predicted by Karg (15); however, *Macrocheles schaeferi* Walter (Macrochelidae) and *Asca nesoica* Athias-Henriot (Ascidae) (Fig. 2B) are equally proficient predators of arthropods and nematodes.

Mites with Type 4 chelicerae readily attack both nematode and arthropod prey, as predicted by Karg (15), although in our experiment there was a tendency to prefer nematode prey in some species. For example, *R. silesiacus* consumed an average of 4.4 nematodes per day (Table 1) but averaged only 1.4 (± 0.2, N = 35) of the smaller collembolans (first-instar *T. granulata*) ($P < 0.05$). These differences in consumption rates, however, usually were not significant. For example, *G. vermivorax* averaged 5.7 nematodes (Table 1) and 4.8 collembolans (± 0.8, N = 24) and *P. mica* consumed 3.7 *Acrobeloides* sp. (Table 1), 4.7 (± 0.6, N = 20) collembolans, and 5.7 (± 0.5, N = 10) *C. propinquus.*

In choice tests with equal proportions of

first-instar collembolans and nematodes (*Acrobeloides* sp.), there was a tendency to prefer nematode prey, but the results were not significant. For example, *D. zwoelferi* ate more nematodes than collembolans (2.3 ± 0.4 nematodes to 1.5 ± 0.3 collembolans, N = 20, NS, $P > 0.09$). *P. hibernicus* consumed an average of 4.0 ± 1.4 nematodes to 2.4 ± 1.4 collembolans (NS, N = 5) when given a choice, although feeding rates on collembola alone, 7.4 ± 0.6, N = 20, were significantly higher than on nematodes alone (Table 1). *G. vermivorax* also consumed equal numbers of nematodes and collembolans in a choice test (36).

Type 2 chelicerae, characterized by a long row of saw-like teeth (Fig. 2C, D), appear to have been derived convergently in a number of unrelated taxa in the Ascidae (some species of *Lasioseius, Cheiroseius, Proctolaelaps, Antennoseius,* and *Protogamasellus*). All of these species do feed on nematodes; they also readily feed on small arthropods, and a number of them have been reported to feed on fungi as well (12,18). Preliminary experiments suggest that the elongate row of teeth on the paraxial face of the chelicerae in *Lasioseius* is associated with omnivorous species that feed on fungal material as well as nematodes and arthropods.

Type 3 chelicerae are characterized by a displacement of teeth to the distal end in a tweezer-like arrangement (Fig. 2E, F). In some cases, this cheliceral morphology is associated with a strong preference for arthropod prey. For example, *V. pusilla* (Fig. 2E) will feed on nematodes only if starved, but it is a very efficient predator of collembolans (37). Predation on pauropods, proturans, prostigmatic mites, and collembolans has been reported for other species of *Veigaia* (11). Irrespective of cheliceral morphology, species of *Cheiroseius* (Fig. 2D, F) feed avidly on nematodes.

Large general predators of arthropods and nematodes in the genus *Geolaelaps* (= *Hypoaspis* in part) do have a distinctive cheliceral morphology (38); however, there is no reason to assume that it represents a specialized trophic function, as suggested by Karg (15), since many other cheliceral morphologies are equally proficient at general predation. Chelicerae attributed to collembola-mite specialists in the genera *Pergamasus* and *Paragamasus* (Mesostigmata: Parasitidae) (15) are also efficient structures for attacking nematodes. Very high rates of predation were observed on infective juveniles of *Steinernema feltiae* by *Pergamasus* sp. (8), and we have found it easier to maintain cultures of *Pergamasus* sp. and *Paragamasus* sp. on nematode than on collembola prey.

Discussion

Taxonomically defined functional groups based on minimal biological information are the norm in soil biology (20). For example, nematodes are generally grouped into five feeding categories: predators, fungivores, bacteriovores, plant feeders, and omnivores, based on the phylogenetic distribution of different buccal morphologies and their correlation to observed feeding in the laboratory and field (2,21,22,41). The least well known of these groups are the omnivorous nematodes that often form a significant part of the nematode community in grassland soils (9). Broad diets including omnivory are also common in nematophagous mites. Phylogenetic relationship is an indication of shared abilities, or at least of shared constraints on morphology, physiology, and behavior; but is phylogenetic relationship a sufficient criterion for predicting ecological function? Our research indicates that critical functional parameters—e.g., feeding behavior, developmental rate, and reproductive mode—are rarely predictable above the generic level.

In grassland soils in Colorado, the class level taxa of arthropods that contain important nematophages are the Acari and Symphyla. Symphylans are a good example of why broad generalizations about trophic function based on limited information are often misleading. In the past, symphylans were considered to be detritivores or plant root-feeders. The symphylans in Colorado, Wyoming, and Nebraska grasslands, how-

ever, have primarily animal prey in their gut contents and little detrital, fungal, or plant materials (38). Since all of the symphylans collected in these grasslands appear to be predatory species in a single genus, it seems reasonable to classify these animals as a feeding guild.

Considering the Acari to represent a feeding guild or functional group, however, is absurd. Most grassland soil mites, both in species number and number of individuals, are fungivores and herbivores. Some of these fungivores are actually omnivores that readily attack nematodes (8,10,26–28,30,33,35,37); however, this is a species level phenomenon and not necessarily characteristic of higher level taxa. All of the acarine suborders present in grassland soils (Prostigmata, Oribatida, Astigmata, and Mesostigmata) include nematophagous species. All of them also include mycophagous species. Family and generic level taxa are better predictors of similar behavior, physiology, and reproductive mode. Exceptions occur in large genera and families, especially when omnivory is a common behavior, or in congeners from different macrohabitats. For example, species of *Dendrolaelaps* from pastures (*zwoelferi, latior*) have significantly lower consumption rates and higher reproductive outputs than do species from dry grasslands (*strenzkei, procornutus*) (Tables 1, 2).

If guilds or functional groups are to be of use in the analysis of ecological communities, they must represent clear functional units with predictive value and cannot be based on convenient taxonomic groupings that are unsupported by functional information. For example, in the shortgrass prairie the SPNM guild is dominated by the rhodacarid mites *R. silesiacus* and *R. denticulatus* and the ascid mites *G. vermivorax, A. cetratus,* and *P. mica* that typically represent > 90% of the Mesostigmata collected. At different seasons and locations, the proportions of the species in the two families can be quite variable. Because of the long developmental times, low reproductive rates, and low consumption rates of the rhodacarid mites, compared with the ascid mites, areas in which most of the guild are rhodacarids could be expected to exert much less impact on nematode populations than areas dominated by ascid mites.

A number of important questions about soil arthropods need to be answered before their role as predators of nematodes can be fully evaluated. Perhaps the most important question is how are nematophagous arthropods distributed in the soil. In grassland systems where most primary productivity occurs below ground, where nematode biomass is correlated to plant root biomass (28), and where nematode densities are highest in the rhizosphere (13), we suspect that nematophagous arthropods are likely to be strongly associated with root systems. If this turns out to be the case, then arthropods may be important predators of ectoparasitic, and perhaps of juvenile stages of endoparasitic, plant-feeding nematodes.

The links between ecosystem level processes and communities of species are forged by the behaviors of the species in those systems (4,20). If the purpose of soil biology is to understand the interactions among the soil fauna and flora with the hope of predicting the dynamics of decomposition, nutrient cycling, and plant growth, this discipline must move beyond the level of counting dead bodies unassociated with meaningful taxonomic and functional information. We suggest that family level and, in many cases, generic level identifications are within the grasp of a competent biologist and should be considered the minimum acceptable level of identification in soil studies. This improved precision in identification should be combined with behavioral studies to yield the kind of information that is essential to construct guilds and functional groups with predictive value.

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