chicken feathers and from B-16 melanoma cells, which were similar to the spectrum of black hair melanin.

Our data thus support the suggestion (*5*, *6*) that many natural melanins are copolymers of dopa and cysteinyldopa. Such copolymers may conveniently be characterized in terms of an *r* value, which is related to the proportions of dopa and cysteinyldopa incorporated into the polymer. We have shown that pheomelanins from red chicken feathers and red hair are spectroscopically dissimilar and that red hair pheomelanin is a copolymer. The argument that some eumelanins are also copolymers, which was based largely on the high sulfur content of some of these materials (*5*, *6*), is supported by our spectroscopic evidence that human brown eye melanin is such a copolymer. It seems that structures characteristic of pheomelanin can be found in tissue other than hair or feathers. It should be possible to use the ESR method to test for the presence of pheomelanin in skin, which is suggested by morphological studies (*2*) but has yet to be chemically verified. This is important in view of a putative link (*15*) between the high incidence of skin cancer in red-haired individuals and the ultraviolet-induced breakdown of pheomelanin presumed to be present in the skin.

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Variation in the Social Grouping Tendency of a Communal Web-Building Spider

Abstract. *The orb web–building spider,* Metepeira spinipes, *from Mexico occurs solitarily and, more frequently, in aggregations of 5 to 150 or more individuals. Although communal, individuals maintain webs and retreats within the colony and capture their own prey. Group size and interindividual distance apparently vary in response to climate and availability of prey.*

Spiders are usually solitary, exhibiting aggressive behavior toward other animals, including conspecifics. Communal and cooperative living patterns have been observed in a few species from several families (*1–3*). Group living patterns in spiders range from simple temporary aggregations to communal web-building, cooperative prey capture, and indiscriminate brood care (*3*, *4*).

Metepeira spinipes Pickard-Cambridge, an orb web–building spider, may be solitary, but more frequently lives in permanent aggregations of 5 to 150 or more individuals (*5*). Observations of this species in central Mexico in 1978 and 1979 showed that it exhibits a communal-territorial living arrangement; that is, individuals maintain their own webs and retreats within a colony and capture their own prey (*2*, *6*). Aggregations of *M. spinipes* remain together for long periods of time (*7*), and individuals taken from colonies hundreds of miles apart may build webs together (*8*). The social grouping tendency of this species appears to be flexible; group size and interindividual distance may vary as a function of environmental severity and the relative availability of prey. The combination of solitary and communal behavior exhibited by this species suggests that it may represent an intermediate stage in the evolution of social behavior in spiders.

The web of individual *M. spinipes* is characteristic of the genus: a three-dimensional space web and catching spiral composite with a retreat in the space web. Signal threads connect the hub of the spiral and the retreat, where the spider rests (*5*). In the groups observed individuals had their own retreats and spirals, but space webs were joined (*2*, *5*, *6*). The sticky catching spirals are taken down and renewed daily, but the communal space web, which serves as a framework for the web-building activities of numerous individuals, is left intact. The communal web is a mass of interconnected webbing that is attached to the vegetation, usually *Agave* and *Opuntia*. Although the communal web is built and maintained by the efforts of all colony members, individuals defend their spirals and retreats against intruders and interact while on the space web. Prey captured on spirals are not shared.

Group size in *M. spinipes* varies by habitat (Fig. 1). In those where prey availability is low and environmental conditions are extreme, such as a high-altitude habitat (Parque Sierra Morelos) or a desert grassland (San Miguel de Allende), individuals are predominantly solitary or live in small groups. In intermediate sites such as agricultural areas with seasonal rainfall (Toluca, Tepotzotlán, and Guadalupe Lake) spiders occur more frequently in aggregations. Differences in group size between these sites appear to be attributable to availability of prey. In the moist tropical site, where climate is favorable all year and insect abundance is great, colony size is large (*9*). The distributions of group size in all but one habitat we studied (Parque Sierra Morelos) were significantly different ($P < .05$) from a Poisson distribution truncated at zero, indicating nonrandom clumping at large colony sizes (*2*, *6*).

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Table 1. Mean distance of nearest neighbor (± 2 standard errors of the mean) of *M. spinipes* individuals within colonies and estimates of availability of prey for sites in central Mexico.

Site			Colony (No.)	Nearest-neighbor distance (cm)	Estimated prey (number per cubic meter per day)	
Name	Elevation (m)	Description			Mean	Range
San Miguel de Allende	2400	Arid grassland with *Opuntia* and other cactus	24	17.49 + 3.17	59	49 to 70
Toluca	2600	Agricultural area with *Agave*; much human and animal waste	26	11.73 + 1.24	96	64 to 116
Tepotzotlán	2100	Roadside *Agave* border	21	12.65 + 1.96	130	112 to 160
		Agave plantation with dumping of feedlot waste	37	8.22 + 0.70	205	160 to 300
Guadalupe Lake	2270	East shore of reservoir with *Opuntia*: insects blown ashore by prevailing winds	27	6.85 + 0.83	316	296 to 336
Córdoba	929	Tropical mountainside with coffee and banana plantations	10	3.78 + 0.42	840	600 to 1000

The distance of nearest neighbors within a colony (Table 1) was negatively correlated ($r = .97$, $P < .01$) with prey availability (*10*), indicating that *M. spinipes* can tolerate conspecifics at closer distances as the availability of prey increases. Riechert (*11*) found that distances between individuals of a solitary desert funnel web spider, *Agelenopsis aperta* (Agelenidae), decreased as a function of decreasing latitude.

To examine further the relation between climate, prey availability, spider group size, and spacing, we designed a series of field experiments. In Toluca, colonies were moved from a site in the agricultural valley (elevation, 2600 m), where prey were abundant and the climate was moderate, to a higher altitude (3000 m) on a mountainside, where there were high winds and wide fluctuations in temperature and moisture. Twenty colonies of ten individuals each were measured for nearest-neighbor distance, collected, and then released into agaves at Parque Sierra Morelos. At this site, spiders were usually solitary or in groups of only two or three. Prey abundance on the mountainside is much lower than that in the valley where the experimental colonies were collected. Measurements made after 10 days showed that 12 of the 20 transplanted groups had remained at the new site and built webs together, but the size of these groups had decreased from 10 to 7.75 ± 3.36 (mean ± standard deviation). Nearest-neighbor distances had almost doubled, from 11.73 ± 1.24 cm (mean ± standard error of the mean, $N = 26$) to 19.63 ± 4.38 ($N = 11$), which is statistically significant ($t = 3.32$, $P < .05$).

In Tepotzotlán, an agricultural area north of Mexico City, the influence of prey availability on social grouping and spacing could be tested in a more moderate environment. Colonies were moved from a site where insect activity was high, because of the dumping of feedlot waste, to a nearby area of lower insect activity. We assumed that there were no differences in microclimate between the areas. Ten groups of 20 spiders each were measured, collected, and transplanted to agaves in the same manner as at Toluca. Mounds of cow dung were piled near five of the transplanted groups to increase the availability of prey, and 10 days later there was no statistically significant change in group size or nearest-neighbor distance among these five (Table 2). In the other five groups there was a statistically significant reduction in colony size (to 16.6 ± 1.67) and nearest-neighbor distance had almost tripled, from 8.22 ± 0.70 ($N = 37$) to 22.15 ± 4.95 ($N = 5$; $t = 3.32$, $P < .05$).

The results indicate that the differences in both group size and nearest-neighbor distance are largely due to varying prey availability. Individuals of *M. spinipes* tolerate conspecifics at closer distances in areas with abundant prey. In contrast to territorial desert spiders whose territory size is genetically fixed in each population (*12*), *M. spinipes* shows a flexible social spacing pattern and rapid responses to changes in prey availability. This is probably possible because the spiders renew their catching spirals daily. It is during the time of web construction that most aggressive inter-

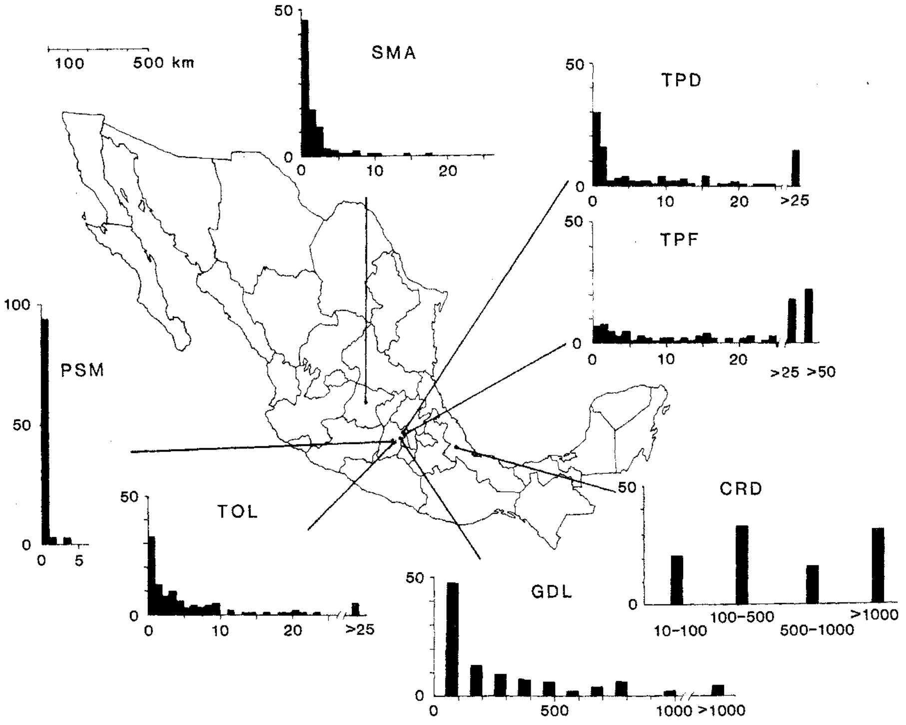

Fig. 1. Frequency distributions of group size for *M. spinipes* in various sites in central Mexico; average numbers of individuals are represented on the ordinate and frequency of groups on the abscissa. Abbreviations: *SMA*, San Miguel de Allende; *TPD*, Tepotzotlán, roadside dump; *TPF*, Tepotzotlán, feedlot waste disposal area; *CRD*, Córdoba; *GDL*, Guadalupe Lake; *TOL*, Toluca; and *PSM*, Parque Sierra Morelos.

actions and contests occur (*13*). In view of the wide range of nearest-neighbor distances exhibited by the population observed, it is possible that there are several ecotypes of this species—that is, geographically distinct populations with genetically determined ranges of interindividual spacing, adapted to the environments in which they occur (*14*).

The combination of solitary and communal behavior exhibited by this species suggests that it represents an intermediate stage in the evolution of social behavior in spiders. Perhaps the communal behavior of *M. spinipes* evolved as the result of an increased tolerance of conspecifics in habitats where prey was locally or seasonally abundant. In such habitats, territory size and interindividual distance could at times be reduced, and populations would be large. If web sites with proper architectural support were patchily distributed, as *Agave* and *Opuntia* are, selection might favor individuals capable of tolerating conspecifics and attaching webs together. In such situations, the advantages of group living—exploitation of habitats free of competing species, increased prey capture efficiency, architectural stability of webs, and so on—would usually outweigh the advantages gained by maintaining maximum distances from conspecifics at the cost of aggressive behavior (*3, 4*). Retention of interindividual spacing mechanisms like web defense, however, would ensure survival when prey availability fluctuates. The end result would be a group-living species which displays considerable variation in social grouping tendency, as *M. spinipes* does.

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7. In most localities, colonies represent annual cohorts of individuals hatched at approximately the same time, or successive cohorts hatching from serial egg sacs. Mating and oviposition occur in the late fall; *M. spinipes* overwinters (the dry season) as an egg or spiderling in the egg sac. Only in the moist tropics, where reproduction occurs year-round, is there overlap of a wide variety of contemporary age classes. Marked groups of adults and juveniles showed little change during several months and usually consisted of the offspring of the residents from the previous year.
8. J. W. Burgess, personal communication.
9. Enormous colonies of web-building spiders have been observed in power lines in mountain areas in Central America, but the species was not identified because the power lines were not accessible. Near Cordóba, colonies had spilled over onto the ground and were identified as those of *M. spinipes*. We estimated colony size in several large groups by measuring the volume of the communal web and then extrapolating from density counts. Several of the larger groups contained an estimated 5800 to 6500 individuals.
10. Prey availability was estimated by observation of the number of insects approaching a 1-m^3 colony web for a specified time period and then correction of this estimate by the number of hours of favorable weather conditions in a day.
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14. It is also possible that the several populations observed represent distinct species or subspecies. Although the genitalia of all specimens match the drawings in the species description of F. O. Pickard-Cambridge [*Biol. Cent. Am.* **2**, 457 (1903)], there are considerable differences in body size, leg length, and life history, as well as social grouping tendency. *Metepeira spinipes* is the only group living spider known in the genus *Metepeira* [H. W. Levi, *Bull. Mus. Comp. Zool. Harv. Univ.* **148**, 185 (1977)], although T. W. Schoener (personal communication) has found groups of *M. daytoni*.

15. We thank R. Hollis and M. K. Uetz for assistance in the field. Supported by the National Geographic Society, the American Philosophical Society, and the University of Cincinnati Research Council.

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Diverse Mechanisms in the Generation of Human β-Tubulin Pseudogenes

Abstract. *The sequence of two human β-tubulin pseudogenes is described. One contains an intervening sequence but lacks sequences encoding the 55* N*-terminal amino acids of the polypeptide chain. A second has no introns but has a polyadenylate signal and an oligoadenylate tract at its 3′ end, and it is flanked by a short direct repeat. These sequences have arisen by different mechanisms, including one that probably involves reverse transcription of a processed messenger RNA and reintegration of the complementary DNA copy into the genome.*

With few exceptions, all expressed eukaryotic genes contain intervening sequences (introns), regions of DNA that interrupt the coding sequence and that are spliced out of the primary gene transcript as part of the generation of cytoplasmic messenger RNA (mRNA). Any of a number of genetic events including deletion, insertion, or acquisition of one or more stop codons within the coding sequence can lead to a failure to yield a functional transcript. Such a gene is therefore termed a pseudogene. Among the pseudogenes thus far described, a curious form is that in which the intervening sequences present in the ex-

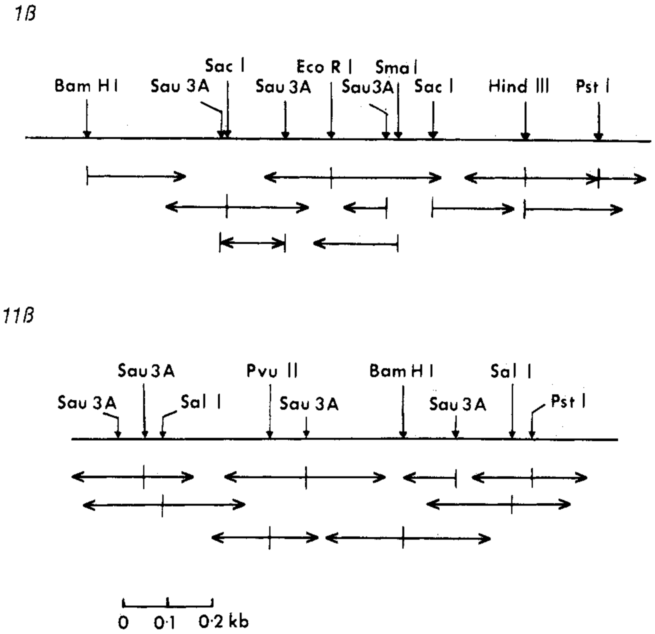

Fig. 1. Sequencing strategies. A 4.1-kb Hind III–Eco RI restriction fragment (11β) and a 1.55-kb Eco RI fragment (1β), each containing β-tubulin sequences, were isolated from the appropriate Charon 4A lambda clones (*3*) by electrophoresis in low melting temperature agarose and extraction with phenol. A further 1.65-kb Bam HI–Hind III fragment containing β-tubulin (1β) was subcloned into pBR322. Restriction endonuclease digestion of these DNA's was performed with the enzymes indicated and the fragments ligated into appropriately cleaved replicative forms of bacteriophage M13 mp8 and mp9. In some cases, plaques containing the DNA to be sequenced were identified on nitrocellulose replicas (*16*) by hybridization with a nick-translated chicken β-tubulin cDNA probe (*17*).

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