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EVIDENCE FOR KIN-STRUCTURED GROUP FOUNDING AND LIMITED JUVENILE DISPERSAL IN THE SUB-SOCIAL SPIDER *STEGODYPHUS LINEATUS* (ARANEAE, ERESIDAE)

Jes Johannesen: Institut für Zoologie. Abteilung für Ökologie, Universität Mainz, Saarstrasse 21, D-55099 Mainz, Germany. e-mail: Jesjo@oekologie.biologie.uni-mainz.de

Yael Lubin: Mitrani Department of Desert Ecology, Blaustein Institute for Desert Research, Ben Gurion University of the Negev, Sede Boqer Campus, 84990 Israel.

ABSTRACT. In sub-social spiders, restricted dispersal of young (i.e., natal philopatry) and the potential for inbreeding could contribute to within-population subdivision, thus resulting in a population structure similar to that found in social congeners. In this context, we analyzed the origin and mode of individual distribution patterns and their contribution to within-population structure in juveniles of the sub-social spider *Stegodyphus lineatus.* We investigated the distribution of juveniles for four months after leaving the maternal nest using allozyme genetic markers. We found that isolated groups of juveniles consisted predominantly of siblings, whereas larger aggregations of individuals showed mixing of different juvenile sibling groups. However, even within such aggregations, sibling groups could be identified. Within the population at large, a heterozygote deficit and an uneven distribution of alleles were found. This was caused by limited movement of juveniles and males away from the natal site. Thus, the within-population (intrademic) structure could be partitioned into two components, resulting from kin-groups and population subdivision into demes. We compare this type of population structure with that found in non-social and social species, and discuss whether it provides conditions that could favor the evolution of sociality.

Keywords: Dispersal, sibling groups, allozymes, relatedness, group founding, intrademic structure.

Species of the genus *Stegodyphus* Simon 1873 (Eresidae) experience extended maternal care, in which spiderlings continue to be fed beyond their first instars and remain together after the mother's death (Schneider 1995). There are three social species (non-territorial permanently social, *sensu* Aviles 1997) in the genus. The widespread occurrence of extended maternal care and juvenile cohabitation in the sub-social congeners suggests that permanent sociality evolved in species that were preconditioned for a prolonged phase of tolerance. This has been termed the sub-social route to sociality (Buskirk 1981). Other eresids (e.g., *Eresus* Walckenaer, 1805, *Seothyra* Purcell 1903) exhibit sub-social behavior (Kullmann & Zimmermann 1975; Y. Lubin personal observation).

High population turnover, inbreeding in closed colonies and colony founding by one or a few related females are demographic characteristics typically associated with sociality in spiders (Riechert & Roeloffs 1993; Avilés 1997). Such populations may have low levels of genetic variation overall, and in particular, individuals within groups will be genetically similar. The spatial distribution of genetic variation within a population is important, because the evolution of social traits may depend on the degree of genetic similarity among interacting individuals.

Sub-social species examined so far differ from social species in having greater genetic variability, no permanent group living, and less population structuring (Johannesen et al. 1998; Johannesen & Lubin 1999). The eresid *Stegodyphus lineatus* Latreille 1817, is considered sub-social. After a phase of living communally in the maternal nest, young *S. lineatus* disperse and settle singly. Spiders live one year, and their nests are often found in clusters separated by large distances of similar, but uninhabited habitat (Lubin et al. 1998). Dispersing young initially settle in the vicinity of the maternal web (Lubin et al. 1998) but nest relocation is not uncommon (Ward & Lubin 1993). Lubin et al. (1998) suggested that limited movement of young during dispersal and their preference for certain species of shrubs results in clumped distributions. Using

genetic markers, Johannesen & Lubin (1999) showed that *S. lineatus* form relatively stable clusters in trees and that in such clusters, adult spiders experience limited dispersal. Furthermore, these groups showed evidence of being established by single females, a pattern similar to that found in social species. However, such stable environments may be atypical sites for this species, and data on juvenile movements in more typical habitats following the initial natal dispersal phase are still lacking.

The aim of the present study was to investigate juvenile dispersal of *S. lineatus* to explain the origin and amount of within-population genetic variance and the processes that produce this variance. We investigated the distribution of juveniles 4 mo after dispersal from the maternal nest. We examined whether clusters consisted of sibling groups, and if these remained separated or if they mixed with juveniles of other clusters. Finally, we tested for the occurrence of random mating at the population level. On the basis of a previous study (Johannesen & Lubin 1999) we predicted that clusters are predominately kin-groups. In contrast to the previous study, the present study analyzes a population in a wadi (dry riverbed), which is an unstable environment that is subject to occasional flooding and frequent disturbance from grazing. We ask if a stable environment is required to generate structuring within the population or if intrademic structure is an intrinsic part of the life history of *S. lineatus* in both stable and unstable environments.

METHODS

Juvenile spiders were collected from several clusters in a small wadi near Sede Boker in the Negev Desert, Israel (Fig. 1) on 25–26 October, 1998, about 4 mo after they left the maternal nest. A juvenile cluster was subjectively defined: either according to a clustered location in a specific plant or if the cluster was near to an old maternal nest showing signs of reproduction (remains of the consumed mother, exuviae of spiderlings). For every cluster, the number of occupied and unoccupied juvenile nests was noted. Two groups, 24A and 24B, were not discretely clustered but consisted of several single nests radiating from the bush-cluster of group 23 (Fig. 1). More than 200 juvenile nests were located: 79 webs were occupied by *S. lineatus,* four by another species, and 65 webs were empty. The remaining webs were not checked. The 79 juvenile spiders belonged to sixteen clusters. Thirteen of these clusters consisted of three or more individuals.

The population and family structure was investigated by means of genetic similarity estimates using enzyme electrophoresis. Electrophoresis staining procedures followed Johannesen & Lubin (1999). The enzymes *Aat-1, Pep-A* and *Adh* were omitted from the analysis because they did not stain or stained too weakly to be interpreted in all juveniles. These three enzymes stained weakly in adult animals. To improve the resolution of *esterase* alleles, the enzyme was run in Tris-Maleate pH = 7.8 instead of Tris-Maleate pH = 7.0.

To help investigate for an unequal distribution of alleles within the wadi, it was divided into an upper and lower half. Each wadi-half comprised about half the individuals. Random mating (Hardy-Weinberg proportions) within the total wadi population and within the upper and lower wadi, respectively, was tested by the Louis & Dempster (1987) exact test using the program GENEPOP (Raymond & Rousset 1995). Genotypic linkage disequilibria were estimated according to Weir (1991). Allele frequency differences between upper and lower wadi were tested applying a RxC—test (GENEPOP) (Fig. 1). Estimates of genetic differentiation among spider groups were obtained by the *F*-statistic estimators of Weir & Cockerham (1984), using the program Biosys (Swofford & Selander 1989). Standard deviations were obtained by jackknifing over loci. *F*-statistics assume that populations (or groups) are defined as breeding units, i.e., the individuals in a group originated from random matings of the previous generation. However, if a cluster consists primarily of siblings, the random mating assumption is violated (Chesser 1991), because by having the same parents, genes of siblings are correlated. Thus, within-population structure may be confounded owing to sampling both sibling groups and breeding units (multi-parental groups). This may lead to a population subdivision estimate based on variance between families, and not actual population subdivision.

To distinguish between genetic structure caused by breeding units and that caused by sibling groups, we used the approach outlined in Johannesen & Lubin (1999), combining a test for group relatedness and heterozygote ex-

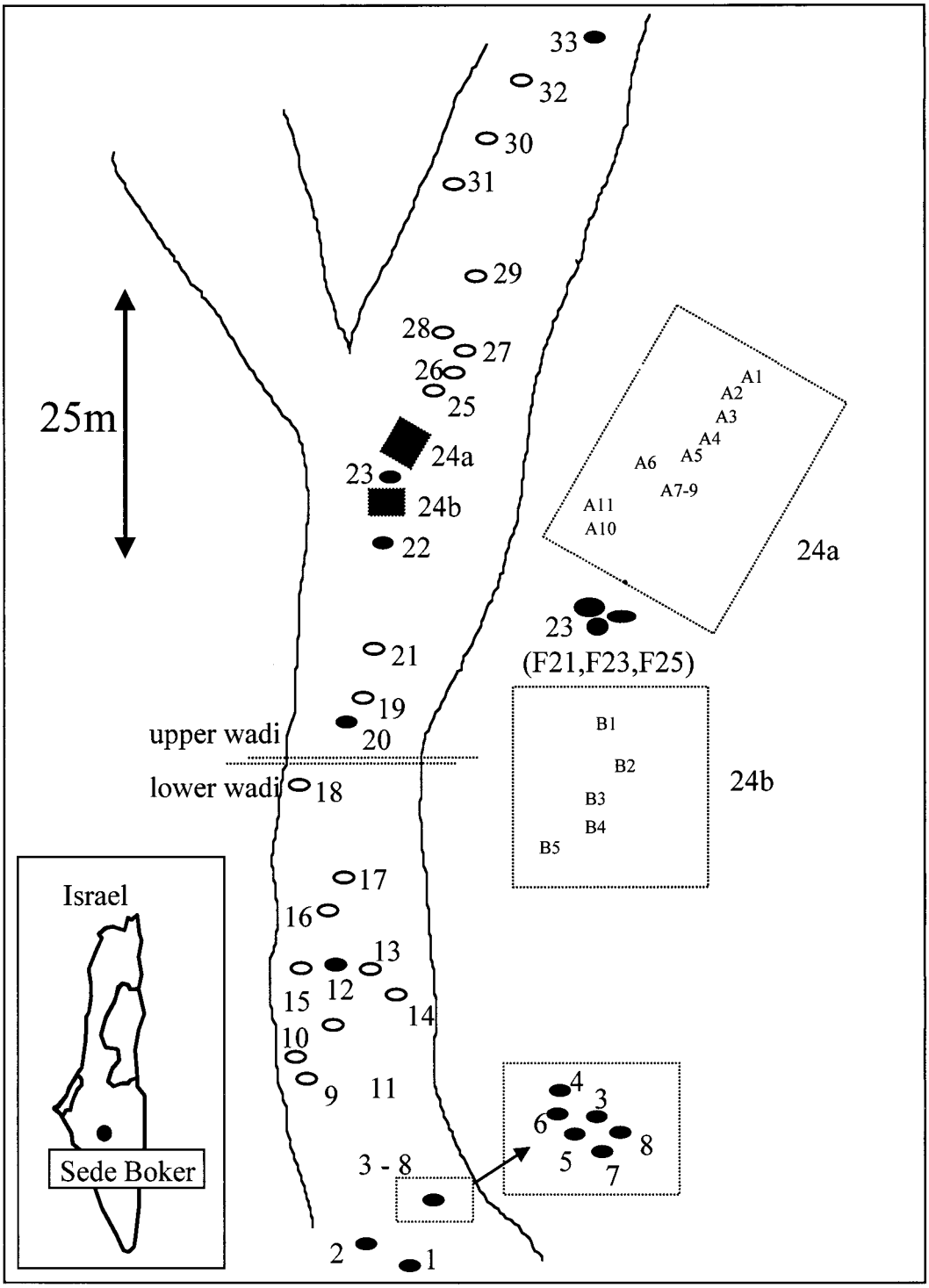

Figure 1.—Sampling location and positions of juvenile *Stegodyphus lineatus* in a wadi near Sede Boker, Israel. Filled circles represent sampled clusters.

cess. The test provides an indication of whether the relatedness of individuals in specific clusters is caused primarily by population subdivision (Wahlund effects) or by sibling relationships. In a two-allelic full-sibling group the average heterozygote excess due to the sibling effect is 7/6 *pq* (Rasmussen 1979). If individuals of a cluster are related, $R_{group} > 0$, and have an inbreeding index, $F_{group} < 0$, then this indicates a group of predominantly siblings. In a structured population, where the population inbreeding index $F_{IT} > 0$, if $R_{group} > 0$ and $F_{group} = 0$, then this may indicate that a cluster consists of offspring from several parents; here the positive value of R is a consequence of subdivision of the population (the Wahlund effect). It should be noted, however, that this test is a crude measure when dealing with only one or two polymorphic loci. If only one polymorphic locus is present and parents of a full-sibling group carried alternative alleles, then $F_{group} \approx 0$. F_{group} values were tested for significance using permutation tests (see Johannesen & Lubin 1999). The population-wide Wahlund effect (measured here as F_{IT}) is little affected by the sibling effect if more than four sibling groups are sampled (Rasmussen 1979). In a random mating population consisting of family groups, F_{IT} quickly approaches zero as the number of sibling groups increases.

Relatedness of group individuals was estimated according to the method of Queller & Goodnight (1989). The population R estimate was obtained by jackknifing over clusters. Only clusters having three or more individuals were analyzed in the group comparisons. For estimates concerning the total wadi population, all sampled individuals were included in the analysis. Kinship assignment of individuals to sibling groups was performed under the primary hypothesis of individuals being full siblings (paternal relatedness pR = 0.5, maternal relatedness mR = 0.5) against the null hypothesis pR = 0 and mR = 0 using the program Kinship 1.0 (Queller & Goodnight 1989). The above hypothesis of full sibling is conservative, given that we lack information about the frequency of multiple mating in natural populations.

RESULTS

A deviation from random mating (Hardy-Weinberg proportions) was found within the wadi-population, $P < 0.001$. *Pep-B1, Est* and *Idh* experienced a deficit of heterozygotes, whereas the two remaining high- polymorphism loci *Ak* and *Sorbdh* and the two low-polymorphism loci *Ldh1* and *Fum* did not. All rare alleles were found only as heterozygotes. Furthermore, significant deviations from Hardy-Weinberg proportions were found within both sections of the wadi (lower half $P < 0.05$, upper half $P < 0.01$). Significant differences in allele distributions was found between the upper and lower half of the wadi population ($P < 0.001$), e.g., the *Est* alleles *2* and *6* were found only in the lower half, whereas the *Ldh* allele *87* and *Fum* allele *124* were found only in the upper half. In the total wadi sample, genetic linkage disequilibrium was observed in 8 out of 21 pair-wise locus comparisons (38%). Genotype distributions are given in the Appendix.

An average group relatedness of $R = 0.25 \pm 0.12$ was observed. The relatedness estimate for single clusters ranged between −0.21 and 0.82 (Table 1). The relatively large standard deviation indicated that some groups consisted of individuals differing in their genetic background. This was confirmed by the F_{group} estimators (Table 1), where F_{group} ranged between −0.58 and 0.41. Out of the 13 examined clusters, seven showed a heterozygote excess. Based on permutation tests, nine groups had a heterozygote excess, two of which were significant. The remaining groups exhibiting homozygote excess were part of larger clusters. The finding is corroborated by the F-statistics, $F_{IT} = 0.150 \pm 0.067$; $F_{IS} = -0.070 \pm 0.073$; $F_{ST} = 0.209 \pm 0.086$, which showed that both kin (negative F_{IS}) and Wahlund effects (positive F_{IT}) enhance F_{ST}, which is the differentiation among groups (Table 1).

Kinship-analyses were performed within four groupings: clusters 3–8, cluster 12, aggregated clusters 24A, 24B, F21, F23, F25, and cluster 33, under the assumption that individuals in these clusters were full siblings. Figure 2 (see also Appendix) illustrates the kinship assignment based on the rare non-overlapping *Ak*/*Est*/*Pep-B1* allele combinations in clusters 3–8. Individuals carrying the allelic combinations tested as full-siblings belonging to one of two sibling groups. Individuals from clusters 3–8 were regrouped into two groups consisting of the predicted full-sibling assignments based on *Ak*/*Est*/*Pep-B1* allelic distributions, and the R and F_{group} values were estimated for these groups. The in-

Table 1.—Relatedness and inbreeding index estimates for clusters of juvenile *S. Lineatus* within a wadi population. Sibling group 1 and 2 estimates are based on rearrangement of individuals from groups 3–8 into two sibling groups based on allelic distributions (see text). Significant permutation F_{group}'s ($P < 0.05$) are presented in bold.

Group estimates cluster	N	Relatedness	F_{group}	Mean permutation F_{group}	Mean permutation sd
1	2	—	—	—	—
2	4	−0.21	0.30	0.19	0.13
3	6	0.28	0.01	−0.12	0.28
4	7	0.11	0.13	0.05	0.12
5	3	0.00	0.41	0.29	0.12
6	5	0.45	0.24	0.09	0.33
7	1	—	—	—	—
8	6	0.64	−0.13	−0.27	0.19
12	6	0.30	−0.05	−0.17	0.24
20	1	—	—	—	—
24A	11	0.22	−0.13	−0.20	0.11
24B	5	−0.07	0.05	−0.10	0.22
F21	5	0.72	−0.58	**−0.76**	0.30
F23	5	0.09	−0.11	−0.25	0.22
F25	5	0.06	−0.11	−0.25	0.15
33	8	0.82	−0.52	**−0.64**	0.19
Sibling Group 1	6	0.52	−0.31	**−0.24**	0.08
Sibling Group 2	14	0.55	−0.20	**−0.21**	0.08

Population estimates Relatedness	F_{IT}	F_{IS}	F_{ST}
0.25 ± 0.12	0.15 ± 0.05	−0.070 ± 0.073	0.209 ± 0.086

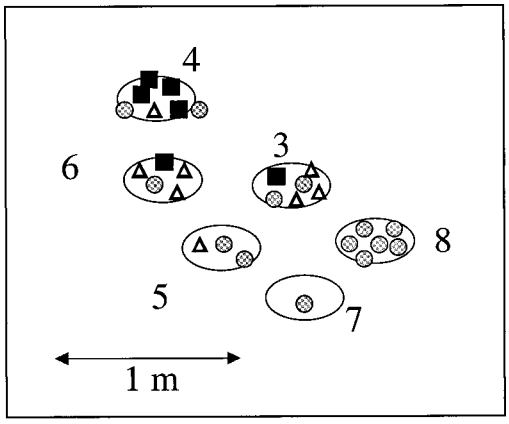

Figure 2.—Kinship assignment based on allele combinations of clusters 3–8. Ellipses indicate juvenile clusters on separate plants. Individuals belonging to sibling group 1 are depicted with squares (■), sibling group 2 members with circles (●), and non-assigned individuals by triangles (△). Two centers of distribution can be recognized.

dividuals that were not regrouped were omitted from the population analysis to avoid biasing population estimates. The two predicted sibling groups showed a relatedness estimate of $R \approx 0.50$ and a significant excess of heterozygotes, $F < 0$ (Table 2). However, the genotype composition of sibling group 2 revealed that it does not consist of only full-siblings. At least one second mating must be assumed. Each group has a center of origin, and juveniles of the two groups mix (Fig. 2).

Kinship analysis of cluster 12 showed two significant full-sibling groups for individuals 1, 3 and 5, and for 4 and 7, respectively. In the upper wadi, the kinship analysis for the group aggregation 24A, 24B, F21, F23 and F25 did not give unequivocal results. The distribution of rare alleles indicated, as previously, mixing of juveniles but an individual assignment to sibling groups was only possible for the F21 cluster, which indicated individuals of a single sibling group. The analysis gave ambiguous results for the remaining individuals due to the lack of rare-allele varia-

Table 2.—A comparison of within-locality genetic structure in sub-social and social spiders. Genetic variance components are divided into three categories and refer to the location at which an individual can be found relative to the population at large: (i) variance among kin-groups (after juvenile dispersal); (ii) demic effects at a locality (intra-locality Wahlund effect); and (iii) more than one genetically independent population unit within a locality (i.e., closed colonies).

	Source of variance, among:			
Species	(i) Kin groups	(ii) Demes	(iii) Closed colonies	Reference
Sub-social species				
Eresus cinnaberinus	Yes	No	No	Johannesen et al. 1998
Stegodyphus. lineatus	Yes	Yes	No	Johannesen & Lubin 1999
Social species				
Stegodyphus sarasinorum	?	Yes	Yes	Smith & Engel 1994
Anelosimus eximius	?	Yes	Yes	Smith 1986; Smith & Hagen 1996
Agelena consociata	?	Yes	Yes	Roeloffs & Riechert 1988; Riechert & Roeloffs 1993
Achaearanea wau	?	Yes	?	Lubin & Crozier 1985

tion. All individuals of cluster 33 indicated full-siblings. However, individual 4 is more likely a half-sibling to the remaining individuals, as indicated by the *Pep-B1* genotype. Combining the kinship analysis and F_{group} estimators suggests that most clusters consisted predominantly of siblings.

DISCUSSION

Intrademic structure of *S. lineatus*.—We found that despite juvenile nest relocation within the first months of leaving the maternal nest (Ward & Lubin 1993; Lubin et al. 1998), most juveniles remained distinctly clustered and did not disperse over greater distances. Several months after leaving the maternal nest, juveniles in isolated clusters consisted mostly of sibling groups, whereas larger aggregations of juveniles originated from several parental pairs. In these larger groups, juveniles of different parentage can mix. However, even within such aggregations, sibling groupings could be identified. Furthermore, we found evidence for the occurrence of multiple mating; thus, some of the variation is likely to be due to multiple fathers. The suggestion that multiple mating is not uncommon derives also from field studies showing a high frequency of male infanticide and probable remating in a natural population (Schneider 1997; Schneider & Lubin 1996, 1997).

In the present study, the lack of heterozygotes at the population level suggests that mating-dispersal did not take place throughout the population. If mating is random throughout a population, the population at large should obey Hardy-Weinberg proportions. Indeed, if a population is subdivided into family units, the population inbreeding coefficient is expected to be very slightly negative, i.e., showing an excess of heterozygotes (Cockerham 1969; Rasmussen 1979). A heterozygote deficit for an entire population that is divided into sibling groups is a strong indication for non-random mating within the population and, therefore, of population sub-structuring. Thus we conclude that *S. lineatus* juveniles settle, and later mate, largely in the vicinity of the maternal nest. The existence of clusters of siblings suggest that new groups arise by single females colonizing new nesting sites.

Despite male dispersal during the mating period (Schneider & Lubin 1996), female group founding must have a greater relative impact on population structure because the propagule-type of cluster founding (Slatkin 1977), combined with generally philopatric behavior, enhances genetic differences among groups more rapidly than male mating-dispersal can break them down. Furthermore, if females disperse to previously empty sites, then the two phenomena of female philopatry and female dispersal will combine to create neighborhood-structured demes. Therefore, occasional dispersal by females to new local-

ities away from the cluster does not conflict with the observed structure. Female distributions are the basis for kin-groups. This is supported by a previous study of population structure, which showed that sibling groups could be found even among adult spiders and also suggested that male mating-dispersal was limited (Johannesen & Lubin 1999). The previous results may have been biased because spiders were sampled from long-lived Acacia trees, which are relatively uncommon habitats for *S. lineatus* in the Negev region. The two studies combined show that a stable environment is not necessary to create sub-structuring of a *S. lineatus* population. In addition, the present study shows that intrademic structure does not depend on the life stage sampled: juvenile and adult populations exhibited similar population structures. Rather, population sub-structuring into sibling groups is likely to be an inherent consequence of philopatric breeding and dispersal behavior.

The type of population structure seen in *S. lineatus,* where spiders occur in family neighborhoods and further population subdivision results from restricted movement of males, may lead to the differential proliferation of both kin-groups and population subsets. One may think of a *S. lineatus* population as a dynamic population where new patches arise constantly and old o nes disappear. Female group-founding and limited mating-dispersal within the population lead to the differential distribution of genetic variation within populations This pattern can be seen in other populations in the Negev (Johannesen & Lubin 1999).

Intrademic structure and social spider evolution.—The genetic structure observed among *S. lineatus* clusters complies with predictions of increased intra-locality structure for social evolution. However, we need to know whether genetic similarity within groups per se can be extrapolated to provide a basis for the evolution of social behavior. If kin-groups in an open mating system are defined as population units then a significant among-group variance, i.e. similarity of group members, is inherent (e.g., Ingvarson & Giles 1999), but does not necessarily imply an advantage to sociality. Genetic indices can be used to infer the origin and mode of individual distribution patterns (and structuring processes) and may as such, be more informative explaining social spider evolution than merely similarity of group members.

Common for social spiders is the establishment of new colonies or populations by mated females or by several related individuals (Vollrath 1982; Lubin & Robinson 1982), and the presence of closed colony clusters. In other words, genetic similarity is achieved by female lineages (propagule migration model), not by migrants from different populations mating randomly in isolated populations (migrant-pool model). The former type of structuring process seems also true for the sub-social *S. lineatus,* albeit in an open system. A comparison of *S. lineatus* and another sub-social eresid, *Eresus cinnaberinus* (Olivier 1789) indicates that the genetic variance in *S. lineatus* is partitioned a step further than in *E. cinnaberinus,* where family groups are observed, but there is no intralocality subdivision (Johannesen et al. 1998). However, in neither *S. lineatus* nor *E. cinnaberinus* were localities divided into more than one population unit, as has been found in social spiders (Table 2). Intralocality differentiation also seems limited or lacking in two non-social species that have been investigated in more detail at the within population level. In *Pholcus phalangioides* (Fuesslin 1775) there is suggestive evidence that philopatry may cause some micro-structuring among cellar populations within the same building, but also that frequent dispersal breaks it down repeatedly (Schäfer et al. 2001). For *Atypus affinis* Eichwald 1830, no within-population divergence was observed. Structuring processes are active, however, at distances of a few kilometres. Ballooning *A. affinis* probably seldom drift beyond the bounds of the population (Pedersen & Loeschcke 2001). In contrast, virtually no structure was detected in the excellent ballooner *Argiope trifasciata* (Forskal 1775) (Ramirez & Haakonsen 1999).

The four social species that have been investigated genetically, *Stegodyphus sarasinorum* Karsch 1891, *Anelosimus eximius* (Keyserling 1884), *Agelena consociata* Denis 1965 and *Achaearanea wau* Levi et al. 1982 have taken population subdivision one step further than *S. lineatus* by creating a closed genetic system of regularly inbreeding colonies. The general lack of allozyme allelic variation in social relative to sub-social species may also be evidence for a process of group closure

(Table 2). We emphasize that Table 2 at present is only suggestive and that three caveats should be noted: 1) The family component in the sub-social species can be estimated because individuals could be assigned to specific grid-positions. This has not been possible in the social species where individuals were taken at large from a colony and within-colony family components have not been determined. 2) The term ''closed colony'' refers to at least two genetically independent colony clusters at one locality. Many localities probably contain clusters derived from a single founding event. Because of the general lack of genetic polymorphism in social spiders, it could not be determined if these colonies have diverged into independent population units or not. 3) Because the localities of social spiders may consist of more than one population unit, the deme genetic variance is given *a priori.*

A closed population structure will generate extreme variances between groups. If groups have different relative fitness, this may result in selection among groups. Groups with higher productivity (due to cooperation) should produce more young, and therefore more dispersing propagules, than groups lacking this trait. To avoid invasion of selfish individuals, high population turnover (Avilés 1993) and dispersal to establish new trait groups (Sober & Wilson 1998) are essential. Two of the three social species of *Stegodyphus* were shown to experience high population turnover (Seibt & Wickler 1988; Crouch & Lubin 2000). Further evidence for a change in population system, from an open system to a closed one, comes from the study of female-biased sex ratios in social spiders. High population turnover alone is not sufficient to produce these ratios. Two additional components, group-level selection and enough population subdivision to create a ratio of the genetic variances favorable to the group level, are required (Avilés 1993). Intercolony selection can only take place once closed colonies have been established (Avilés 1997).

The genetic data presently compiled on social and sub-social spiders allows preliminary comparisons of genetic patterns among species of different social levels relative to their breeding behavior (Table 2). One possible test to evaluate the significance of breeding structure in spider social evolution would be to compare the population genetic structure of social and sub-social species with communal non-social species. The latter form coherent groups, and perhaps even kin-groups, but are unlikely to inbreed. A comparison of genetic systems might identify patterns for the elucidation of underlying evolutionary processes. However, one should keep in mind that patterns do not create processes, rather patterns may be used only to infer processes (Templeton 1998).

The central unsolved questions are thus how and why do open systems become closed, what ecological conditions make individuals refrain from dispersal altogether and remain clustered (see discussions in Avilés & Gelsey (1998) and Avilés (1999), and is a closed system required for the evolution of sociality in spiders? Thus, in a genetic context, one needs to distinguish between traits leading to and resulting from demic structure.

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Appendix. Genotypes of seven polymorphic loci in *S. lineatus* juveniles smapled at Sede Boker. Missing genotypes were too weak to score. Allele designations are relative distances, except for *esterase* which was run in two buffers and alleles were given numbers according to their mobility.

Id.	AK	EST	FUM	IDH	LD2	PB1	SO2
Cluster1							
1	100100	44	100100	100100	100100		
2	100113	45	100100	90100	100100	94106	77100
Cluster 2							
1	100100	44	100100	90100	100100	94100	100100
3	100113	44	100100	100100	100100	9494	7777
5	93100	55	100100	100100	100100	100106	7777
6	100113	44	100100	90100	100100	100106	7777
Cluster 3							
1	100100	45	100100	100100	100100	100100	7777
2	100113	24	100100	90100	100100	100100	7777
3	100100	44	100100	100100	100100	100100	77100
4	100100	44	100100	100100	100100	100100	7777
5	100100	46	100100	100100	100100	100106	77100
6	100113	24	100100	9090	100100	100100	77100
Cluster 4							
1	100100	44	100100	100100	100100	100100	7777
2	100100	46	100100	100100	100100	100100	77100
3	100100	46	100100	100100	100100	106106	7777
4	100100	46	100100	90100	100100	100106	7777
5	100100	44	100100	100100	100100	106106	77100
6	100113	24	100100	90100	100100	100100	77100
7	100113	24	100100	9090	100100		7777
Cluster 5							
1	113113	24	100100	90100	100100	100100	77100
3	100100	44	100100	100100	100100	100100	7777
4	100100	24	100100	9090	100100	100100	100100
Cluster 6							
1	100100	44	100100	100100	100100	100100	7777
2	100100	44	100100	100100	100100	100100	7777
3	100100	46	100100	100100	100100	100106	77100
4	100100	44	100100	9090	100100	100100	77100
5	100113	44	100100	100100	100100	100100	7777
Cluster 7							
1	100113	44	100100	100100	100100	100100	77100
Cluster 8							
1	100113	24	100100	9090	100100	100100	7777
2	113113	24	100100	90100	100100	100100	100100
3	100113	44	100100	9090	100100	100100	100100
4	100113	44	100100	9090	100100	100100	100100
5	100113	44	100100	90100	100100	100100	77100
6	100113	44	100100	9090	100100	100100	77100
Cluster 12							
1	100113	45	100100	100100	100100	106106	7777
3	100113	45	100100	100100	100100	106106	7777
4	100113	44	100100	90100	100100	100106	77100
5	100100	44	100100	100100	100100	106106	7777
6	100100	44	100100	100100	100100	100106	77100
7	100100	44	100100	90100	100100	100106	10010
Cluster 20							
1	100100	45	100100	100100	100100	106106	77100
Cluster 24A							
1	100100	45	100100	100100	100100	100106	7777
2	100113	55	100100	100100	100100	100100	77100
3	100113	45	100124	100100	100100	94106	77100
4	100100	55	100100	100100	87100	100100	77100
5	100113	45	100124	100100	100100	100100	7777
6	100100	55	100100	90100	100100	100100	7777
7	100113	45	100124	90100	100100	100100	77100
8	100100	45	100124	100100	100100	94100	77100
9	100100	55	100124	100100	100100	100100	7777
10	100100	44	100100	100100	100100	100106	77100
11	100100	55	100100	100100	100100	100106	7777
Cluster 24B							
1	100100	44	100100	90100	87100	100100	77100
2	113113	55	100100	100100	100100	100100	10010
3	100100	44	100100	100100	87100	100106	77100
4	100100	44	100100	100100	100100	100106	77100
5	100113	44	100100	90100	100100	100106	77100
Cluster F21							
1	100113	45	100100	90100	100100	100106	7777
2	100100	44	100100	90100	100100	100106	7777
3	100100	45	100100	90100	100100	100106	7777
4	100100	44	100100	90100	100100	100106	7777
5	100100	45	100100	90100	100100	100106	7777
Cluster F23							
1	100113	45	100124	100100	100100	100100	77100
2	100113	44	100100	100100	100100	100106	7777
3	100100	55	100100	100100	100100	100100	77100
4	100100	45	100100	90100	100100	100106	77100
5	100100	55	100100	90100	100100	100100	77100
Cluster F25							
1	100100	55	100100	100100	87100	100106	77100
2	100113	44	100100	100100	100100	94106	77100
3	100100	55	100100	100100	100100	100106	77100
4	100113	44	100100	100100	100100	100106	7777
5	100100	45	100100	100100	87100		
Cluster 33							
1	100100	45	100124	100100	100100	9494	77100
2	100100	55	100100	100100	100100	9494	77100
3	100100	45	100124	100100	100100	9494	77100
4	100100	45	100124	100100	100100	94106	77100
5	100100	45	100124	100100	100100	9494	77100
6	100100	55	100100	100100	100100	9494	77100
7	100100	55	100124	100100	100100	9494	77100
8	100100	55	100124	100100	100100	9494	77100