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POPULATION GENETICS OF *ANELOSIMUS EXIMIUS* (ARANEAE, THERIDIIDAE)[1]

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ABSTRACT

Anelosimus eximius is a cooperative, group-living neotropical spider. Colonies consist of up to several thousand individuals, and colonies may be aggregated into local colony clusters. The colony clusters are patchily distributed, and are often separated from their neighbors by a km or more. In this study individuals were collected from colonies located in Panama and Suriname. These individuals were subjected to horizontal starch gel electrophoresis and screened for polymorphisms in 46 enzyme systems. A total of 51 scorable loci were found, of which seven were polymorphic. The results were analyzed with Wright's F statistics which were used to investigate the amount of genetic differentiation in the population attributable to subdivision of the population into colonies, colony clusters, local populations and the geographic regions of Panama and Suriname.

Most of the genetic differentiation in the *A. eximius* sampled was due to subdivision of the population into colony clusters and into geographic regions. There was no evidence of differentiation among colonies in a colony cluster, and little differentiation among collection sites within Panama or Suriname. In contrast, within a local population, samples from adjacent colony clusters were sometimes fixed for different alleles at one or more loci, and the Panama and Suriname samples were fixed for different alleles at three loci.

INTRODUCTION

Anelosimus eximius (Keyserling) (Theridiidae) is among the best known of the cooperative or quasisocial spiders. Its natural history has been studied most recently by Brach (1975), Christenson (1984), Overal and Ferreira da Silva (1982), Vollrath (1982), Vollrath and Rohde-Arndt (1983) and others (L. Aviles, Y. Lubin, A. Rypstra, pers. comm.). *Anelosimus eximius* is found in rainforest and second growth habitat from Panama to southern Brazil, and from Peru to Trinidad and eastern Brazil (Levi 1963). The webs of *A. eximius* consist of a large, more or less oval horizontal sheet of nonsticky silk, one or more retreats made of green and dry leaves curled and held in place with silk, and vertical threads ("knock down threads") extending from the sheet and retreat to leaves and branches above the web. Webs can be found from ground level to at least 20 m up in the forest canopy (personal observation). Webs range in size from tiny structures 10-25 cm long containing only one or a few spiders, to large

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colonies 2-3 m or more in length containing hundreds or thousands of individuals.

Established colonies contain adult females and males, and immatures. The social interactions of *A. eximius* have been described by Brach (1975), Christenson (1984), Vollrath (1982), and Vollrath and Rohde-Arndt (1983). These behaviors include cooperative construction, maintenance and cleaning of the web; cooperative prey capture and feeding on large prey by several individuals; and regurgitation feeding of young. Females regurgitate food for offspring other than their own (Christenson 1984) and there is some evidence that some adult females in colonies do not reproduce (Vollrath and Rohde-Arndt 1983; Overal and Ferreira da Silva 1982). The adult sex ratio is highly biased towards females; males make up only a small portion of the adult population of colonies: 5% to 22% (six colonies of 100 to 200 individuals; Overal and Ferreira da Silva 1982); 7% (4 of 55 adults in one web; Christenson 1984). The bias in sex ratio is already apparent in the penultimate instar, when males and females can be distinguished (Aviles 1983). Reproduction takes place year round, at least in some populations (Overal and Ferreira da Silva 1982).

Two types of colony foundation have been described for this species: budding and dispersal (Vollrath 1982). In budding a large established colony splits into two or more webs, either because the web is broken by falling branches, debris etc., or because small groups of spiders leave the main web and begin a new web nearby (Overal and Ferreira da Silva 1982). During dispersal, large numbers of mated females leave their original colony and disperse singly to build new solitary webs. The females in the solitary webs may later be joined by other females, apparently dispersing females whose new webs have failed. All newly founded webs have a very high failure rate, but they stand a better chance for survival if they are later joined by other females (Christenson 1984). Vollrath notes (1982) that dispersing females always traveled alone, and only after the webs were built did other females join. These multi-foundress colonies were generally in the proximity of a larger established colony. Webs more distant from a large established web were usually single female webs.

These two methods of colony foundation, budding and dispersal, may be the cause of two superimposed patterns of colony distribution. Colonies or webs are often found in local aggregations, or colony clusters which may contain two to 40 or more distinct webs. This pattern of distribution may be the result of budding; if so, colonies within colony clusters should be genetically very similar. The colony clusters themselves are patchily distributed, separated from neighboring clusters by as little as a few tens of meters or as much as several km. This may be partly due to new colony foundation by dispersal and founder events.

Based on observations of natural history, it is likely that gene flow among the colonies within a colony cluster is high. The webs are in close proximity, sometimes touching, and may share parts of the knockdown threads. The extent of gene flow among colony clusters is unknown. There are four potential avenues for gene flow among colony clusters: 1) new colonies may be founded by unrelated dispersing females; 2) males may disperse out of their natal colony clusters and into different clusters to mate; 3) immatures or females may disperse and join established colony clusters; and 4) spiders may be accidentally transported to new webs (e.g. by wind, rivers, animals or humans).

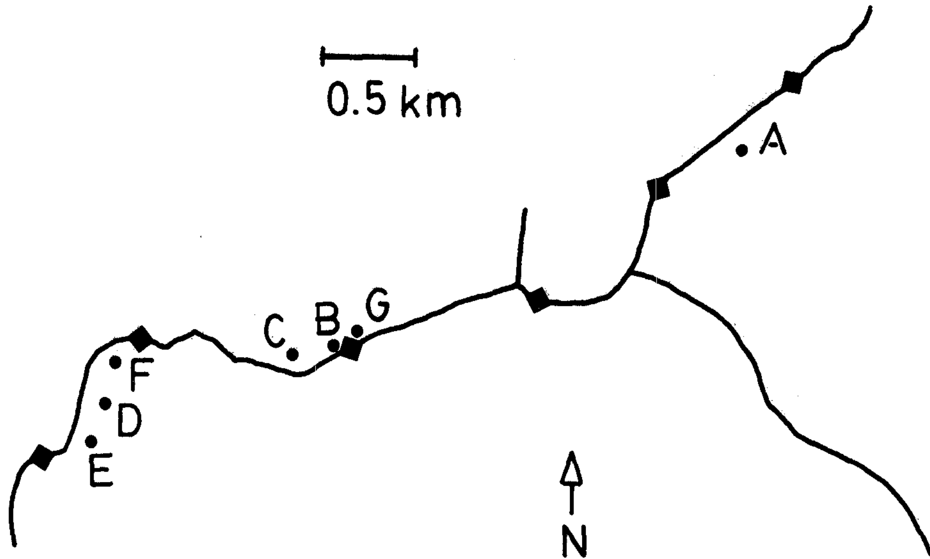

Fig. 1.—Map of Browns Berg collection site, Brokopondo, Suriname. Solid lines indicate trails, solid circles indicate *Anelosimus eximius* colonies or colony clusters, and solid diamonds are km markers.

If colonies are founded by a single female lineage (one female or a group of sibling females who mated before leaving their natal nest), and if there is no subsequent migration into a colony by any age-sex class, then the individuals within colonies and colony clusters would by necessity inbreed. In addition each family lineage would be isolated from others in the population as it went through cycles of dispersal, colony foundation, growth, budding and more dispersal. Subdivision of the population into isolated genetic lineages may contribute to more rapid or more frequent speciation than would be found in a more freely mixing population.

Genetic variability at loci coding for structural proteins can be detected using protein electrophoresis. This technique has been widely used in population studies of both vertebrates and invertebrates (Selander and Whittam 1983, and references therein). Pennington (1979) used protein electrophoresis to distinguish immatures and females of similar species of *Meta* (Araneidae). The data presented here are the results of a pilot study investigating the feasibility of using protein electrophoresis to study genetic variation within and among colonies, colony clusters, and populations of *A. eximius*. The questions addressed are:

1) Is there a high level of genetic similarity within colonies?

2) Is there a high level of genetic similarity within colony clusters?

3) Is there genetic differentiation among populations, and if so on what geographic scale?

METHODS AND MATERIALS

Collection.—*Anelosimus eximius* were collected from colonies in Panama (August 1983) and Suriname (April and May 1984). The Panama collections were made in two locations. The first was along the El Llano—Carti Road in Panama province east of the Panama Canal (9° 15′N, 79° 5′W), at an elevation of

approximately 100-200 m. The area along the road was recently forested, but is now mainly agricultural land and second growth forest. The second collection site was outside of the town of El Valle in Penonome Province west of the Panama Canal (8°37'N, 80°6'W). This area was higher in elevation (approximately 400-500 m) in the bowl of an extinct volcano, and is covered with cooler, wet cloudy forest. Here and at El Llano the spiders were collected by bagging a retreat and cutting it out of the web.

Suriname collections were also made at two localities, the Browns Berg Nature Park and the Voltzberg-Raleighvallen Reserve. The Browns Berg Reserve (Brokopondo province, 4°50'N, 55°15'W) is located along the western shores of the Brokopondo reservoir. The study area was on the Mazaroni plateau at an elevation of 400-450 m. The vegetation here is rainforest which had been selectively logged at some time in the past. Colony clusters were found along a 12 km trail across the plateau.

The Voltzberg-Raleighvallen reserve (Saramacca province,4°45'N, 56°10'W) is located along the Coppename river in central Suriname. Park headquarters are on Foengoe Island. Colonies were found on Foengoe Island, on the west bank of the river (outside the reserve lands) and at the Voltzberg camp in the forest east of the river. Both here and at Browns Berg spiders were collected by shaking the web and catching the spiders in a bag or box as they jumped off the edge of the web.

All spiders collected in Panama and Suriname were transported live to the United States. The animals were starved for at least 1 week and stored frozen at −70°C.

Electrophoresis.—Spiders were analyzed for enzyme polymorphisms using horizontal starch gel electrophoresis. The techniques employed are described in detail in May et al. (1979), May (1980), Harris and Hopkinson (1976), and Brewer (1970); recipes for stains follow Harris and Hopkinson (1976) and Shaw and Prasad (1970). Four buffer systems were used: "R" (Ridgway et al. 1970), "C" (Clayton and Tretiak 1972), "M" (Markert and Faulhaber 1965), and "4" (modified from Selander et al. 1971) (recipes for the buffers are given in Appendix 1). Gels were made of 42 g (thin gels) or 70 g (thick gels) of a 1:1 mixture of hydrolyzed potato starch and electrostarch, and 300 or 500 ml respectively of one of the four buffers. Individual spiders were homogenized in 2-3 drops of 0.05 M Tris HCl (Appendix 1). Heavy weight filter paper wicks (Whatman #3 filter paper) approximately 0.5 x 3 x 8 mm were used to carry samples of the homogenates; one spider provided enough homogenate for two to four wicks. Running conditions followed those described in May et al. (1979) and May (1980). After the proteins migrated a sufficient distance each gel was sliced horizontally into four (thin gel) or six (thick gel) layers approximately 1.5 mm thick and each slice was stained to indicate the position of a single enzyme.

A screen of 46 enzyme systems using each of the four buffer systems was carried out to determine 1) which enzymes could be detected in *A. eximius,* 2) which buffers gave the best results for each enzyme system, and 3) which enzymes showed detectable polymorphisms. In the screen two thick gels of each buffer system were run, for a total of 8 gels. Ten spiders were run on each gel; one spider produced enough homogenate for four wicks, so that four replicates of the ten spiders were placed on a gel. (Sometimes it was not possible to get four wicks from a single homogenized spider, so samples from another ten spiders from the

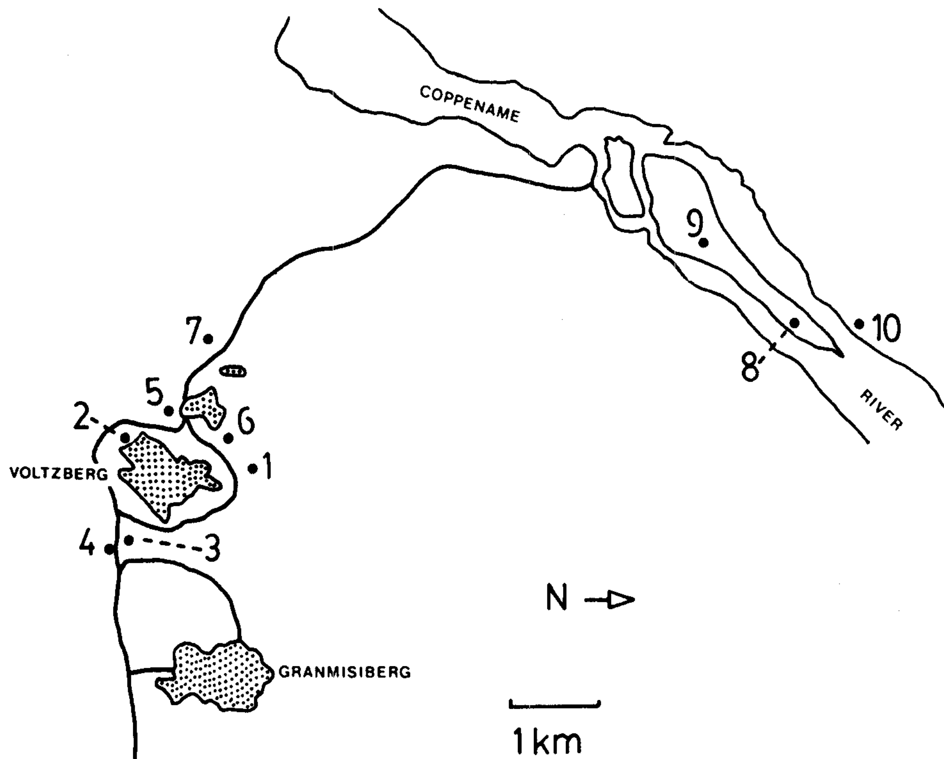

Fig. 2.—Map of Voltzberg collection site, Saramacca, Suriname. Thick sold lines indicate trails, solid circles indicate *Anelosimus eximius* colonies or colony clusters, and stippling indicates granite outcrops in the form of bergs and plates. Colonies 8 and 9 are on Foengoe Island in the Coppename River.

same web were used for one of the replicates). After the gels had been subjected to electrophoresis they were cut into four "mini gels." Each mini gel was sliced horizontally into six layers, giving a total of 48 gel layers for each type of buffer. One slice of each buffer type was stained for one of the 46 enzyme systems investigated. The ten spiders in the replicates were chosen so that every buffer and stain combination was tried on spiders from each of the four collection sites and from as many different colonies as possible. The list of enzyme systems screened and the buffers which gave best results is given in Appendix 2.

Based on the results of the screen, a survey of each colony was carried out examining each apparently polymorphic locus on the buffer system giving the best results. In the survey of polymorphic enzymes 7 to 14 spiders were sampled from each of 23 webs for a total of 187 spiders. An additional 22 spiders were sampled from one web in which heterozygotes were discovered (see results below).

Analysis.—Mean heterozygosity in the *Anelosimus eximius* samples was calculated as the arithmetic mean of the heterozygosities calculated for every scorable locus. Heterozygosity at a single locus was calculated as though all members of the population were potentially freely interbreeding, so that heterozygosity of a single locus with two alleles occurring with frequencies "p" and "q" is 2pq; for three alleles with frequencies "p," "q" and "r" it is 2(pq + pr + qr), etc. I computed mean heterozygosities and standard errors according to the method of Nei (1978) and Nei and Roychoudhury (1974) for populations

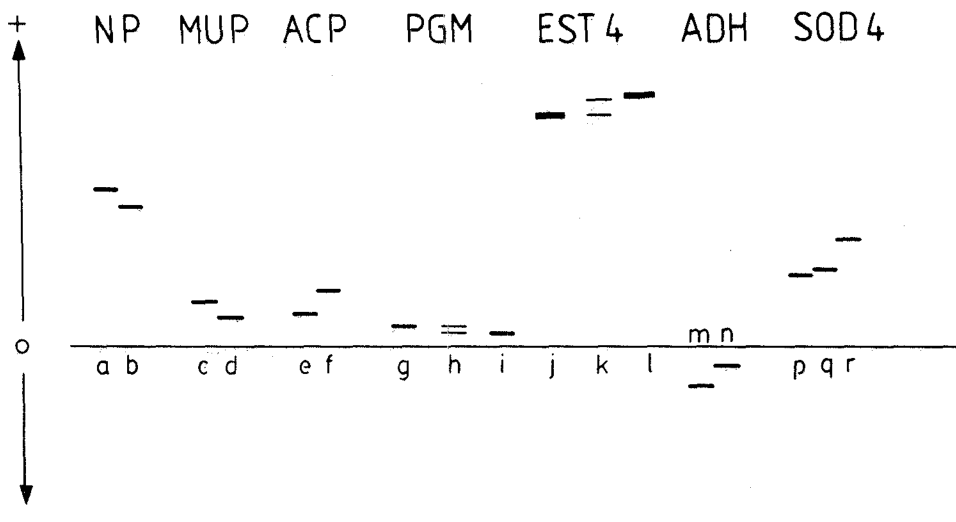

Fig. 3.—Banding patterns observed for seven polymorphic enzymes. "o" is the point of origin on the gel, and arrows indicate the direction of migration by the protein (+ towards positive terminal, −towards negative terminal). The presumed genotype for each band is given in the arbitrary numbering system used in the text (e.g. 11, 12, 22) and in the percentage system described in Allendorf et al. (1977). NP: a = 11 or 100/100, b = 22 or 89/89; MUP: c = 22 or 158/158, d = 11 or 100/100; ACP: e = 11 or 100/100, f = 22 or 164/164; PGM: g = 11 or 100/100, k = 12 or 100/106.5, l = 22 or 106.5/106.5; ADH: m = 11 or 100/100, n = 22 or 42/42; SOD-4; O = 11 or 100/100, p = 33 or 107/107, q = 22 or 145/145.

consisting of the total *A. eximius* sample, the Panama and Suriname samples separately, and for colony clusters which contained heterozygotes, using a program written by Dowling and Moore (1984) modified for the IBM PC.

When colony clusters contained individuals heterozygous at a particular locus, I calculated the frequencies of genotypes expected given the allele frequencies calculated from the samples, and compared them with observed frequencies using a Chi^2 goodness-of-fit test.

I calculated Wright's F statistics (F_{dt}, F_{st} and F_{ds}) for each polymorphic locus (Wright 1951, 1978; Hartl 1980). F statistics provide measures of the extent of population structuring based on the departure of the frequencies of genotypes observed from those expected under conditions of panmixia. Non-random mating within populations and division of the population into sub-populations and demes are examples of departure from panmixia which may lead to a reduction in the observed frequency of heterozygotes compared to homozygotes. F statistics are hierarchical in nature. Reduction in heterozygosity in the population as a whole (F_{dt}), can be partitioned into that due to sub-populations within the total population (F_{st}), and in demes within sub-populations (F_{ds}). I performed two sets of calculations; in both I treated the colony clusters as demes, and all *A. eximius* sampled as the total population. In one set of calculations I treated the four collecting sites (El Llano, El Valle, Browns Berg and Voltzberg) as sub-populations, and in the other I considered the Panama and Suriname samples to be sub-populations.

Table 1.—Presumed genotypes found for seven polymorphic loci in El Llano (EL), El Valle (EV), Browns Berg (BR) and Voltzberg (VB) samples of *Anelosimus eximius*. N is number of individuals sampled.

Locality	ACP	ADH	MUP	NP	SOD-4	PGM	EST-4	N
EL	11	11	11	11	11	11	11	26
EV	11	11	11	11	22	11	11,12,22	37
BR	22	22	22	22	22,33	11	22	23
VB	22	22	22	11,22	22,33	11,12,,22	22	101*

*plus an additional 22 spiders sampled for PGM.

RESULTS

Collections.—At the El Llano collection site two colony clusters were found about 1 km apart, each consisting of a single web. I collected spiders from each of these two webs. At the El Valle site a group of webs was found along a 135 m portion of a path. At this site there were 40 webs ranging in size from 10 cm across to 4 m across, and containing one spider to several hundred spiders. No web was more than 22 m from its nearest neighbor, so that it appeared likely that this was one very large colony cluster. I took spiders from five webs. Seven colony clusters (which I labelled a A through G) were found at the Browns Berg park. Cluster A consisted of four webs and cluster B consisted of three; the rest consisted of single webs. The relative positions of these colony clusters are shown in Figure 1. I collected spiders from each colony cluster except for cluster G, which was 10 m up a tree. However, after collection a problem with excess moisture killed all but the samples from two webs in cluster A and the sample from cluster C. Ten colony clusters were found at the Voltzberg reserve. The locations of these clusters are shown in Figure 2. Clusters 2, 3 and 7 contained two webs each, the rest only single webs. I collected samples from each web in each colony cluster.

Electrophoresis.—Thirty-seven of the 46 proteins screened gave clear and scorable results on at least one buffer system. Ten enzymes were apparently coded for by more than one locus (indicated in Appendix 2 by a numerical suffix, e.g. MDH-1, MDH-2) giving a total of 51 scorable loci. Of these, 44 were monomorphic for all individuals sampled, and only seven, or 13.7%, were polymorphic. These seven were methylumbelliferyl phosphatase (MUP), alcohol dehydrogenase (ADH), acid phosphatase (AC), an esterase (EST-4), a superoxide dismutase (SOD-4), nucleoside phosphorylase (NP), and phosphoglucomutase (PGM). SOD-4 was represented by three presumed alleles, the rest by two. The banding patterns found, along with the presumed genotypes producing the patterns, are presented in Figure 3.

The genotypes at these seven loci in each collection site are presented in Table 1. Of the seven polymorphic loci, three (MUP, ADH and ACP) show fixed differences between the Panama and Suriname samples. NP and PGM were monomorphic in the Panama samples, and EST-4 was monomorphic in the Suriname samples. Thus in the Suriname sample three (5.9%) of the 51 loci sampled were polymorphic, and in the Panama sample two (3.9%) were polymorphic.

The gene frequencies found for EST-4, NP, PGM and SOD-4 in each web are given in Table 2. Most samples taken from any one colony are made up of

Table 2.—Gene frequencies of NP, SOD-4, PGM and EST-4 in webs sampled from El Llano (EL), El Valle (EV), Browns Berg (BR) and Voltzberg (VB). The convention 1-1 is used to indicate colony cluster 1, web 1, etc. N is number of individuals sampled from each web.

	NP		SOD-4			PGM		EST-4		N
allele:	1	2	1	2	3	1	2	1	2	
EL 1-1	1	0	1	0	0	1	0	1	0	14
EL 2-1	1	0	1	0	0	1	0	1	0	12
EV 1-1	1	0	0	1	0	1	0	0.86	0.14	9
EV 1-2	1	0	0	1	0	1	0	0.36	0.64	7
EV 1-3	1	0	0	1	0	1	0	0.64	0.36	7
EV 1-4	1	0	0	1	0	1	0	0.86	0.14	7
EV 1-5	1	0	0	1	0	1	0	0.86	0.14	7
BR A-1	0	1	0	1	0	1	0	0	1	8
BR A-2	0	1	0	1	0	1	0	0	1	7
BR C-1	0	1	0	0	1	1	0	0	1	8
VB 1-1	0	1	0	10	01	0	0	1	7	
VB 2-1	0	1	0	1	0	1	0	0	1	7
VB 2-2	0	1	0	1	0	1	0	0	1	7
VB 3-1	1	0	0	1	0	1	0	0	1	7
VB 3-2	1	0	0	1	0	1	0	0	1	7
VB 4-1	1	0	0	0	1	0	1	0	1	7
VB 5-1	1	0	0	0	1	0	1	0	1	9
VB 6-1	1	0	0	1	0	0	1	0	1	8
VB 7-1	0	1	0	1	0	0.58	0.42	0	1	8*
VB 7-2	0	1	0	1	0	0.47	0.53	0	1	8**
VB 8-1	0	1	0	1	0	0	1	0	1	8
VB 9-1	0	1	0	1	0	1	0	0	1	8
VB 10-1	0	1	0	1	0	0	1	0	1	10

* three individuals unscorable.

** plus an additional 22 individuals to calculate frequencies of PGM alleles.

individuals identically homozygous at all loci sampled. Samples from colonies within a cluster (the El Valle samples, cluster A from Browns Berg and clusters 2, 3, and 7 from Voltzberg) did not differ in alleles present. There are two instances of heterozygosity. Within colony cluster 7 at Voltzberg the enzyme PGM was polymorphic, and within the El Valle colony cluster the enzyme EST-4 was polymorphic; in each instance all three potential genotypes were present (11, 12, 22). In Voltzberg cluster 7, 30 spiders from one web and 5 from the other in the cluster were scored for their PGM phenotype. In El Valle a total of 37 spiders were examined for their EST-4 phenotype. In both, the proportion of individuals of each genotype in the cluster (data for the two webs which comprised cluster 7 combined, and data for the 5 El Valle webs combined) did not differ from that predicted by the Hardy-Weinberg equation given the allele frequencies calculated from the data (Table 3). There were no significant differences in the frequencies of the three genotypes (11, 12, 22) found in the two webs which made up colony cluster 7 ($chi^2 = 1.75$, 2 df, $p = 0.42$). Sample sizes were not large enough to make comparisons among the five El Valle webs sampled.

Comparison of the genotypes found within colony clusters presented in Table 2 with the spatial locations of colony clusters in Browns Berg and Voltzberg (Figs. 1 and 2), shows that adjacent colonies (e.g. Voltzberg clusters 3 and 4, separated by 70 m) may be fixed for different alleles of one or more enzyme.

Table 3.—Observed frequencies of genotypes found in Voltzberg 7 and El Valle 1 colony clusters compared with the frequencies expected under Hardy-Weinberg conditions, given gene frequencies calculated from the samples.

EST-4: El Valle webs 1 through 5 combined, frequency of allele 1 = 0.72, frequency of allele 2 = 0.28			
Genotype:	11	12	22
observed	19	15	3
expected	19.2	14.8	3
chi^2 = 0, 2 d.f., p = 1			

PGM: Voltzberg webs 1 and 2 from colony cluster 7 combined, frequency of allele 1 = 0.53, frequency of allele 2 = 0.47			
Genotype:	11	12	22
observed	8	21	6
expected	9.8	17.4	7.7
chi^2 = 0.93, 2 d.f., p = 0.63			

Mean heterozygosity for the total *A. eximius* sample is 0.060 with a standard error of 0.021, and the values for the Panama and Suriname samples are 0.017 (s.e. 0.012) and 0.024 (s.e. 0.012) respectively. Heterozygosity values within colony clusters are zero, except for the El Valle cluster (0.0080) and Voltzberg cluster 7 (0.0099).

For each enzyme studied the biochemical phenotypes of 7 to 14 spiders from each web were determined. In any individual web sampled, alleles that occurred with a frequency of 0.19 or more would have been detected with a probability of 0.05 or better. In future studies larger sample sizes (> 30 spiders per web) will increase the probability that all alleles present in a colony are detected, and that samples which show only one allele are representative of a monomorphic colony. The pooled samples total 187 spiders; thus the conclusion of extreme monomorphism in *A. eximius* is based on strong evidence.

F statistics for the seven polymorphic loci are presented in Table 4. F_{dt} describes the reduction in observed heterozygosity in the population as a whole; a value of zero implies that there is no difference between the observed and expected frequency of heterozygotes, whereas values close to 1 imply a great reduction in heterozygosity. F_{st} tells how much of the reduction in heterozygosity observed in the population is associated with division of the total population into sub-populations. A value of F_{st} close to zero indicates that little of the observed loss of heterozygosity is associated with division of the total population into sub-populations, and values close to 1 indicate that all or most of the observed loss is associated with division of the population into sub-populations. F_{ds} describes what portion of the reduction in observed heterozygosity is associated with the division of sub-populations (e.g. El Valle, El Llano, Browns Berg and Voltzberg) into demes (colony clusters). A value of F_{ds} close to zero would indicate that little of the observed reduction in heterozygosity is associated with division of the sub-populations into colony clusters, whereas values close to 1 indicate that most or all of the observed reduction is associated with division of the sub-population into demes.

All of the values of F_{dt} presented in Table 4 are large, indicating a large reduction in the occurrence of heterozygotes in the population. The polymorphic enzymes fall into two groups. For the enzymes EST-4, MUP, ACP and ADH all of the observed reduction in heterozygosity is associated with division of the total

Table 4.—Partitioning of total genetic variance in *Anelosimus eximius* into components associated with division of the total population into demes (F_{ds}) and sub-populations (F_{st}) for polymorphic enzyme systems.

A. demes = colony clusters, sub-populations = El Valle, El Llano, Browns Berg and Voltzberg.

	F_{ds}	F_{st}	F_{dt}
NP	1.0	0.37	1.0
PGM	0.90	0.18	0.92
SOD-4	1.0	0.43	0.93
EST-4	0.0	0.93	0.93
MUP	0.0	1.0	1.0
ACP	0.0	1.0	1.0
ADH	0.0	1.0	1.0

B. demes = colony clusters, sub-populations = Panama and Suriname.

	F_{ds}	F_{st}	F_{dt}
NP	1.0	0.32	1.0
PGM	0.91	0.05	0.92
SOD-4	1.0	0.17	1.0
EST-4	0.53	0.86	0.93
MUP	0.0	1.0	1.0
ACP	0.0	1.0	1.0
ADH	0.0	1.0	1.0

population sample into sub-populations, in particular into the Panama and Suriname sub-populations, and none is associated with division of the local populations into colony clusters. For the enzymes NP, PGM and SOD-4 the observed reduction in heterozygosity is largely associated with division of the total population and the sub-populations into colony clusters; relatively little is associated with division of the total population into sub-populations. The F statistics for EST-4, MUP, ACP and ADH imply that the Panama and Suriname populations are highly differentiated. The corresponding values for the enzymes NP, SOD-4 and PGM indicate that within large geographic areas (i.e. Panama and Suriname) there is little differentiation among local populations but a great deal of differentiation among colony clusters.

DISCUSSION

Social Structure and the Genetic Composition of Colonies.—*Anelosimus eximius* is highly monomorphic; within the Suriname samples only three loci out of 51 were polymorphic, and within the Panama samples only two. To interpret these results, that is, to decide whether these levels of homozygosity are unusually high or simply typical of spiders in general, it is necessary to compare these data with studies of genetic variability in other cooperative and non-cooperative spiders; however, very little comparative information is available. Riechert, Roeloffs and McCracken are studying genetic variation in the cooperative West African spider, *Agelena consociata* Denis (Agelenidae), and have found very few polymorphic systems and few heterozygotes (Riechert, pers. comm.). Lubin and Crozier (1985) examined 22 loci in 615 individuals of the New Guinea cooperative spider *Achearanea wau* Levi (Theridiidae) taken from four localities, and found only one polymorphic locus with two alleles. Using these data and Dowling and Moore's program for mean heterozygosity (1984), I calculated a mean

heterozygosity for *A. wau* of 0.02. I also calculated the mean levels of heterozygosity from data for three non-cooperative species: two species of *Philophonella* (Uloboridae) from Arizona (Smith, ms in prep) and for the California trap door spider *Bothriocyrtum californicum* (O. P.-Cambridge) (Ctenizidae) (Galindo-Ramirez and Beckwith 1983). Calculated mean heterozygosity for *Philophonella oweni* (Chamberlin) is 0.085, s.e. 0.048 (11 loci sampled in 18 individuals). For *Philophonella* sp. (undescribed species) calculated mean heterozygosity is 0.12, s.e. 0.052 (11 loci sampled in 12 individuals). For *B. californicum,* mean heterozygosity was 0.09, s.e. 0.06 (11 loci sampled in at least 64 individuals). These three non-cooperative species show higher levels of heterozygosity than the two cooperative species, perhaps because the cooperative societies examined are characterized by high levels of inbreeding within colonies. However, to establish that this is due to inbreeding and not to generally low levels of heterozygosity in the genus *Anelosimus* or the family Theridiidae, similar studies of related non-cooperative species are needed.

Colonies within a colony cluster do not appear to be genetically differentiated, given the limitations imposed by sample size. This suggests that the colony clusters are the result of budding rather than (for example) aggregations of unrelated webs at particularly favorable sites. However, samples taken from neighboring colony clusters, even when separated by as little as 70 m, may be fixed for different alleles at one or more loci. This implies that adult males probably do not leave their natal colonies and enter new webs to mate, and also suggests that effective migration by females and immatures into established webs does not occur. These data do not exclude the possibility that unrelated females may join (either occasionally or routinely) to found a new colony during the dispersal phase. The two colony clusters which contained heterozygotes might in fact be the result of colony foundation by unrelated females.

Social Behavior, Population Structure, and Speciation.—The genetic variation that occurs in the populations of *A. eximius* sampled is attributable to subdivision of the population into demes (colony clusters), and into geographic regions (Panama versus Suriname). Little or no variation is due to division of the population into sub-populations within a geographic area. Thus in comparing Browns Berg and Voltzberg, genetic variation appears to be attributable to division of the population into colony clusters, not to differences between Browns Berg and Voltzberg sub-populations as a whole. Thus, based on this sample, one can say that the structure of the *A. eximius* population is a genetic mosaic, with each piece in the mosaic consisting of one colony cluster. However, the samples were relatively small and sampled only two points out of the large range of *A. eximius;* thus what appears as a fixed difference at three loci between Panama and Suriname populations may actually be two extremes in a continuum of allelic frequencies across northern South America. Larger samples from Panama and Suriname encompassing more colony clusters and more localities, and samples from more of the range of *A. eximius* are needed.

Animal social systems have been proposed as an important agent shaping the genetic structure of populations and rates of speciation. Mammals show a rapid speciation rate and a high level of chromosomal diversity in comparison to other vertebrate groups (Bush et al. 1977). Several authors have attributed this to the mammalian propensity for social structuring (Wilson et al. 1975, Bush 1975), proposing that many types of mammalian social structure lead to the formation

of breeding units with small effective size and little gene flow among demes. This theoretically would create the same genetic environment as a founder event — a small, isolated gene pool in which stochastic events can act rapidly to fix unique genotypes or chromosomal types that are maladaptive in the heterozygous state and that would rapidly be eliminated by selection in a large panmictic population.

This hypothesis has been investigated many times by many authors (e.g. Daly 1981 with wild rabbits; McCracken 1984 with two species of bats; Patton and Feder 1981 with pocket gophers; review by Patton and Sherwood 1983). All reported that gene flow among social units, particularly by dispersing young, was sufficient to overcome any genetic effects caused by social structuring of the population. The hypothesis that social structuring alone has an effect on speciation rates does not appear to hold for mammals, the group for which it was originally proposed; however the cooperative or quasisocial spiders may be a perfect model for testing this hypothesis.

Templeton (1980a, 1980b) has provided a more refined analysis of the role of founder events in speciation in the context of a more general discussion of types of speciation. The three major elements in his analysis are: 1) the mechanism of speciation; 2) the structure of the ancestral population; and 3) the type of split between two potentially speciating populations.

1) Templeton (1980b) describes three mechanisms for speciation: genetic transilience, chromosomal transilience, and divergence. In the genetic transilience mechanism a founder event leads to a period of inbreeding during which alleles are subject to selection for their contribution to fitness in the homozygous state and against a more stable genetic background than (presumably) existed in the ancestral population. But rather than relying on accumulation of fixations and novel combinations at many loci, this model relies on changes in a few loci with major developmental and regulatory effects leading rapidly to a new "adaptive peak." In chromosomal transilience, a chromosomal translocation which is detrimental in its heterozygous form can quickly become established in small populations and provide a rapid barrier to gene flow with the ancestral population. Genetic divergence occurs by the accumulation of neutral and adaptive changes in allelic frequencies in populations separated by physical barriers, distance along a cline, host differences, etc.

2. The genetic structure of the ancestral population can be considered as one of two extreme types: a large panmictic population with high genetic variability, or a population divided into many tiny demes with little gene flow between them.

3) The type of split between populations can also be considered as one of two extremes: division of a population into two large, roughly equal populations, or a separation of small populations from a large parental population.

Genetic transilience is most likely to occur when a small founder population splits off from a large panmictic population; it is least likely to occur when the founding population splits off from an ancestral population which is already low in genetic diversity. In particular, it is unlikely to occur when the ancestral population consists of small highly inbred demes, because the founder population is unlikely to produce any novel genetic combinations by selection of alleles that are more fit against a uniform and homozygous background because the genome of the parent population has already been subject to selection for fitness in a uniform genetic background.

Chromosomal transilience is most likely to occur when the ancestral population consists of small inbreeding demes. Because chromosomal translocations are often deleterious in the heterozygous state, they are likely to persist only in small populations where they can rapidly become fixed by stochastic processes. Gradual divergence, with or without a physical barrier to gene flow, is also most likely to occur against a genetic background of small, isolated demes. Carson and Templeton (1984) conclude that although speciation via founder events probably occurs only under a restricted set of conditions, this mode of speciation may nonetheless be important for certain groups of organisms, or for organisms living under certain ecological conditions (but see Barton and Charlesworth 1984). The cooperative social spiders may be one such group of animals. *Anelosimus eximius* as it exists today apparently consists of many small inbred demes with little genetic variability; when a founder event takes place (such as foundation of a new colony), the emigrants also possess little genetic variability and there is little or no scope for novel genetic combinations to enter a new adaptive peak. Thus it is unlikely that *A. eximius* has given rise to new species by genetic transilience. Speciation by chromosomal transilience is more probable for modern *A. eximius* populations; if a chromosomal translocation occurred in one of the dispersing foundress females, it could rapidly become established in a homozygous form among her descendants. Finally, speciation by gradual divergence may also occur; in particular, the viscous nature of the population, and subdivision into small non-interacting demes, would accentuate the effects of natural geographic barriers to gene flow.

Speciation by chromosomal and genetic transilience are not expected to lead to high levels of genetic differentiation as detected by electrophoresis, producing full species which may be very similar electrophoretically. As a result, genetic distance measures are not expected to be good indicators of the species status of populations in which genetic or chromosomal transilience are frequent speciation mechanisms. Thus before any conclusions can be drawn about genetically differentiated populations, such as the Panama and Suriname populations of *A. eximius,* it will be necessary to do comparative studies of the genetic distances among morphologically recognized species of *Anelosimus.*

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Appendix 1.—Recipes for buffering systems and running conditions for gels.

R: described by Ridgway, Sherburne, and Lewis (1970). Electrode buffer = 0.06 M lithium hydroxide, 0.3 M boric acid, pH 8.1; gel buffer = 0.03 M Tris, 0.005 M citric acid, 0.0006 M lithium hydroxide, 0.003 M boric acid. Running conditions = pre-run 75 mA, main run < 225 V and < 75 mA.

C: described by Clayton and Tretiak (1972). Electrode buffer = 0.04 M citric acid, pH adjusted to 6.1 with N-(3-Aminopropyl)-morpholine; gel buffer = electrode buffer diluted 1:10. Running conditions = pre-run 75 mA, main run 75 mA and < 200 V.

M: described by Markert and Faulhaber (1965). Electrode buffer = 0.18 M Tris, 0.1 M boric acid, 0.004 M Na EDTA; gel buffer = electrode buffer diluted 1:4. Running conditions = pre-run 250 V, main run 275 V and < 75 mA.

4:adjusted from Selander et al. (1971). Electrode buffer = 0.223 M Tris (pH 7.0), 0.094 M citric acid, pH adjusted to 6.3 with NaOH; gel buffer = Tris and Tris HCl to pH 6.1, 0.003 M citric acid, final pH adjusted to 6.7 with 1 M NaOH. Running conditions = pre-run 75 mA, main run 75 mA.

grinding or extraction buffer: 5.36 g Tris, 5.16 g Tris HCl, 8 l H_2O, pH 7.10.

Appendix 2.—List of enzymes screened, standard abbreviations and buffer systems which gave the best results in each case. The buffers are R, C, M, and 4 (see appendix 1 for references); NA indicates no detectable activity on any gel/buffer system.

ENZYME	*ABBREVIATION*	*BUFFER*
acid phosphatase	ACP	C
aconitase	AC	R
adenosine deaminase	ADA	4
adenylate kinase	AK	C
alcohol dehydrogenase	ADH	4
aldolase	ALD	R
alphaglycerophosphate dehydrogenase	AGP	R
aspartate aminotransferase	AAT	R
diaphorase	DIA	4
esterase	EST-1	R,M,4
	EST-2	R,M,4
	EST-3	R,M,4
	EST-4	R,M,4
fructose diphosphatase	FDP	M
fumarase	FUM	4
galactosaminidase	GAM-1	C
	GAM-2	C
beta-glucosidase	beta-GLU	NA
glyceraldehyde-3-phosphate dehydrogenase	GAPDH	4
guanine deaminase	GDA	NA
glucokinase	GK	R
glucose-6-phosphate dehydrogenase	G6P	R
glucosephosphate isomerase	GPI	R,C,M,4
glutamic dehydrogenase	GDH	NA
glutamic pyruvic transaminase	GPT-1	C
	GPT-2	C
glutathione reductase	GR	4
hexoseaminidase	HA-1	R
	HA-2	R
hydroxybutyric dehydrogenase	HBDH	R
isocitrate dehydrogenase	IDH-1	C
	IDH-2	C
lactose dehydrogenase	LDH-1	C
	LDH-2	C
leucine aminopeptidase	LAP	NA
malate dehydrogenase	MDH-1	C
	MDH-2	C
malic enzymes	ME	R
mannosephosphate isomerase	MPI	R
alpha-mannosidase	alpha-MAN	NA
methylumbelliferyl phosphatase	MUP	C
nucleoside phosphorylase	NP	4
octanol dehydrogenase	ODH	NA
peptidase with leucyl-alanine	PEP-LA	M
peptidase with leucyl-leucyl-leucine	PEP-LLL-1	M
	PEP-LLL-2	M
peptidase with phenyl-alanyl-proline	PEP-PAP	M
phosphoglucomutase	PGM	4
phosphogluconate dehydrogenase	PGD	C
phosphoglycerate kinase	PGK	4
pyruvic kinase	PK	NA
protein	PRO	C
sorbitol dehydrogenase	SDH	R

Appendix 2.—cont.

superoxide dismutase	SOD-1	C,4
	SOD-2	C,4
	SOD-3	C,4
	SOD-4	C,4
triosephosphate isomerase	TPI	R,C,M,4
xanthine dehydrogenase	XDH	NA