GEOLAELAPS OREITHYIAE, N. SP. (ACARI : LAELAPIDAE), A THELYTOKOUS PREDATOR OF ARTHROPODS AND NEMATODES, AND A DISCUSSION OF CLONAL REPRODUCTION IN THE MESOSTIGMATA

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SOIL MICROFAUNA
GAMASIDA
SYSTEMATIC
PREDATION
PARTHENOGENESIS
COLORADO

ABSTRACT : In the soils of fields and grasslands of Colorado, mesostigmatid mites are the most abundant predators of nematodes in the below-ground food web. A new species in the assemblage of predators, *Geolaelaps oreithyiae*, is described. *G. oreithyiae* is closely related to *G. aculeifer* (Canestrini), but differs in size, details of ornamentation of the ventral shields, lengths of dorsal shield setae, and mode of reproduction. Virgin females of *G. oreithyiae* lay up to 5 eggs per day at 25°C and all offspring develop into females, indicating a thelytokous mode of parthenogenetic reproduction. In grassland soils of the central United States, *Cosmolaelaps cf. vacua* (Michael) (Laelapidae), *Rhodacarellus silesiacus* Willmann (Rhodacaridae), *Amblyseius (Neoseiulus) setulus* (Fox) (Phytoseiidae), *Protogamasellus mica* (Athias), *P. hibernicus* Evans, *Lasioseius youcefi* Athias, *L. berlesi* (Ouds.) (Ascidae), and *Veigaia pusilla* (Berlese) (Vergaiidae) are thelytokous.

MICROFAUNE DU SOL
GAMASIDA
SYSTÉMATIQUE
PRÉDATION
PARTHÉNOGENÈSE
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RÉSUMÉ : Dans le sol des champs et dans les sols herbeux du Colorado les acariens Mesostigmatides sont les prédateurs de nématodes et d'arthropodes les plus abondants du réseau de consommation souterrain. Dans cet assemblage de prédateurs, *Geolaelaps oreithyiae*, une nouvelle espèce, est décrite. *G. oreithyiae* ressemble de très près à *G. aculeifer* (Canestrini) mais en diffère par sa taille, les détails de l'ornementation des boucliers ventraux, la longueur des soies dorsales et le mode de reproduction. Les femelles vierges de *G. oreithyiae* pondent jusqu'à 5 œufs par jour à 25°C et tous les rejetons deviennent des femelles, indiquant un mode de reproduction thélytoke et parthénogénétique. Dans les sols herbeux du centre des États Unis, *Cosmolaelaps cf. vacua* (Michael) (Laelapidae), *Rhodacarellus silesiacus* Willmann (Rhodacaridae), *Amblyseius (Neoseiulus) setulus* (Fox) (Phytoseiidae), *Protogamasellus mica* (Athias), *P. hibernicus* Evans, (Ascidae), *Lasioseius youcefi* Athias, *L. berlesi* (Ouds.), et *Veigaia pusilla* (Berlese) (Vergaiidae) sont thélytokes.

INTRODUCTION

A major component of the below-ground food web are arthropods that act as predators of nematodes, mites, springtails, insects, and other invertebrates that mediate the decomposition of organic residues or attack plants, including economically important crops (MOORE *et al.* 1988). In the fields and grasslands of Colorado, these predators are primarily mites, especially mites in the suborder Mesostigmata (WALTER 1987). Although these animals occupy a key juncture in the rhizosphere food web (Fig. 1), little research has been devoted to their systematics or ecology.

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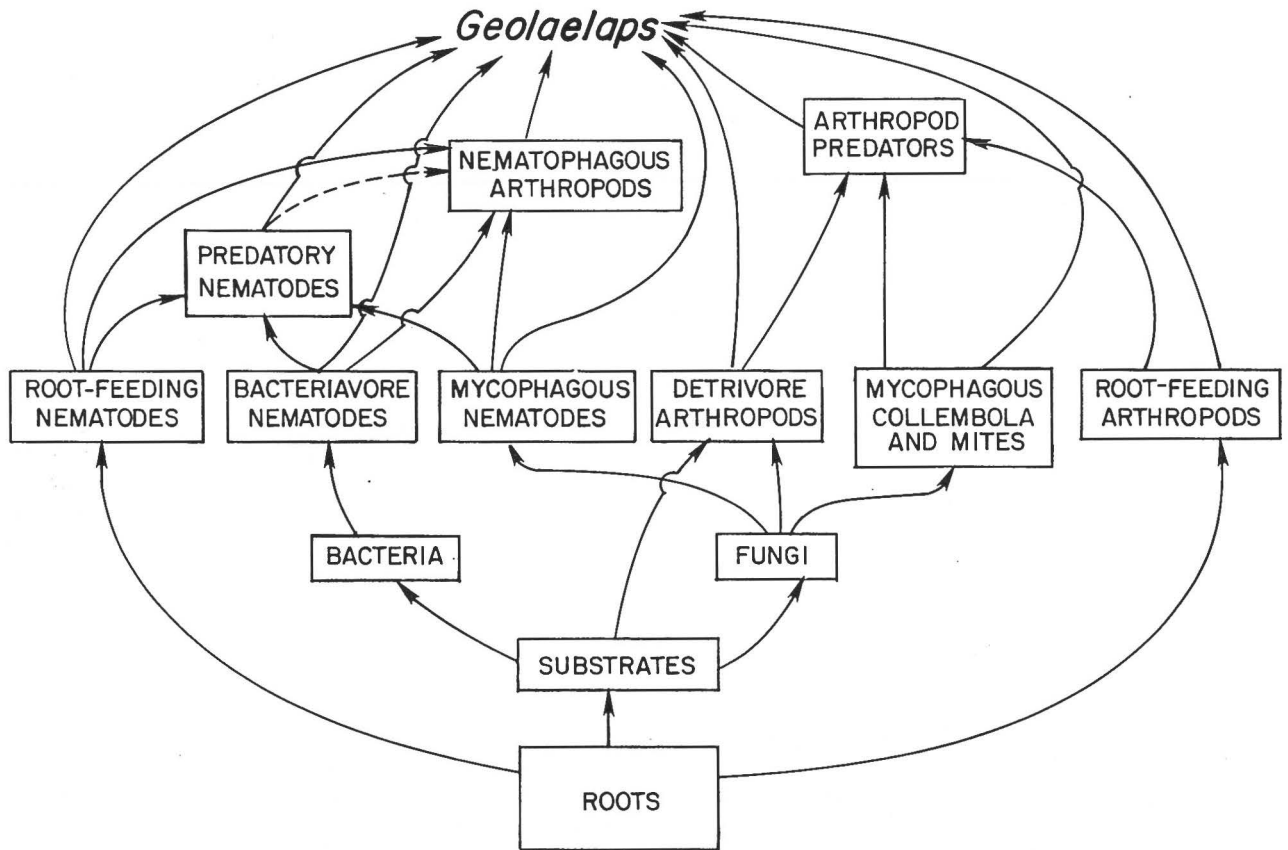
FIG. 1 : Trophic sink web for *Geolaelaps* in croplands in Colorado. Because of their large size, aggressive behavior, and broad diet, species of *Geolaelaps* occupy a key juncture in the below-ground food web.

Thelytokous parthenogenesis is a reproductive strategy in which unfertilized eggs develop into only female offspring. Although there is little information about the frequency or ecological distribution of thelytokous animals in terrestrial ecosystems, obligate parthenogenesis is known to occur in a number of soil invertebrate taxa (Gastrotricha, Rotifera, Nematoda, Oligochaeta, Tardigrada, Opiliones, Insecta, Symphyla, Pselaphognathida, and Acarina) (HUGUES & CANCINO 1985). In the Mesostigmata, a number of taxa are known to be composed of thelytokous species (OLIVER 1971).

In this paper, a new, thelytokous species of hypoaspidine mite, *Geolaelaps oreithyiae*, is described. The genus *Geolaelaps* is redefined, and the biology and behavior of the known species are reviewed. The occurence of thelytokous species of

mesostigmatic mites in Colorado grasslands is discussed.

METHODS AND MATERIALS

Soil arthropods were collected using Tullgren funnels. Live collections were made into containers with moistened plaster-charcoal floors, and removed with a small brush. Cultures were maintained at room temperature (20-26°C) or in a constant temperature incubator at 25°C following the methods in WALTER *et al.* 1988. A variety of potential prey items were offered to predators, and scored for attacks, consumption, reproduction, and development of predators. Consumption rates determined by adding individual *G. oreithyiae* to constant

densities of prey items in one dram shell vials with plaster-charcoal floors sealed with Parafilm@. Consumption was scored daily. Parthenogenetic reproduction was confirmed by obtaining virgin females from isolated immature stages, rearing any progeny produced to adults, and determining their sex. Measurements were obtained from slide-mounted specimens using an ocular grid calibrated with a stage micrometer. Fresh weights were obtained on a microbalance using freeze-killed individuals or unfrozen eggs ; dry weights were obtained after 24 h at 60°C.

SYSTEMATICS

The genus *Hypoaspis sensu lato* Canestrini has been used as a catchall for a large variety of free-living soil mites, inhabitants of animal nests, and associates of insects. The species of the genus, *H. krameri* (Can.), is an associate of log-inhabiting beetles and along with other related species exhibits a number of morphological apomorphies lacking in free-living hypoaspidines. *Hypoaspis* s.l. has been variously divided into subgenera (EVANS & TILL 1966, KARG 1979, 1982) which are often given generic status (e.g. *Hypoaspis sensu strico, Cosmolaelaps, Stratiolaelaps, Gymnolaelaps, Pneumolaelaps, Alloparasitus, Laelaspis* and *Geolaelaps*) (EVANS & TILL 1979). Many morphological, behavioral, and ecological attributes are associated with the various hypoaspidine genera, and we believe that a clearer understanding of the ecology of hypoaspidine species results if large, ungainly taxa such as *Hypoaspis* s.l., that are not clearly monophyletic, are avoided. As a result, we propose a narrow definition of *Geolaelaps* Berlese 1924 (type species = *Hypoaspis aculeifer* Can.) to accomodate our new species.

GEOLAELAPS SENSU STRICTO

DIAGNOSIS : Free-living hypoaspidine Laelapidae. Females with sternal shield longer than wide with three pairs of setae and two pairs of pores ; metasternal setae and associated pores in soft integu-

ment ; epigynial shield drop-shaped with one pair of setae ; anal shield subtriangular with three setae ; 8 pairs of ventral setae in soft integument ; movable digit bidentate. Males with holoventral shield ; spermadactyl simple with curved tip ; movable digit unidentate. Both sexes with curved row of small teeth flanked by larger teeth on fixed digit (Fig. 3 e) ; dorsal shield setae simple ; tarsus II with thickened super-like setae (Fig. 3 d) ; distal segments of legs II-IV with spine-like ventral setae ; tarsus IV with thick, elongate setae ; palp apotele 2-3 tined. Leg chaetotexy normal.

Under this définition the genus *Geolaelaps* includes the following species : *aculeifer* (Canestrini), *augustus* (Karg), *queenslandicus* (Womersley), *neaculeifer* (Hirschmann), *disjuncta* (Hunter & Yech), and the new species described below.

Geolaelaps oreithyiae, new species

DIAGNOSIS : With the characteristics of the genus s.s. All female species ; adult fixed digit with 5-6 small teeth flanked by larger teeth (Fig. 3 e) ; movable digit bidentate ; dorsal shield with 39 pairs of simple setae, similar in size (most 40 $\pm$ 5 μm) (Fig. 3 a) ; sternal shield with unpaired cell along midline between setae 2-3 ; palp apotele 2 tined. *G. oreithyiae* is easily distinguished from *G. aculeifer* by relative lengths of the setae on the anterior dorsal shield (compare Fig. 3 b to 3 a), and by its smaller size.

The specific name is derived from the legendary Oreithyia (*Greek* = she who rages on the mountain), a war leader of the Amazons during their siege of Athens.

FEMALE : Dorsal shield (Fig. 2 a) 515-605 μm long ($\bar{x}$ = 556, SE = 3.9, N = 25 for all measurements) averaging 306 μm wide (SD = 2.9) with 39 pairs of short, smooth-acicular seta, j-, z-, (except z1), s-, and r-series 31-37 μm in length, shield remaining relatively broad posteriorly, J5 21 μm and Z5 26 μm in length. Sternalshield (Fig. 2 b) 151-169 μm long ($\bar{x}$ = 161, SE = 1.0) with three pairs of setae, two pairs of pores, reticulate pattern with distinctive unpaired cells along midline between
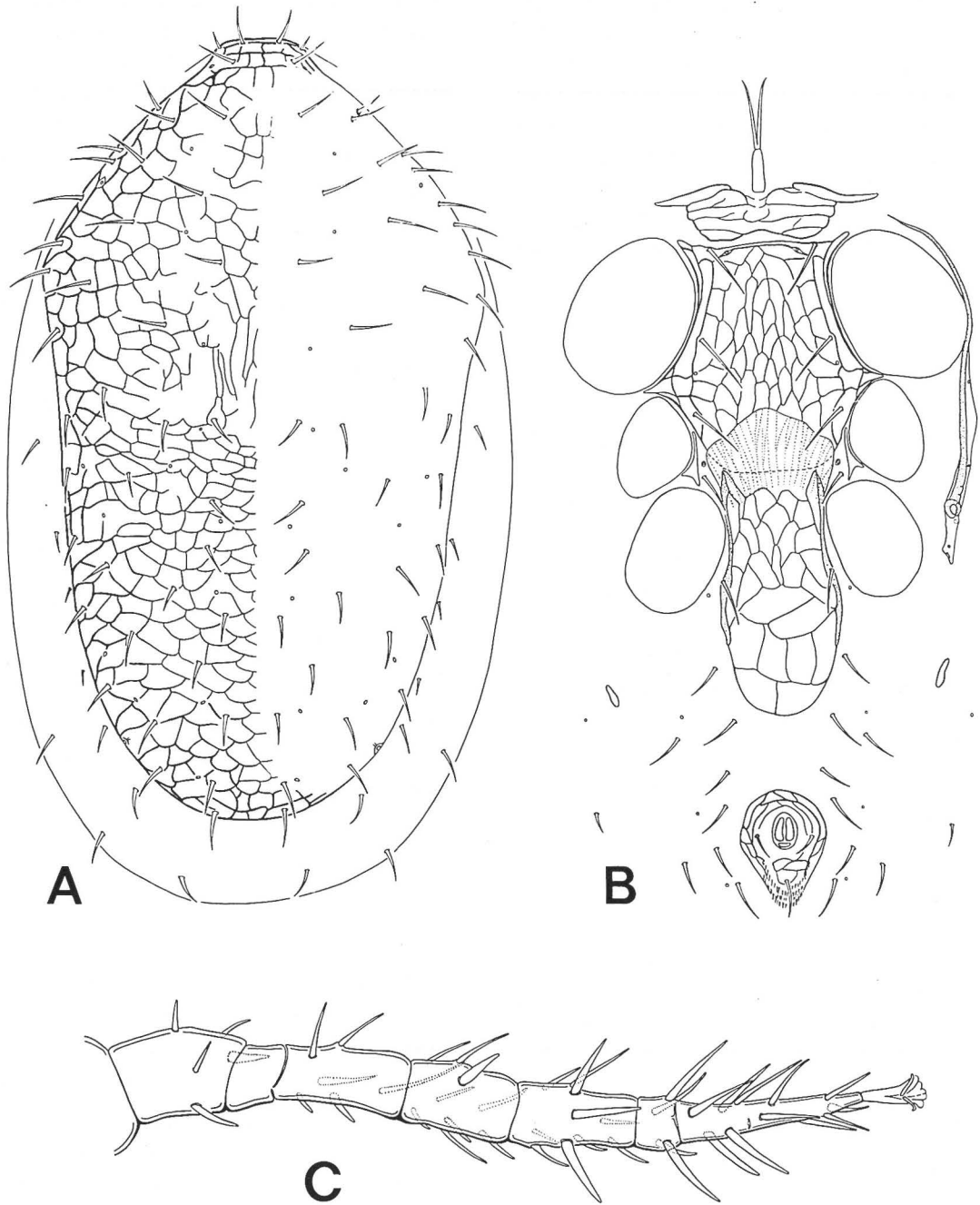
FIG. 2 : *Geolaelaps oreithyiae*, new species, adult female a) dorsum ; b) venter ; c) leg IV.
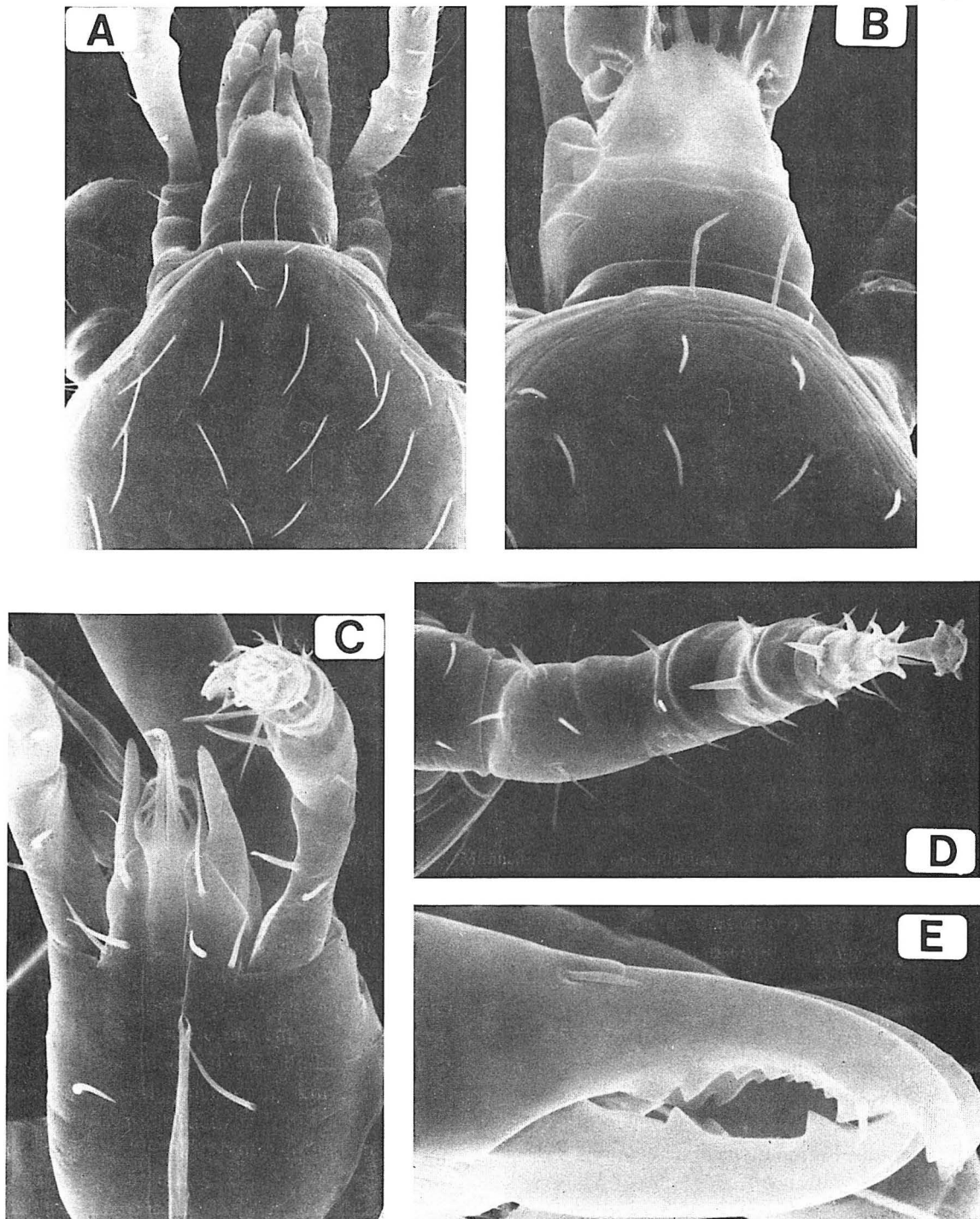
Fig. 3 : Scanning electron micrographs of a) *G. aculeifer* (Can.) from Colorado, adult female anterior dorsal shield and gnathosoma ; b) *G. oreithyiae* n. sp., adult female anterior dorsal shiel and gnathosoma ; c) venter hypostome and palp ; d) venter leg II ; e) antiaxial view of chelicera.

st2-3. Epigynial shield tongue shaped with 1 pair setae on margin, associated pore in integument, inverted V-shaped line differentiates small, tightly-packed cells in anterior from large, more rounded cells posteriorly. Metasternal seta and associated pore in smooth integument. Anal shield small, dropshaped, reticulate ornamentation anteriorly, well developed cribrum posteriorly, with pair smooth paranal setae, short, smooth postanal seta. Soft-integument plicate with 8 pairs smooth ventral setae, two pairs pores, small elongate metapodals. Marginal setae short, smooth, 9 pairs in two series. Leg chaetotaxy normal. Tarsus I 139-155 μm long ($\bar{x}$ = 149, SE = 0.8). Leg II (Fig. 3 d) with spine-like ventral setae on femur (1), genu (1), tibia (2), tarsus (3). Tarsus II terminating in 4 spur-like setae. Leg III spine-like ventral setae on genu (2), tibia (2). Leg IV with spine-like setae on genu (1), tibia (3). Tarsus IV 144-166 μm long ($\bar{x}$ = 157, SE = 1.0) with lateral setae on basitarsus, and other setae on telotarsus thickened and elongate. Cheliceral segment II 175-193 μm long ($\bar{x}$ = 184, SE = 0.9); dorsal setae simple; fixed digit with basal shear followed by curved row of 5-6 small teeth bracketed by larger teeth (Fig. 3 e), acicular pilus dentilis, and 2 offset distal teeth; movable digit bidentate 67-76 μm in length ($\bar{x}$ = 73, SE = 0.5); arthrodial process a simple fringe. Hypostome (Fig. 3 c) with six rows of deutosternal denticles, each with 15-20 small teeth; corniculae reaching approximately to mid-palpfemur; internal malae with divided median element and 3 fringed lobes. Epistome procurved, denticulate.

TYPE DEPOSITION : The holotype female is from a culture initiated from females collected in an abandoned alfalfa field in Fort Collins, Colorado in May 1987. Paratypes include additional females from culture, and collections from a cow pasture (10 & 25 May 1987) and a plowed field (15 April 1987) at Bay Farm, Colorado State University, Fort Collins, Colorado. The holotype and a paratype series will be deposited with the U.S. National Museum, Washington, D.C. Paratypes will be deposited at the Acarology Laboratory, The Ohio State University, Columbus, OH; the acarology collection, Department of Entomology, Oregon State University, Corvallis, OR; the Museum of Zoology, University of Michigan, Ann Arbor, MI; the Canadian National Collection, Ottawa; the Field Museum of Natural History, Chicago, IL; and the Soil Microarthropod Research Collection, NREL, Colorado State University, Fort Collins, CO.

BIOLOGY

Two species of *Geolaelaps* often coexist in Colorado. The larger species (dorsal shield 601-756 μm in length, tarsus IV 211-250 μm in length) appears to be *G. aculeifer* (Can.) (KEVAN & SHARMA 1964), and is morphologically identical to specimens of *G. aculeifer* (Can.) collected in Europe (supplied by Dr D. E. JOHNSTON). Virgin females of the larger species produce only male offspring (confirmed for 2 populations : Fort Collins and Parachute, CO), suggesting an arrhenotokous mode of reproduction that has been confirmed in European *G. aculeifer* (DE JONG *et al.* 1981). As KEVAN & SHARMA suggest, *G. aculeifer* occurs throughout the United States, and we have studied collections from Pennsylvania to California. In Colorado, *G. aculeifer* has been collected from cow pastures and compost heaps in Fort Collins, from ponderosa pine savanna and grassy riparian zones at mid-elevations (up to 2200 m) in the Rocky Mountains, and from a pasture along the Colorado River near Parachute, CO. *G. oreithyiae*, has been collected from fields in Fort Collins in the Platte River drainage, and from native grassland and pasture along the Colorado River near Parachute, CO. Both species are aggressive predators of nematodes and arthropods, and will attack animals that are many times their size.

In the laboratory, *G. oreithyiae* readily attacks soil-inhabiting nematodes, springtails, mites, and small insects (thrips, root-aphids, scale crawlers). Adult females will attack arthropods that are several times their size by seizing an area of soft cuticle with their chelicerae and eventually chewing through. In this manner small millipedes, caterpillars (*Plodia interpunctella* (Hubner)), and beetle larvae (*Oryzaephilus surinamensis* (L.) may be partially or completely consumed. Individual adult female *G. oreithyiae* fed on a maximum of 25 small collembolans (*Tullbergia granulata* (Mills)) in a day

and averaged about 14/ day (Table 1). A maximum of 34 nematodes (*Acrobeloides* sp. 11, c. 0.810 μg in mass) were consumed in a day, with an average consumption rate of 23/ day (Table 1). The entomogenous nematode, *Steinernema feltiae* Filipjev, was readily eaten, but did not support mite development (EPSKY *et al.*, 1989).

TABLE 1 : Consumption rates of two collembolan and a nematode preys and egg laying rates using those prey as the sole source of food for adult female *Geolaelaps oreithyiae* at 25°C.

Prey Species	Mean # Eaten/day	(S.E)	N
Collembola			
Tullbergia granulata (Mills) (adults)	13.7	(0.8)	30
Hypogastura scotti Yosi (1-2nd instars)	10.5	(1.4)	13
Rhabditida			
Acrobeloides sp.	23.0	(2.1)	10
	Mean # Eggs/day	(S.E)	N
Collembola			
Tullbergia granulata (Mills) (adults)	1.1	(0.2)	50
Hypogastura scotti Yosi (1-2nd instars)	1.0	(0.2)	20
Rhabditida			
Acrobeloides sp.	2.2	(0.2)	45

G. oreithyiae eggs averaged 4.7 μg in weight (11.5 % of female body mass), adult females averaged 41.0 μg wet weight, and 17.3 μg dry weight (dry weight/wet weight = 0.42). Development was most rapid on nematode prey, as was egg production rate (Table 1). At 25°C on a diet of rhabditid nematodes (*Acrobeloides* sp.), developmental time (egg to adult, N = 12) averaged 14.5 days, the egg stage lasting 3.7 days (SD = 0.5), larva (nonfeeding) 1.2 days (SD = 0.4), protonymph 4.2 days (SD = 0.9), deutonymph 5.4 days (SD = 0.8). Time from adult female to first egg averaged 2.8 days (SD = 0.4, N = 8), giving a generation time of 17.3 days.

DISCUSSION

Previous considerations of feeding habits of soil arthropods have concentrated on their role as predators of other arthropods and largely ignored their effects on other invertebrates with which they coexist (but which are not extracted by Tullgren funnels). Many prostigmatid mites do appear to be specialized predators of arthropods (WALTER *et al.* 1988), but most mesostigmatic mites include nematodes, and probably other softbodied invertebrates, in their diets (KARG 1983, WALTER *et al.* 1987, 1988, SARDAR & MURPHY 1987). Because of their large size and aggressive predatory behavior, species of *Geolaelaps* attack a greater variety of prey than other soil-inhabiting *Hypoaspis s.l.* (*see Figure 1*).

KARG (1961) used *G. aculeifer* as an example of a polyphagous predator that feeds on a variety of arthropods (insect larvae, mites, collembola), and to a lesser extent on nematodes. Similarly, SARDAR & MURPHY (1987) and IGNATOWICZ (1974) found that *G. aculeifer* would feed on a variety of mites, collembola, insect larvae, and enchytraeid worms. KEVAN & SHARMA (1964) found that *G. aculeifer* preferred a mite *Tyrophagus putrescentiae* Schrank to a collembolan, *Isotoma notabilis* Shaefferi, and that it was possible to maintain cultures with only collembola as a food source. However, USHER & DAVIS (1983) were able to maintain *G. aculeifer* in culture using springtail prey. They found that fecundity was very low when large *Hypogastura denticulata* (Bagnell) were used as prey, and higher when small *H. denticulata*, and large or small *Sinella coeca* (Schott) were presented.

G. oreithyiae was able to successfully complete development from protonymph to adult on the two collembola tested, adults of *Tullbergia granulata* and first and second instars of *Hypogastura scotti* (Yosii). However, later instar and adult *H. scotti*, although readily eaten, supported only very low egg production rates, and were excluded from the experiment. Females feeding on the nematode *Acrobeloides* sp. laid twice as many eggs/ day as females feeding on either species of collembolan (Table 1). INSERRA & DAVIS (1983) found a species near *aculeifer* (specimens unavailable, D.W. DAVIS, pers. comm.) feeding on the egg masses of both root-knot nematodes (*Meloidogyne chiwoodi* Golden et al. and *M. hapla* Chitwood) and a cyst nematode (*Heterodera schachtii* Schmidt) on greenhouse tomato and sugarbeets in Utah.

Thelytoky has often been considered to be an

evolutionary dead end since the genetic diversity to adapt to environmental change has been assumed to be lacking. This misconception is based on the assumption that thelytoky results in the production of only genetically identical female offspring (clones). In fact, however, the genetic consequences of thelytoky differ with the cytological features of the parthenogenetic system under consideration. If the system is apomictic (ameiotic), neither chromosome reduction, nor fusion of nuclei nor any similar phenomenon, occur and the offspring are genotypically identical to the mother. If, however, parthenogenesis is of the automictic (meiotic) type there is regular chromosome pairing and reduction of chromosome number, followed by restoration of the zygotic chromosome number. The latter may be restored by fusion of two haploid nuclei in diploid species and by various other means in polyploid species (OLIVER *et al.* 1973). The genetic consequences of these two cytological mechanisms may be quite different. Genetic differences may also be significant even in automictic populations depending on whether first or second polar body nuclei fuse with the egg cell nucleus, and/or if chromomes show pre- or postreductional disjunction (separate at meiosis I or II). Heterozygosity is replaced by homozygosity of progeny when the zygotic chromosome number is restored by fusion of two haploid cleavage nuclei or if alleles of heterozygous loci separate prereductionally (at meiosis I); heterozygosity is maintained if postreductional disjunction (separation at meiosis II) occurs. WHITE (1970) thinks most thelytokous organisms possess considerable amounts of heterozygosity and thus function as genetic systems capable of exploiting the advantages of heterosis and adaptive polymorphisms.

STANLEY (1975) has pointed out that the relative rarity of asexual clones in nature is more likely a result of a higher rate of speciation for sexually reproducing species, than of a higher extinction rate for clones. Indeed, because clones are not constrained by reproductive compatibility (behavorial or genetic), a clonal lineage could theoretically tolerate a higher degree of genetic variability than a related sexual species. In the tick, *Haemaphysalis longicornis* Neumann, OLIVER and HERRIN (1976) attempted to measure genetic heterozygosity via comparing differential morphological variation between 10 thelytokous and bisexual geographical races. The ten races or populations consisted of 6 diploid bisexual and 4 triploid thelytokous populations. Univariate and multivariate statistical analyses of the morphological characters indicated that laboratory-reared thelytokous females ($3n = 33$) had the least overall variation, laboratory-reared bisexual females and males ($2n = 22 ; 21$) an intermediate level, and field-collected bisexual females and males a higher level of variation that was exceeded only by a field-collected thelytokous population ($3n = 33$). In mesostigmatic mites, thelytoky has arisen independently a number of times, and is known to occur in the Veigaiidae (HURLBUTT 1979), Macrochelidae (OLIVER 1971), Phytoseiidae (HOY 1985), PODOCINIDAE (WONG 1967), Rhodacaridae, Ascidae, and Laelapidae (Table 2). Unfortunately, no published data exist that indicate if thelytoky is apomictic or automictic in the above mentioned mites, and only unconvining evidence in *H. longicornis* (TAKENAUCHI *et al.* 1970).

To date 110 species of mesostigmatic mites (excluding Uropodina and Ameroseiidae) have been identified from Colorado grassland habitats (shortgrass prairie, croplands, pastures, abandoned fields, riparian zones, foothill grasslands, ponderosa pine savannah, pinyon-juniper woodland, montane meadows and parkland, and alpine tundra - WALTER, unpublished). For 77 of these species, males have also been collected or reared in the laboratory. Many of these species show arrhenotokous parthenogenesis. Of the 33 remaining species, 22 are represented by rare collections of females (5 or fewer individuals) or deutonymphs, and no conclusions can be formed regarding their reproductive strategies. For 8 of the remaining 11 species, we have demonstrated thelytoky by the rearing of only female offspring from virgin females for many generations. Three other species, *Veigaia planicola* (Berlese), *V. pusilla* (Berlese), and *Asca garmani* Hurlbutt, have previously been reported to be all females (HURLBUTT 1979). A single rearing of 5 female offsprings from an isolated nymph of *V. pusilla* appears to confirm thelytoky in that species.

No males have ever been collected in Colorado

TABLE 2 : Species of Mesostigmata represented by all female races (thelytoky) from grassland soils in Colorado, U.S.A.

Taxon	MALES	Habitats			
		Shortgrass Prairie	Pasture & Cropland	Low-elevation Riparian	Montane Meadows
Rhodacaridae					
Rhodacarellus silesiacus Willmann	No	X	X	X	X
Ascidae					
Protogamasellus mica (Athias)	No	X	X		
Protogamasellus hibernicus Evans	No	X	X		
Lasioseius youcefi Athias	No		X	X	
Lasioseius berlesei (Oudemans)	Yes [1]			X	
Asca garmani Hurlbutt	Yes [2]				X
Phytoseiidae					
Neoseiulus setosus (Fox) [3]	No	X	X		
Laelapidae					
Gosmolaelaps vacua (Michael)	Yes [4]	X	X	X	
Geolaelaps oreithiae n. sp.	No		X		
Veigaiidae					
Veigaia pusilla (Berlese)	No	X	X	X	
Veigaia planicola (Berlese)	No		X		X

1. males reported in Karg 1971.
2. males reported for some populations (Hurlbutt 1971).
3. senior synonym of *Amblyseius brevispinus* (Kennett).
4. males reported in Ghilarov & Bregetova 1977.

or appeared in cultures for the species in Table 2. Literature records for male species could be found for *Cosmolaelaps vacua* (Michael) (GHILAROV & BREGETOVA 1977) and *Lasioseius berlesei* (Oudemans) (KARG 1971). *C. vacua* is an extremely variable species (EVANS & TILL 1966), and it is possible that *C. rectangularis* Sheals, and perhaps other species are often confused with *C. vacua* (COSTA 1968). European collections of *C. vacua* (supplied by Dr. D. E. JOHNSTON) include a lightly sclerotized morph that is identical to the Colorado specimens, and a second, more heavily sclerotized morph that resembles *C. rectangularis* (for which the male is known, see COSTA 1968). It is unclear if thelytokous races of otherwise sexually reproducing species occur in the Mesostigmata, but there are reports of thelytokous *Macrocheles penicilliger* (Berlese) from Italy and the United States and bisexual *M. penicilliger* from the USSR (see OLIVER 1971 for dicussion). Since most macrochelids are arrhenotokous, however, it seems likely that bisexual *M. penicilliger* from the USSR are also arrhenotokous. The phytoseiid *Typhlodromus guatemalensis (= Amblyseius elongatus)* is thelytokous in California (KENNETT 1958), but males are common in Canada (PUTNAM 1962). HOY & CAVE (1986) performed an exhaustive survey for parthenogenetic races in the parahaploid phytoseiid, *Metaseiulus occidentalis* (Nesbitt), but no evidence of thelytoky was found.

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