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PARTHENOGENETIC *ASPIDOSCELIS TESSELATA* C AND GONOCHORISTIC
ASPIDOSCELIS SEXLINEATA (SQUAMATA: TEIIDAE) IN
SOUTHEASTERN COLORADO

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ABSTRACT—Parthenogenetic *Aspidoscelis tessellata* (pattern class C) reaches the northern limit of its distribution in Ninemile Valley, Otero County, Colorado. Its coexistence with gonochoristic *A. sexlineata* permitted comparison of diets between species of different sizes, reproductive modes, and evolutionary histories. Based on numbers of prey in stomachs, *A. sexlineata* had a broader diet than *A. tessellata* C in June and July; however, breadth of diets calculated from volumes of prey were nearly the same for the two species. Despite the larger size of *A. tessellata* C, dietary resources were not partitioned by size and foods present exclusively in one species were rare in its diet. Overlap of diets in June could be explained by chance, but this was not true for July. Remarkably high dietary overlap in July resulted from both species taking advantage of an annual surge in abundance of grasshoppers. There was no evidence that either species was affected adversely by presence of the other.

RESUMEN—La lagartija partenogenética *Aspidoscelis tessellata* (clase de patrón C) alcanza el límite norte de su distribución en Ninemile Valley, condado de Otero, Colorado. Su coexistencia con la lagartija de reproducción sexual *A. sexlineata* nos permitió comparar la dieta entre especies de diferentes tamaños corporales, modos de reproducción e historias evolutivas. Basándonos en el conteo de presas en estómagos, *A. sexlineata* tuvo una dieta más amplia que *A. tessellata* C en junio y julio; sin embargo, las amplitudes de dieta calculadas a partir de volúmenes de presas fueron casi iguales para las dos especies de lagartijas. A pesar del mayor tamaño corporal de *A. tessellata* C, los recursos alimenticios no estuvieron repartidos por tamaño, y las presas encontradas exclusivamente en una especie fueron raras en su dieta. La sobreposición de dietas en junio podría ser explicada por azar, pero esto no fue el caso para julio. La sumamente alta sobreposición de dietas en julio fue el resultado de que ambas especies se aprovecharon del surgimiento anual de chapulines abundantes. No hubo evidencia de que una de estas especies se haya visto adversamente afectada por la presencia de la otra especie.

East of the Rocky Mountains in Colorado, gonochoristic (Tomlinson, 1968) *Aspidoscelis sexlineata* is distributed widely, whereas parthenogenetic *A. tessellata* (pattern class C) has been recorded from relatively small areas of only three southeastern counties (Walker et al., 1997; Hammerson, 1999). Distributions of these lizards in Colorado reflect different tolerances for climatic, edaphic, topographic, and vegetational variables (Walker et al., 1998), largely stemming from different modes of evolutionary origin. Derivation of the allodiploid genome of *A.*

tessellata in either northern Mexico or southern Texas from *A. tigris marmorata* × *A. gularis septemvittata* (Neaves, 1969; Parker and Selander, 1976; Dessauer and Cole, 1989) did not hamper its dispersal northward to Otero and Las Animas counties, Colorado (Parker and Selander, 1976). However, lack of further expansion northward, based largely on this allodiploid genome, coincides with northwestward dispersal of *Aspidoscelis neotessellata*, a triploid parthenogenetic species of recent origin from *A. tessellata* × *A. sexlineata* (Parker and Selander, 1976; Densmore et al.,

1989), beyond the range of *A. tessellata* into Pueblo and Fremont counties (Walker et al., 1997; Taylor et al., 2006).

Coexistence of *A. tessellata* C and *A. sexlineata* in southeastern Colorado provided an opportunity to compare diets between congeners with strikingly different reproductive modes, size of adults, and evolutionary histories. Our study addressed the following questions: Do syntopic populations of *A. tessellata* C and *A. sexlineata* have similar breadths of diet? Does breadth of diet change across months and years? Are there significant differences between observed dietary overlaps and overlaps predicted by chance? Are breadths of diets of *A. tessellata* C and *A. sexlineata* in Colorado similar to those reported for *A. tessellata* E and different gonochoristic congeners in Trans-Pecos, Texas (Schall, 1993)?

MATERIALS AND METHODS—Specimens were pooled from three localities in Ninemile Valley, Otero County, Colorado (described by Walker and Cordes, 1998); H-VC was 4.3 km SW Colorado Highway 109 on road 804; H-SR was 8.6-9.0 km SW Colorado Highway 109 on road 804; and H-NV was 11.5-13.4 km SW Colorado Highway 109 on road 804 (approximate center of this site was at UTM 13S 630854E, 4175545N, WGS84 datum). Specimens listed by date are: 9-10 July 1988, *Aspidoscelis tessellata* C, University of Arkansas Department of Zoology (UADZ) 3147, 3155, 3156, 3159, 3160, 3182, 3184, 3185, 3187, 3188, 3194-3196, 3198, 3199, 3203 ($n = 16$, 3195 and 3198 had empty stomachs) and *A. sexlineata viridis*, UADZ 3148, 3152-3154, 3157, 3158, 3163-3165, 3179-3181, 3190, 3191, 3197, 3200 ($n = 16$); 11 August 1988, *A. tessellata* C, UADZ 3409-3412, 3414-3423 ($n = 14$); 4-5 June 1990, *A. tessellata* C, UADZ 4088, 4090-4093, 4104-4106, 4108, 4109, 4111-4113, 4115-4117 ($n = 16$) and *A. sexlineata viridis*, UADZ 4077-4087, 4089, 4124-4127, 4130 ($n = 17$, 4084 had an empty stomach). There was no apparent ecological difference between localities. Habitat was characterized by scattered shrubs including *Chrysothamnus nauseosus* (rabbitbrush), *Sarcobatus vermiculatus* (greasewood), and *Gutierrezia sarothrae* (snakeweed), and an assortment of weeds on the roadside and severely deteriorated grassland of the Ninemile Valley adjacent to road 804 (Walker et al., 1998:figure 3). In addition to *A. tessellata* C and *A. sexlineata*, other *Aspidoscelis* at this locality included *A. tessellata* D and *A. neotessellata* B. Small samples precluded inclusion of *A. tessellata* D and *A. neotessellata* B in our study. The historical significance of this four-member guild in resolving diverse problems involving parthenogenetic *Aspidoscelis* is summarized by Walker and Cordes (1998).

Adults of *A. tessellata* C and *A. sexlineata* were collected as encountered in July 1988 and June 1990. Stomach contents were removed, labeled, and stored in 70% ethanol. Stomach contents were separated into taxonomic orders and counts and volumetric measurements were made to estimate breadth and overlap of diets. In small graduated cylinders, volumetric mea-

surements of each category of prey were made by displacement in liquid.

We compared overlap in diet between *A. tessellata* C and *A. sexlineata* for each sampling period with expected values for overlap due to chance. Expected values were derived from a null model recommended by Winemiller and Pianka (1990) and available as alternative RA3 (Randomization Algorithm 3) in the Niche Overlap module of Ecosim700 software (<http://homepages.together.net/~gentsmin/ecosim.htm>). Because breadth of diet for each species was retained in this model, results of simulation were not biased by small samples (Gotelli and Entinger, 2001). We estimated overlap of diets using the symmetrical formula of Pianka (1973) and running 1,000 iterations of the simulation to obtain a mean value. Food items were assumed to be equally usable by both species by random, multiple, reshuffles of each row of the resource matrix. We used Levin's measure of breadth of niche: $B = 1/\sum p_{ij}^2$, where p_{ij} was the proportion of a particular taxon (i) in the diet of species j (Levins, 1968). Breadth of niche ranges from 1 to n , and B would be maximized at n with equivalent use of all taxa in the sample.

Because adults of *A. tessellata* C were much larger than adults of *A. sexlineata* (snout-vent length in mm: June 1990, 87.6 ± 4.1 SE and 69.3 ± 1.1 SE; July 1988, 88.1 ± 3.6 SE and 67.2 ± 1.6 SE, respectively), there was a possibility that food resources were being partitioned by size of prey. We tested this possibility by dividing total volume (cc) of each category of prey by number of individual prey in that category for each of the two species of lizards in each sample (June and July). This provided average size (cc) of individual prey in each category for informal interspecific comparisons. We also calculated the grand mean volume of prey in each month for each species and used *t*-tests to determine if there were significant interspecific differences in overall size of foods that were consumed.

RESULTS—Assuming that samples obtained in July 1988 and June 1990 were representative of availability of prey for these months, both species increased use of grasshoppers in July (Tables 1 and 2). For *A. tessellata* C, the shift was from 3.1% in June to 45.8% in July (number of grasshoppers) or 11.3% in June to 81% in July (volume of grasshoppers). The shift to grasshoppers by *A. sexlineata* was from 16.8% in June to 37.3% in July (number of grasshoppers) or 52.3% in June to 77.3% in July (volume of grasshoppers). Adult beetles also were important to both species in July, as suggested by both number and volume (Tables 1 and 2). As in June, number of prey for July provided a broader estimate of diet for *A. sexlineata* (4.68) compared to *A. tessellata* C (3.82), but volume reduced the magnitude of the interspecific difference (1.62 for *A. sexlineata* and 1.50 for *A. tessellata* C). In contrast to samples in June, overlap in diets calculated from numbers (0.95) and volumes (1.00) were too high to

TABLE 1—Percentages of the total number of food items in stomachs of adult parthenogenetic *Aspidoscelis tessellata* C and gonochoristic *A. sexlineata* from a site of syntopy in Ninemile Valley, Otero County, Colorado.

Food item	June 1990		July 1988	
	<i>A. tessellata</i> n = 16	<i>A. sexlineata</i> n = 16	<i>A. tessellata</i> n = 14	<i>A. sexlineata</i> n = 16
Araneae	5.5	16.8	6.8	9.8
Scorpiones	0.0	0.9	0.0	0.0
Solifugae	0.8	0.0	0.0	0.0
Opiliones	0.0	1.8	10.2	2.0
Isopoda	2.3	0.0	6.8	9.8
Microcoryphia	0.0	0.0	0.0	2.0
Collembola	0.0	0.0	1.7	0.0
Orthoptera	3.1	16.8	45.8	37.3
Isoptera	3.9	1.8	0.0	0.0
Hemiptera	10.2	5.3	0.0	2.0
Homoptera	7.8	14.1	3.4	2.0
Coleoptera				
Adults	13.3	4.4	17.0	21.5
Larvae	5.5	11.5	1.7	0.0
Lepidoptera				
Adults	4.7	2.7	0.0	2.0
Larvae	35.2	8.0	3.4	2.0
Diptera	0.8	1.8	1.7	2.0
Hymenoptera	0.8	2.7	1.7	7.8
Insect pupae	4.7	4.4	0.0	0.0
Snails	0.0	5.3	0.0	0.0
Unidentified	1.6	1.8	0.0	0.0
Number of prey	128.0	113.0	59.0	51.0

be explained by chance (Table 3; $P < 0.01$). The general pattern was broader diet and less overlap in June and diets that were less diverse with greater overlap in July.

Numbers of individual prey (Table 1) indicated that principal foods of *A. tessellata* C were caterpillars (Lepidoptera 35.2%), adult beetles (Coleoptera 13.3%), and bugs (Hemiptera 10.2%), and principal foods of *A. sexlineata* were spiders (Araneae 16.8%), grasshoppers (Orthoptera 16.8%), and leaf hoppers (Homoptera 14.1%). Volumes of prey consumed (Table 2) were broadly congruent with numbers of individual prey in identifying caterpillars as the principal food of *A. tessellata* C (48.1%) and grasshoppers as the principal food of *A. sexlineata* (52.3%). Numbers of prey items and volumes of prey categories both showed that three of the top four taxa of prey of *A. tessellata* C were caterpillars, adult beetles, and leaf hoppers, and that three of the top four taxa of prey of *A. sexlineata* were grasshoppers, leaf hoppers,

and spiders (Tables 1 and 2). However, numbers and volumes provided contradictory information on breadth of dietary niches. Based on number of individual prey, *A. sexlineata* had a broader diet (9.24) than *A. tessellata* (5.81), but breadth of diets calculated from volumetric data did not appear to be significantly different between *A. sexlineata* (3.0) and *A. tessellata* C (3.54). Overlaps in diets calculated from numbers of individual prey (0.56; $P = 0.15$) and volumes (0.38; $P = 0.08$) could be explained by chance (Table 3), i.e., as would be expected in the absence of interspecific interactions such as competition.

Aspidoscelis tessellata C and *A. sexlineata* had not partitioned food resources by size as evidenced by similar mean sizes of prey in each food category (Table 4). We tested this hypothesis by using mean size of prey as a variable and by comparing the grand means. Although *A. tessellata* C had a much larger body than *A. sexlineata*, overall mean size of prey was larger for

TABLE 2—Volumetric percentages of food items in stomachs of adult parthenogenetic *Aspidoscelis tessellata* C and gonochoristic *A. sexlineata* from a site of syntopy in Ninemile Valley, Otero County, Colorado.

Food item	June 1990		July 1988	
	<i>A. tessellata</i> n = 16	<i>A. sexlineata</i> n = 16	<i>A. tessellata</i> n = 14	<i>A. sexlineata</i> n = 16
Araneae	1.8	5.3	0.2	2.4
Scorpiones	0.0	0.1	0.0	0.0
Solifugae	0.6	0.0	0.0	0.0
Opiliones	0.0	0.1	2.1	0.4
Isopoda	0.8	0.0	1.3	2.0
Microcoryphia	0.0	0.0	0.0	0.1
Collembola	0.0	0.0	<0.1	0.0
Orthoptera	11.3	52.3	81.0	77.3
Isoptera	<0.1	<0.1	0.0	0.0
Hemiptera	1.1	0.1	0.0	0.1
Homoptera	15.1	20.5	0.2	0.1
Coleoptera				
Adults	9.2	1.7	8.9	12.3
Larvae	0.9	1.7	0.1	0.0
Lepidoptera				
Adults	7.5	11.4	0.0	1.8
Larvae	48.1	3.2	5.2	3.2
Diptera	0.8	0.8	0.9	0.1
Hymenoptera	<0.1	<0.1	0.1	0.1
Insect pupae	2.5	2.5	0.0	0.0
Snails	0.0	0.4	0.0	0.0
Unidentified	0.2	0.1	0.0	0.0
Volume of prey (cc)	23.9	23.7	21.4	17.1

TABLE 3—Comparison of dietary breadth (Levins, 1968) and overlap (Pianka, 1973) between samples of adult parthenogenetic *Aspidoscelis tessellata* C and gonochoristic *A. sexlineata* from a site of syntopy in Ninemile Valley, Otero County, Colorado.

Food parameter	June 1990		July 1988	
	<i>A. tessellata</i>	<i>A. sexlineata</i>	<i>A. tessellata</i>	<i>A. sexlineata</i>
Numbers of prey				
Breadth of diet	5.33	9.24	3.82	4.68
Overlap observed		0.56		0.95
Overlap expected from chance		0.42		0.32
Probability that observed overlap was explained by chance		0.15		<0.01
Volumes of prey				
Breadth of diet	3.54	3.00	1.50	1.62
Overlap observed		0.38		1.00
Overlap expected from chance		0.18		0.10
Probability that observed overlap was explained by chance		0.08		<0.01

TABLE 4—Average size of prey (in cc) consumed by adult parthenogenetic *Aspidoscelis tessellata* C and gonochoristic *A. sexlineata* from a site of syntopy in Ninemile Valley, Otero County, Colorado. Numbers in parentheses are sample sizes.

Food item	June 1990		July 1988	
	<i>A. tessellata</i>	<i>A. sexlineata</i>	<i>A. tessellata</i>	<i>A. sexlineata</i>
Araneae	0.26 (7)	0.28 (19)	0.05 (4)	0.48 (5)
Opiliones			0.35 (6)	0.40 (1)
Isopoda			0.32 (4)	0.40 (5)
Orthoptera	2.82 (4)	2.75 (19)	3.00 (27)	4.10 (19)
Isoptera	0.01 (5)	0.01 (2)		
Hemiptera	0.08 (13)	0.01 (6)		
Homoptera	1.50 (10)	1.30 (16)	0.10 (2)	0.12 (1)
Coleoptera				
Adults	0.54 (17)	0.34 (5)	0.89 (10)	1.12 (11)
Larvae	0.13 (7)	0.13 (13)		
Lepidoptera				
Adults	1.25 (6)	3.80 (3)		
Larvae	1.07 (45)	0.35 (9)	2.58 (2)	3.20 (1)
Insect pupae	0.42 (6)	0.51 (5)		

A. sexlineata, both in June (*A. tessellata* C: 0.81 ± 0.28 cc; *A. sexlineata*: 0.95 ± 1.30 cc) and in July (*A. tessellata* C: 1.04 ± 1.23 cc; *A. sexlineata*: 1.40 ± 1.59 cc). However, this difference in mean size of prey was not significant (June, $t_{18} = 0.781$, $P = 0.78$; July, $t_{12} = 0.642$; $P = 0.64$).

DISCUSSION—Diets in gonochoristic *A. sexlineata* and parthenogenetic *A. tessellata* have been studied (Paulissen, 1987; Paulissen et al., 1993, 1997, 2006), but this is the first comparison for syntopic populations of these species. Schall (1993) determined from volumes of prey that *A. tessellata* E had a narrower breadth of diet than three sympatric, gonochoristic congeners in Trans-Pecos Texas. Although we reached a different conclusion based on volumes of prey consumed by *A. tessellata* C and *A. sexlineata*, the two studies cannot be compared directly. Unlike our study, Shall (1993) increased samples by pooling individuals of each species: *A. tessellata* E ($n = 50$), *A. tigris marmorata* ($n = 66$), *A. gularis gularis* ($n = 81$), and *A. inornata heptagramma* ($n = 120$) that had been collected during 4 months in each of 2 years from 45 sites (breadth of diet) and 5 sites (overlap of diet). This provided a broad, general perspective of diets for species in Trans-Pecos Texas. Shall (1993) also detected that *A. inornata*, a small species similar in size to *A. sexlineata*, was using smaller prey than *A. tessellata* E. In contrast, we revealed that *A.*

sexlineata and *A. tessellata* C were using prey of similar size.

One point of similarity between assemblages of *Aspidoscelis* from Trans-Pecos Texas and Ninemile Valley was the high overlap in diets between *A. tessellata* C and gonochoristic congeners. However, high overlaps in diet in Trans-Pecos Texas were based on abundance of termites throughout the activity season (Schall, 1993); high overlap of diets in Ninemile Valley was based on seasonal abundance of grasshoppers. The reliable presence of large numbers of termites that served as principal prey for *Aspidoscelis* in Trans-Pecos Texas (and for *A. tessellata* C and E at Sumner Lake, DeBaca County, New Mexico; Paulissen et al., 2006) was missing at our study site. Extensive overlap in diets did not imply competition among congeners in either study because these broadly overlapping diets resulted from opportunistic targeting of a particularly abundant prey.

Evidence suggests that *A. tessellata* might be at an ecological disadvantage compared to gonochoristic congeners. For example, *A. tessellata* E was less responsive than gonochoristic *A. tigris marmorata* to simulated predatory threats in the field (Price, 1992), and density of *A. tessellata* E did not increase in response to a systematic removal of *A. tigris marmorata*, a potential competitor, from a site of syntopy in southern New Mexico (Price et al., 1993). In addition,

individuals of *A. tessellata* E had a higher parasitic load than those of *A. tigris marmorata* in samples collected from syntopic populations (Mata-Silva et al., 2008). This difference, along with similar findings for parthenogenetic and gonochoristic *Heteronotia* (Moritz et al., 1991), is related to the Red Queen hypothesis (Van Valen, 1973), i.e., the continuous generation of genetic variation in gonochoristic species has adaptive value in countering parasitic infection. Tangential evidence of ecological vulnerability in a parthenogen is provided by the isolated group of *A. dixonii* C in southwestern New Mexico (a parthenogenetic species derived from *A. tessellata* subsequent to the hybridization origin of *A. tessellata*; Cordes and Walker, 2006). *Aspidoscelis dixonii* C is possibly in a late stage of contraction of range, extirpation, or both, from effects of a recent expansion of gonochoristic *A. tigris punctilinealis* into its range (Cole et al., 2007). Despite negative connotations of this evidence, *A. tessellata* has a geographic distribution spanning ca. 1,100 km between our study site in Otero County, Colorado (UTM 13S 630919E, 4175489N; WGS 84), and the southern limit of its range near Saucillo (UTM 13R 467649E, 3100708N; WGS 84), Chihuahua, Mexico (Taylor et al., 2003). Within its range, *A. tessellata* coexists with an assortment of congeners, including parthenogenetic *A. exsanguis*, *A. dixonii*, *A. neomexicana*, *A. neotessellata* B, *A. uniparens*, and *A. velox*, and gonochoristic *A. gularis gularis*, *A. g. septemvittata*, *A. inornata*, *A. sexlineata*, and *A. tigris marmorata*. Its extensive latitudinal range and successful assimilation into an array of taxonomically diverse communities are indicators of ecological success.

Based on nearly equal numbers of *A. tessellata* C and *A. sexlineata* in our samples (individuals were collected as they were encountered), it was not obvious that fitness of *A. tessellata* C had been affected negatively at Ninemile Valley. We detected no evidence of competition between the two species in either sampling period. For samples collected in June, overlap in diet could be explained by chance, and the extensive overlap in diet in July reflected an opportunistic response of both species to an increase in availability of grasshoppers.

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