Natal dispersal and demography of a subsocial Anelosimus species and its implications for the evolution of sociality in spiders

L. Avilés and G. Gelsey

Abstract: The transition to permanent-sociality in spiders is thought to have involved the suppression of the dispersal phase characteristic of hypothetical subsocial or periodic-social ancestral species. Extant periodic-social species may provide insights into this transition. The periodic-social Anelosimus jucundus in southern Arizona was found to form mother–offspring and sibling associations that disintegrate prior to the mating season. Following the breakdown of the social phase, more than twice as many females as males became established within a few metres of the natal nest. Given that the predispersal sex ratio was 1:1, a fraction of the males may have dispersed beyond the local area. The short dispersal distances of at least a fraction of individuals of both sexes, the clustering of nests in local areas, and at least two possible cases of sibling mating suggest, however, that dispersal may not eliminate the possibility of close inbreeding in this species. Estimated transition probabilities between life-history stages show that the heaviest loss of individuals occurs during dispersal. Once established, 41% of the females that reached maturity succeeded in producing grown progeny. We discuss the implications of these findings in terms of the transition from periodic to permanent sociality in spiders and of current models that consider the interplay between competition and inbreeding avoidance in the evolution of dispersal.

Résumé : On croit généralement que la transition vers une vie sociale permanente chez les araignées est née de la suppression de la phase de dispersion caractéristique d’espèces ancestrales hypothétiques subsociales ou périodiquement sociales. L’examen d’espèces actuelles périodiquement sociales peut jeter de la lumière sur ce phénomène de transition. Chez l’araignée sociale périodique Anelosimus jucundus du sud de l’Arizona, il se forme des liens mère-progéniture et des liens entre rejetons qui se dissolvent avant la saison des accouplements. Après la cessation de la phase sociale, plus de deux fois plus de femelles que de mâles se sont établies dans l’espace de quelques mètres du nid d’origine. Comme les rapports mâles : femelles avant la dispersion étaient de 1 : 1, il se peut qu’une partie des mâles se soient éloignés de l’aire d’origine à la dispersion. Les courtes distances parcourues par au moins une fraction des individus des deux sexes lors de la dispersion, l’agglomération des nids dans des zones locales et l’observation d’au moins deux cas possibles d’accouplements entre membres d’une même famille indiquent que la dispersion ne suffit pas à éliminer la possibilité de consanguinité chez cette espèce. Les probabilités reliées à la transition entre les stades du cycle biologique indiquent que les pertes les plus considérables au sein de la population sont encourues pendant la dispersion. Une fois établies, 41% des femelles parvenues à maturité ont réussi à produire une progéniture adulte. Nous examinons ces résultats en fonction de la transition entre une vie sociale périodique et une vie sociale permanente chez les araignées et en fonction des modèles courants qui envisagent l’existence d’interactions entre la compétition et la prévention de la consanguinité dans l’évolution de la dispersion.

Introduction

The most complex form of social behavior in spiders is characterized by communal prey capture, feeding, and brood care among individuals that build and share a communal nest (Buskirk 1981; D’Andrea 1987; Avilés 1997). One of the most notable characteristics of these cooperative spiders, technically labeled non-territorial permanent-social (D’Andrea 1987) or quasi-social (Wilson 1975), is that colony members of both sexes remain within their natal nest to mate (for a recent review see Avilés 1997). Generation after generation, the colonies grow through this process of within-colony mating, and dispersal events may occur after they reach a relatively large size (for a recent review see Avilés 1997). This type of social structure is thought to have arisen from periodic-social ancestral species via the “subsocial” (Kullmann 1972; Krafft 1979) or “sibling” route (Wickler and Seibt 1993). In contrast to the permanent-social species, the periodic-social spiders consist of mother–offspring and sibling associations that break down prior to the mating season (see reviews by Krafft 1979; Buskirk 1981; D’Andrea 1987). The transition from periodic to permanent sociality, therefore, must have involved suppression of this dispersal phase. Thus, understanding why and how the dispersal phase was suppressed is
central to understanding the evolution of advanced social systems in spiders. Simultaneously, because the transition to permanent sociality in spiders must have included a switch from a breeding system that involved primarily outbreeding to one that involved inbreeding (Rieckert and Roeloffs 1993; Avilés 1997), understanding the conditions that favor dispersal or allow its suppression in spiders may shed light on the interplay between competition and inbreeding avoidance in the evolution of dispersal (Bengtsson 1978; Moore and Ali 1984; Waser et al. 1986; Johnson and Gaines 1990; Negro et al. 1997).

Among the spider genera that contain social species, Anelosimus Simon, 1891 (family Theridiidae) appears to be particularly valuable for studying the transition to permanent sociality. In addition to several periodic-social or solitary species, this genus contains four permanent-social species, the largest number in any spider genus (Avilés 1997). Also, while the permanent-social Anelosimus species are all tropical or subtropical (but see Furey 1998), the ranges of their periodic-social relatives extend into the temperate regions and the highlands (Levi 1956, 1963; L. Avilés, personal observation). This geographic distribution, which is characteristic of social spiders in general (Buskirk 1981; D’Andrea 1987; Avilés 1997), suggests that the environment has an important role in determining dispersal and social patterns. A comparative study of species in the genus Anelosimus and of the environments they inhabit would, therefore, indicate possible selective pressures for or against dispersal and group living in these organisms.

Despite its importance, only one species in the genus Anelosimus, the permanent-social Anelosimus extimus, has been relatively well studied (see references cited in Avilés 1997). Other species have received comparatively little attention (see Brach 1977; Fowler and Levi 1979; Nentwig and Christenson 1986; Vollrath 1986a; Smith 1987; Rypstra and Tirey 1989; Avilés and Maddison 1991; Furey 1998; Avilés and Salazar 1999). Here we describe the life cycle, natal dispersal patterns, and demography of a population of a species of Anelosimus in southern Arizona. Anelosimus jucundus O.P. Cambridge, 1896, whose type locality is Guerrero, Mexico, has been reported from northern Mexico to southern Argentina (Levi 1956, 1963). On the basis of palpal morphology and proximity to the type locality, we have tentatively assigned the Arizona population to this species. Definite placement, however, awaits revision of the genus Anelosimus (J. Coddington and G. Hormiga, in preparation) as it appears that A. jucundus may represent more than one species (Levi 1956; J. Coddington, personal communication).

Anelosimus jucundus has been studied in Panama, where it was found to be periodic-social (Nentwig and Christenson 1986; Vollrath 1986a). Here, we show that A. jucundus in southern Arizona is also periodic-social and discuss aspects of its biology that may be of relevance to understanding the transition to permanent sociality in spiders. We discuss our findings in the light of existing models for the evolution of dispersal (reviewed in Johnson and Gaines 1990). We suggest that this and other periodic-social spiders may serve as model systems in which to investigate the relative roles of competition and inbreeding avoidance in the evolution of dispersal (Bengtsson 1978; Moore and Ali 1984; Waser et al. 1986; Negro et al. 1997).

Materials and methods

We studied A. jucundus at the Patagonia–Sonora Creek Preserve (PSCP), a semi-arid riparian area in southeastern Arizona (31°30′N, 110°50′W, 1500 m) maintained by the Arizona chapter of the Nature Conservancy. We surveyed the entire length of the Creek Trail (1.4 km) for the presence–absence of nests and selected three areas for extensive study: a 10 × 10 m quadrat surrounding an isolated nest (area A), a 10 × 20 m quadrat surrounding 7 original nests (area B), and a 28-m transect (to a height of 2.5 m) along a forest edge where 16 original nests were located (area C). The sizes of the quadrats (but not that of the transect) were adjusted to include all first- and second-generation nests within a given cluster. We visited the sites at 3-week intervals from the end of April through November 1996, and every 4 weeks from the beginning of the overwintering period until May 1997. During these visits we searched for new nests within and around the study areas and inspected all previously recorded nests. When first recorded, the nests were mapped and marked individually. During subsequent visits, we measured all nests (approximate volume, estimated as the product of the three linear dimensions) and recorded their inhabitants. In mature nests we could only record presence–absence of spiders and their approximate instars. In newly founded nests, on the other hand, we determined the sex and instar of the one individual or, occasionally, two individuals they contained. Because the spiders did not discard the exuviae of previous molts, we could determine the instar in which the spider had dispersed in cases where we failed to discover the nest when it was first established. By censusing mature and newly founded nests periodically, we were able to determine the timing of nest and individual life-history events, such as dispersal, mating, egg laying, and eventual disappearance. We estimated the distance at which new nests were established relative to either the sole dispersing nest in area A or the closest possible source in areas B and C. In each of the clusters we also estimated sex ratios among nest founders and among adults in the mating population.

In the laboratory, using specimens newly collected from the field, we estimated clutch size, number of instars constituting the life cycle of the spiders, and predispersal sex ratios. We estimated clutch size for five laboratory-eclosed clutches, the eggshell and exuviae remains within 3 field-eclosed sacs, and the spiderling remains within an uneclosed sac. To determine the number of instars, we collected whole nests at various times of the year (a total of 17 nests in their social phase and 12 in their solitary phase). Differences in size, body proportions, and the state of the genitalia allowed us to visually separate live or preserved spiders into distinct size classes. We confirmed that these size classes corresponded to instars by recording molting in the laboratory. We have characterized these instars by measuring the tibia plus the patella of leg pair I and the distance between the posterior lateral eyes in the field-collected specimens. We estimated predispersal sex ratios among spiders raised in the laboratory from six nests collected prior to the dispersal season. Finally, in the laboratory, we also made casual observations of the spiders’ behavior during the social phase. We report on these behavioral observations when it is necessary to complement the demographic information presented here.

Nonparametric actuarial analyses (Survival Tools for Statview, Abacus Concepts, 1994) were used to characterize the timing of dispersal and of individual and nest persistence. Weeks to dispersal since the first recorded dispersal event and weeks to individual disappearance or to nest extinction since nest establishment were used as the event time variables in the dispersal and the survival analy-
Results

Spatial distribution of the nests

The nests of *A. jucundus* along the 1.4 km of the Creek Trail were clustered in 11 areas that contained from one to a few dozen nests (exact numbers could not be estimated in clusters where the nests occurred high up on trees). Within clusters, the median nearest-neighbor distance among mature nests prior to dispersal was 0.9 m in 1996 (range = 0.2–5.9 m, \(N = 31\) nests in four clusters) and 0.9 m in 1997 (range = 0.1–7.2 m, \(N = 29\) nests in four clusters; the isolated nest in area A was excluded in both years). The median distance between contiguous nest clusters along this trail was 55 m (range 20–430 m).

Phenology

The area of the PSCP is characterized by mild winters (range –10 to 26°C in January–February 1997), warm summers (temperature range 3–40°C in June–August 1996), and low precipitation throughout the year (335 mm from May 1996 through April 1997), except for scattered winter rains and a distinct monsoon season in July–August, when 50% or more of the yearly precipitation may fall. By examining an average of 30 nests (range 4–58) at each of our visits to the field (Fig. 1), we found that *A. jucundus* at the PSCP is univoltine, forming mother–offspring and sibling associations that persist for several months but break up prior to mating.

The life cycle of individual spiders comprised seven instars after emergence from the sac, the sexes being identifiable from the fifth instar onwards (Table 1). Both male and female spiders were adult in their seventh instar. In the three study areas, new nests were established from the middle of May to the middle of August, when spiders in their fourth through seventh instars dispersed from their natal nest (Fig. 1). Male and female spiders molted to maturity in their individual nests and presumably mated during late July and early August, when male–female cohabiting pairs were observed. Starting in August, female dispersers that survived to maturity laid their eggs. Most males had disappeared by this time. The egg sacs started to eclose in mid-August. Mothers remained with the spiderlings until early December, when they either died or were cannibalized by their progeny. By this time, the nests, which were initially clear three-dimensional structures measuring from 50 to 900 cm\(^3\), had accumulated dry leaves and measured up to 4000 cm\(^3\) (Fig. 2). The spiderlings spent the winter within these masses of leaves and silk, overwintering in their third, fourth, or fifth instar (Fig. 1). Growth resumed in the spring, when the spiderlings started to molt again prior to undertak-
ing a new dispersal cycle. Maximum nest size was reached just prior to dispersal, when the largest of 22 nests observed prior to the 1996 dispersal season measured 11 300 cm³. Casual observations of field and laboratory groups indicate that cooperative prey capture and prey sharing are characteristic of younger spiders during their social phase. However, tolerance and cooperation broke down in the laboratory under conditions of crowding or low food supply, when the spiders readily cannibalized each other.

Natal dispersal

During the dispersal season, we recorded the initiation of 86 nests in the areas surrounding the 22 original nests. Natal dispersal distances in area A, which contained a single isolated source colony, ranged from 0.12 to 8.5 m, with half of the 18 occupants of 17 new nests established within only 2.5 m of the source colony (Fig. 3). Although we could not match new nests with a particular source colony in the other two areas, it appeared that dispersal distances were also short, as new nests appeared in the immediate vicinity of preexisting ones. Excluding 10 cases of nest reoccupation (see below), the distances to the nearest preexisting nests in these two areas ranged from 0.14 to 3.64 m (median 1.00 m, N = 21 occupants of 20 nests) in area B and from 0.20 to 2.3 m (median = 0.70, N = 40 occupants of 39 nests) in area C. There were no significant differences between males and females in dispersal distances in area A (Mann–Whitney U = 15.5, p = 0.44; Fig. 3) or in the distance to the nearest preexisting nest in area B (U = 29.0, p = 0.79) or area C (U = 99.0, p = 0.31).

A steep decline in the proportion of males from pre- to post-dispersal periods, however, suggests that male-biased dispersal beyond the local area may have taken place. While the sex ratio in nests prior to the dispersal season was 1:1 (53.1% males, 95% CI = 43.3–62.4% males, N = 145 spiders in 6 nests; Table 2), postdispersal sex ratios were significantly female-biased (p = 0.01, Fisher’s exact test). Only 28.2% of the individuals that established nests in the study areas were male (95% CI = 16.6–41.4% males, N = 71), with no significant differences among areas in the magnitude of this bias (LR χ² = 0.41, 2 df, p = 0.81). In the absence of longer distance migration, the alternative hypothesis of higher male mortality appeared less likely, because male and female spiders that did become established in the areas did not differ in their probability of survival to adulthood (p = 0.78, Fisher’s exact test). As a result, a bias of similar magnitude to that present among nest founders, 27.5% males (95% CI = 14.1–43.3% males), was present among the 51 spiders that reached adulthood.

Dispersal schedules for males and females are given in Table 3. There were no significant differences in dispersal...
instar between the sexes (LR $\chi^2 = 4.5$, 3 df, $p = 0.21$, $N = 60$ non-reoccupants of known instar and sex). Males, however, completed dispersal somewhat earlier than females (log rank $\chi^2 = 3.0$, 1 df, $p = 0.08$, $N = 60$). There were significant differences in dispersal timing among the three areas (log rank $\chi^2 = 7.9$, 2 df, $p = 0.02$, $N = 74$ non-reoccupants of known instar), as spiders in area B dispersed more than 2½ weeks later than in the other two areas (dispersal week (median ± standard error) = 7.8 ± 1.7, 5.1 ± 1.5, and 5.1 ± 0.7 in areas B, A, and C, respectively). Despite this difference in timing, spiders in all three areas dispersed in comparable instars (LR $\chi^2 = 7.5$, 6 df, $p = 0.27$).

Nest reoccupation

Of the 86 nests established in the study areas, 10 were established on portions of one of the 22 original nests. Slightly fewer than half of the original nests, therefore, were reoccupied. We do not know whether this was the result of recolonization or absence of dispersal. In only one case was a nest reoccupied by more than one spider, when two females in area B occupied separate portions, 16 cm apart, of the same original nest. Nest reoccupation occurred only in the two areas with a higher density of original nests. Females were significantly more likely than males to reoccupy old nests (Mantel–Haenszel $\chi^2 = 4.8$, $p = 0.03$, controlling for the factor area), as all nine nest reoccupants that we could sex were female. Not surprisingly, individuals that reoccupied nests were in an older instar (five in instar 6 and four in instar 7) than those that dispersed (LR $\chi^2 = 15.5$, 3 df, $p = 0.002$, $N = 49$ females), and reoccupation occurred later in the dispersal season (median reoccupation week = 12.5 ± 2.0 vs. median dispersal week = 5.8 ± 0.7; log rank $\chi^2 = 9.6$, 1 df, $p = 0.002$, $N = 49$ female-founded nests).

It is worth pointing out that reoccupied nests had a lower, although, with our sample sizes, not significantly so, probability of becoming extinct than newly founded ones (Fig. 4). Only 19% of newly established nests, compared with 50% of the reoccupied nests, persisted until the next dispersal period.
season (Mantel–Haenszel $\chi^2 = 2.9, p = 0.09, N = 10$ reoccupied and 47 new female-maintained nests, after apparently lower survival in one of the areas is controlled for). This pattern suggests a potential selective advantage in remaining in the natal nest that may have influenced the transition to permanent-sociality in spiders.

Nest takeovers, male–female cohabitation, and possible sibling mating

We recorded nine instances of simultaneous or sequential nest sharing. One case was a temporary male–male pair seen in a nest that was subsequently abandoned. The remaining eight cases were male–female pairs formed during or just prior to the mating season. In two of these cases, an adult male moved into an adult female’s nest, in four cases a female moved into a male’s nest and eventually inherited the nest, and in the remaining two cases a male’s cannibalized corpse was found in a nest occupied by a female. The period of overlap in all these cases was probably brief, as we never observed a pair cohabiting during more than one of our visits to the field. In six of the eight cases, the spiders were adults during the period of cohabitation and therefore could have mated. In the remaining two cases, mating could not have occurred, as one or both individuals were subadults at the time of overlap; these two cases, which corresponded to a female moving into a male’s nest, could thus be described as nest takeovers.

Sibling mating appears likely in at least two cases (one each in areas A and B) in which we could infer where the second individual in a cohabiting pair came from, based on the simultaneous disappearance of an individual of the same sex and instar from a nearby nest (0.2 and 0.4 m distant, respectively). If we made the correct inference in these cases, the members of these cohabiting pairs, which were adult at the time of overlap, were siblings.

Transition probabilities between life-history stages

Figure 5 shows estimated transition probabilities between life-history stages for male and female A. jucundus at the PSCP. It is clear from this figure that the greatest loss of individuals occurred during the dispersal phase. Based on the number of spiders in five nests collected just prior to the 1996 dispersal season (Table 2), we estimate that, prior to dispersal, the original nests contained an average of 25 spiders each. It is expected, therefore, that the eight original nests in areas A and B contained a total of 200 spiders (we excluded area C from these calculations because, unlike the quadrats in areas A and B, the study transect did not include all nests in the area). Since we recorded 42 nest founders in these two areas, 21% of the spiders were recovered after dis-
pupation (14% of the males and 27% of the females, assuming a sex ratio of 1:1 in the original nests).

Following the establishment in their individual nests, male and female spiders in the three areas had a similar probability of surviving to adulthood ($p = 0.78$, Fisher’s exact test). Fifty percent of 34 subadult females and 44% of 18 subadult males reached adulthood in their individual nests (Fig. 5). Given that some degree of mobility of spiders of both sexes is suggested by the above observations on cohabitation and nest takeover, at the moment we cannot distinguish between mortality and relocation as the cause of the disappearance of the remaining spiders.

Because only females engaged in maternal care, however, overall female persistence in the newly founded nests was significantly longer than that of males (log rank $\chi^2 = 15.18$, 1 df, $p < 0.0001$) (Fig. 6a). From nest establishment, the tenure time of females was 6.1 ± 2.4 weeks (median ± 1 SE), while that of males was only 2.7 ± 0.6 weeks. The maximum recorded life-span (of individuals initially in instars 4–7) was 24 weeks for females and 12 weeks for males. We recorded eight cases of cannibalism: two males were cannibalized by a female and six adult females were cannibalized by their progeny.

Of 37 females that became adult or were adult when first recorded, 27 laid one sac each and 1 laid two sacs, the second of which did not eclose (Fig. 5). Twenty-seven of these 29 sacs (93%) eclosed and gave rise to clutches that continued to develop within the maternal nests. Clutch sizes, estimated from nine collected egg sacs, ranged from 21 to 53 spiderlings ($35.4 \pm 3.7$ mean ± 1 SE). After the death of their mother, the developing offspring took over the maintenance of these nests. Nests maintained by females, therefore, outlived their founders (Fig. 6b). The nests maintained by males, on the other hand, disappeared at a rate comparable to that of their keepers, as no spiders stayed behind to maintain them. The persistence time was $3.6 \pm 1.48$ weeks (median ± 1 SE) for nests maintained by males and 17.1 ± 7.5 weeks for nests maintained by females. While the sex of the original keeper had a highly significant effect on nest persistence (log rank $\chi^2 = 15.2$, 1 df, $p < 0.0001$, with area as a stratification factor), area did not (log rank $\chi^2 = 2.0$, 2 df, $p = 0.36$, with sex as a stratification factor).

Overall, 15 out of 27 nests with developing clutches (56%) persisted until the next dispersal season. Assuming that these colonies contained an average of 25 spiders each, as in the previous year (Table 2), spiderling survival in the colonies that persisted to the next dispersal season would have been 71% (assuming an initial average of 35 spiderlings per clutch). Including colonies that went extinct, roughly 40% of the first-instar spiderlings would have survived to dispersal in the overall population.

**Discussion**

**Natal dispersal and the breakdown of the cooperative phase**

The defining characteristic of a periodic-social species is the termination of its group-living phase at some point of the group’s life cycle, a termination that is necessarily accompanied by dispersal from the natal nest. In *A. jucundus*, the group-living phase, which consisted of mother–offspring and sibling associations, lasted for 9 months, or 3/4 of the yearly cycle (Fig. 1). Two related questions emerge from this situation: (1) what determines the timing of dispersal in periodic-social species and (2) what allows prolongation of the group-living phase in permanent-social species. The results of studies that have succeeded in prolonging the group-living phase of periodic-social species by supplementing the colonies with food (Krafft et al. 1986; Ruttan 1990; Gundermann et al. 1993; Schneider 1995; see also Rypstra 1986) suggest that the level of resources available in the environment may be critical.

In *A. jucundus*, dispersal from the natal nest preceded a period of rapid growth prior to the egg-laying season. During this time, the spiders more than doubled their body size (Table 1). Since there is a correlation in spiders between female size and fecundity (Eberhard 1979; Marshall and Gittleman 1994; Simpson 1995; Schneider 1996) and male size and various traits affecting male fitness (Vollrath 1987), there is probably strong selection pressure to maximize food intake during this period. In areas where periodic-social species occur, insufficient food may be obtainable at any one site to feed a group of increasingly larger spiders. Therefore, dispersal from the natal nest may be driven by resource competition. Absence of dispersal during winter, on the other hand, may reflect the protection against predators and
the elements afforded by the communal nest during a period in which the development of the spiders is arrested (Fig. 1). These are hypotheses that could be tested by comparing *A. jucundus* populations in different geographic regions and by manipulating food supply and nest integrity in any one region.

**Larger scale sex-biased dispersal and inbreeding**

The results of this study point to the possibility that dispersal beyond the local area may also be taking place in *A. jucundus*. The fact that newly founded nests contained more than twice as many females as males, while the pre-dispersal sex ratio was 1:1, is indirect evidence of this. Two hypotheses would explain the decline in the proportion of males: higher male mortality within the study sites, and male-biased dispersal to more remote areas, also accompanied by mortality. We favor the second hypothesis, since it appears unlikely that predation or other sources of mortality would affect initially undifferentiated individuals of similar size (Table 1). Also, the transition probabilities from subadult to adult of males and females that did become established in the study areas (Fig. 5) were not significantly different from each other. Assuming that the second hypothesis is correct, and that foreign males were as likely to immigrate into the study areas as local males were to emigrate out of them, the over 50% drop in the proportion of males suggests a relatively high cost of male dispersal. Although the decline in the proportion of males suggests male-biased migration to remote areas, the possibility of female migration cannot be discounted, as a large fraction of females was also lost from the local populations (Fig. 5).

Despite the possibility of migration away from local areas, it appears that natal dispersal does not eliminate the possibility of close inbreeding, as suggested by (i) the extremely short dispersal distances of at least a fraction of the spiders of both sexes, (ii) the suspected cases of sibling mating described in the Results, and (iii) the clustering of nests in local areas that, combined with some asynchrony in dispersal among areas, would reduce the success of dispersing males. In a future study, we plan to assess the extent to which gene flow between areas is taking place in *A. jucundus* by analyzing the genetic structure of its populations using molecular markers.

**Competition versus inbreeding avoidance in the evolution of dispersal**

Models for the evolution of dispersal have stressed different factors as being responsible for dispersal patterns in plants and animals. These factors are resource competition, mate competition, and inbreeding avoidance (reviewed in Johnson and Gaines 1990). Although these factors are not mutually exclusive, it is useful to distinguish among predictions formulated when one factor is stressed over the others (Dobson 1982). While all three hypotheses predict that juveniles will be more likely to disperse than adults, the resource-competition hypothesis predicts that members of both sexes will disperse with equal probability. The inbreeding-avoidance hypothesis predicts that only members of one sex will need to disperse, but which sex disperses is more or less irrelevant (Dobson 1982; but see Greenwood 1980; Waser et al. 1986). The mate-competition hypothesis predicts that the sex subject to stronger competition for mates will disperse, so that dispersal patterns will depend on the breeding system.

In *A. jucundus*, different selective pressures may favor dispersal at different spatial scales. As suggested, dispersal from the natal nest is probably driven by resource competition: spiders of both sexes dispersed primarily as juveniles, and no more than one individual remained or recolonized an original nest. This situation closely resembles theoretical models for the evolution of dispersal that are based on resource competition (e.g., Hamilton and May 1977). The short distances traveled (Fig. 3) suggest that individuals may simply be moving to the first available site (Murray 1967, cited in Johnson and Gaines 1990, p. 459), rather than seeking to avoid inbreeding. That only females reoccupy old nests may be due to selection pressure on the caregiving sex to secure the safest and most productive sites to raise their progeny, and on males to allow their female partners to do so.

Male-biased dispersal out of the local area, if confirmed to be taking place, could be explained by intrasexual competition for mates and (or) inbreeding avoidance. The fact that in *A. jucundus*, females are the exclusive caregivers to their progeny suggests that males may be limited by the number of females they can fertilize. Although postdispersal female-biased sex ratios would tend to lower the intensity of male-male competition, operational sex ratios may not be as biased. Males, rather than females, may thus be competing for mates. The intrasexual-competition hypothesis would therefore predict that males will be more likely to disperse than females. *Anelosimus jucundus* may fulfill this prediction resembling, in this sense, the mating system and dispersal pattern of mammals rather than birds (Greenwood 1980; Johnson and Gaines 1990).

According to the inbreeding-avoidance hypothesis, it is more or less immaterial which sex disperses (Dobson 1982). However, because in polygynous mating systems males are less likely than females to forfeit outbreeding opportunities by mating with a relative, males should tolerate inbreeding under a wider set of conditions than females (Waser et al. 1986). If inbreeding avoidance is the primary reason for dispersal in such systems, females will be more likely to disperse. This prediction is apparently not supported by our observations in *A. jucundus*, if its mating system does indeed resemble that of polygynous mammals, as discussed above.

Overall, the various models have emphasized that the extent to which inbreeding is tolerated should depend on the relative costs of inbreeding versus dispersal. According to Bengtsson (1978) and Waser et al. (1986), if dispersal costs are high, then inbreeding could be common. In this paper, we have presented evidence that male dispersal away from the local area in *A. jucundus* may carry a high cost. Some degree of inbreeding, therefore, may be acceptable in this species. Detailed measurement of inbreeding depression and dispersal costs in this species, therefore, is critical not only for understanding the transition from periodic to permanent sociality in spiders (see below), but also for resolving a sometimes heated controversy (e.g., Moore and Ali 1984; Dobson and Jones 1985; Packer 1985) concerning the rela-
tive roles of inbreeding avoidance and competition in the
evolution of dispersal.

The transition from periodic to permanent sociality in
spiders

Why and how did a periodic-social ancestral spider spe-
cies give up natal dispersal and turn to inbreeding? The
tropical and subtropical environments in which the permanent-
social species occur could have been instrumental in changing
the balance between the costs and benefits of remaining in
the natal nest versus dispersing (Avilés 1997). The tentative
pattern of increased survival probability of reoccupied nests (Fig. 4) suggests that there are potential benefits of remain-
ing in the natal nest. These benefits would include increased
protection offered by an existing nest and the possibility of
inheriting an already successful site. Tropical environments
could have further tilted the balance in favor of group living
by simultaneously decreasing the costs of remaining in
groups and increasing the costs of leading a solitary exis-
tence. The availability of large prey items, which only
groups can access (Nentwig 1985; Ward 1986; Rypstra 1990;
Pasquet and Kraftt 1992) and use effectively (Rypstra and
Tirey 1990), and the relative stability and abundance of the
prey supply in the tropics, could have decreased the intensity
of competition within nests relative to the situation in tem-
perate regions. Simultaneously, the costs of dispersal and of
establishing and maintaining solitary nests in the tropics
could be higher than in temperate zones, as a result of in-
creased levels of predation (Wickler and Seibt 1993) and (or)
frequent destruction of nests in rainy habitats (Riechert
et al. 1986). The consequent shift in balance between the
costs and benefits of group living could have been large
enough to compensate for any initial loss in fitness resulting
from inbreeding.

The fact that the colonies of some of the permanent-
social species may grow for several generations without dispersing
(reviewed in Avilés 1997) does suggest that group living,
despite demonstrated levels of intragroup competition
(Riechert 1985; Ward and Enders 1985; Vollrath 1986b;
Seibt and Wickler 1988; Henschel 1991/92; Rypstra 1993),
is still favorable within a range of colony sizes. In A. eximius, for instance, Avilés and Tufiño (1998) found that
even though the probability of female reproduction de-
creased with colony size (possibly reflecting resource com-
petition), the probability of offspring survival increased with
colony size. As a result, individuals in intermediate-size col-
yonies had the highest lifetime reproductive success. Data
from other authors suggest comparable costs and benefits of
group living for other permanent-social species (for reviews
see Wickler and Seibt 1993; Avilés 1997; Uetz and Hieber
1997).

In addition to the tentative patterns of nest persistence
shown in Fig. 4, two other results are illuminating with re-
spect to the transition to permanent sociality in spiders. The
first result involves a comparison of the success of solitary
females in A. jucundus (Fig. 5) and the permanent-social
A. eximius. While 41% of the females that became adult in
this study (Fig. 5) succeeded in producing offspring that sur-
vived until the next dispersal cycle, only 1 out of 11 solitary
adult female A. eximius at a tropical rain forest site had com-
parable success (Avilés and Tufiño 1998; see also Vollrath
1982). This result suggests that a solitary life-style may be
evolutionarily stable in the temperate regions but not in trop-
cical rain forest habitats. Anelosimus jucundus, however, ex-
tends into the habitat of A. eximius in some areas of its range
(Nentwig and Christenson 1986; Vollrath 1986a; L. Avilés,
personal observation). This opens up the question of how fe-
male A. jucundus in those areas compensate for the hard-
ships of a solitary life-style.

The second result is the observation that natal dispersal in
periodic-social species may not prevent inbreeding. A his-
ory of some inbreeding in the ancestral species from which
permanent-social species originated could have eliminated
from the population the most damaging recessive alleles. In
the transition from one system to another, therefore, inbreed-
ing depression may not have been as large an obstacle as
was previously believed (e.g., Avilés 1997). Determining
whether, in this respect, A. jucundus can be taken as repre-
sentative of the hypothetical ancestral species from which
permanent-social species in the genus Anelosimus origi-
nated, however, requires confirmation that its periodic-
social system is primitive rather than a reversal from a
permanent-social stage. Tentatively, in the absence of a phy-
logeny for the genus Anelosimus, the most parsimonious
assumption is that its periodic-social system is primitive, given
that most species in the genus Anelosimus, the family
Theridiidae, and the order Araneae are periodic-social or
solitary.

To conclude, we would like to highlight a point that, in
our opinion, has not been sufficiently stressed in models for
the evolution of dispersal: while competition is not likely to
go away unless the environment changes, inbreeding depres-
sion should diminish over evolutionary time as recessive
deterious alleles are weeded out of the population. The
very existence of completely inbred permanent-social spider
species (Riechert and Roeloffs 1993), apparently derived in-
dependently several times (Avilés 1997), is living proof that
inbreeding depression is not an insurmountable obstacle for
extreme philopatry when the benefits of staying at home are
sufficiently large.

Acknowledgments

We thank the Undergraduate Biology Research Program
at the University of Arizona for making this collaboration
possible and the Arizona Chapter of the Nature Conservancy
for allowing us to conduct this study at the PSCP. Special
thanks are extended to G. Binford for pointing out to us this
population of A. jucundus and to Jeffrey Cooper and Ed
Wilkins of the Nature Conservancy for their hospitality and
access to weather records. J. Aukema, C. Varas-Vieira, and
D. Hahn assisted in the field with either initial studies or set-
ing up a quadrat; A. Danielson-François kindly supplied the
photographs of the male and female spiders in Fig. 2. We
thank J. Bronstein, W. Maddison, D. Papaj, Y. Ziv, and an
anonymous reviewer for comments on the manuscript. This
research was funded in part by the Research Training Group
for the Analysis of Biological Diversification at the Univer-
sity of Arizona.

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