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RELATIONSHIP OF HABITAT AGE TO PHENOLOGY AMONG GROUND-DWELLING LINYPHIIDAE (ARANEAE) IN THE SOUTHEASTERN UNITED STATES

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ABSTRACT. Ground-dwelling Linyphiidae from eight South Carolina inner coastal plain habitats were sampled for one year using pitfall traps. Habitats formed an age gradient, from a field disturbed yearly and pine stands aged 5, 25 and 40 years, to xeric, mesic and hydric hardwoods (50–75 years) and an old-growth forest (200 years). Sixteen of the 55 trapped species were represented in sufficient numbers (n adults ≥ number of sampling periods, 26) to examine patterns of correlation between phenology and habitat distribution. Half of the species are multivoltine, characterized by adults present throughout the year, continuous reproduction, and overlapping generations. Adult abundance of these species peaked during spring through autumn. Other species were univoltine, with adults present briefly, indicating synchronous reproduction and non-overlapping generations. Adult abundance of these species always peaked during winter months. This study examines relationships between observed voltinism patterns and characteristic habitat (distribution among the habitats) among the 16 most abundant species. Species from older habitats tend to be univoltine, whereas species inhabiting more recently disturbed habitats were more likely to be multivoltine. Stenochronous winter reproduction (univoltines) probably increases survivorship by limiting individuals' exposure to the harsh conditions of the southeastern summer during vulnerable periods of immaturity and reproduction. This phenological specialization appears optimal in this region except in frequently disturbed habitats, where rapid multivoltine reproduction is most advantageous.

Knowledge of cyclic temporal aspects of organisms' life cycles (phenology) is crucial for understanding population dynamics and community ecology, and lends realism to evolutionary and ecological hypotheses (Lieth 1974; Tauber & Tauber 1981). This basic data can be time-consuming to obtain, as it requires sampling a population repeatedly throughout the year, and phenology may vary geographically or from one year to the next. Although Linyphiidae is by far the most diverse spider family in North America (Coddington et al. 1990), little is known about the phenology of most North American species. This is particularly true of the ground-dwelling forms, whose small size (1–3 mm), high diversity (ca. 800 species in North America), and cryptic microhabitats within litter interstices, etc., make them difficult to observe in the field.

This paper is part of a research program examining life history variation among ground-dwelling Linyphiidae. As phenology and other life history information is time-consuming to obtain, our goal is to determine the extent to which more easily obtainable kinds of information (such as the habitats used) are predictive of life history variation among ground-dwelling linyphiids. By understanding this, we may begin to apply information derived from careful phenological and laboratory studies to unstudied taxa as they are encountered in sampling.

Although linyphiids are most diverse in Northern Hemisphere mid-temperate latitudes and increasingly dominate spider assemblages farther north, they are still fairly diverse and form a conspicuous portion of spider assemblages in more southerly humid temperate regions, such as the southeastern Atlantic coastal plain of the United States (Draney 1997a, b). The present study examines species from the inner coastal plain of South Carolina (approximately 33° N).

Pitfall trapping during the course of this research yielded 55 species, of which 16 were judged abundant enough to use in elucidating phenological patterns. Two general phenological patterns emerged (Draney 1997a): In about half of the species, the adults are eurychronous (present during most of the year); these species appear to be multivoltine, with overlapping generations and continuous reproduction. For all these species, adults trapped peaked during the warm season. The other species have stenochronous adults (present during only a short time during the year); these species appear to be univoltine in our region, with non-overlapping generations and a winter mating period. Although other phenological patterns doubtless exist in our region, these two general patterns of voltinism appear to be very common among ground-dwelling linyphiids in the southeastern US.

The objective of the present article is to examine the extent to which these observed voltinism patterns are correlated with the distribution of individuals of a species among our sampled habitats. It might be expected that habitats differing in time since last disturbance would favor different life history responses, corresponding to r- and K-selection models (Stearns 1992). Our sampled habitats were specifically selected to provide a wide gradient of habitat age, as measured by time since the soil/litter layer has been significantly disturbed (as by clear-cutting, burning, mowing, plowing, etc.). We expect that species occurring in younger, more recently disturbed habitats would be more likely to be multivoltine than species occurring in older, more permanent habitat types, for reasons discussed more fully in the Results and Discussion section.

METHODS

Study sites.—The study areas were located on the Savannah River Site (SRS), a 780 km^2 area adjacent to the Savannah River in Aiken, Allendale, and Barnwell Counties, South Carolina. SRS has been maintained by the US Department of Energy since 1951. Because a primary objective of this study was to determine whether habitat age is related to life history parameters of the linyphiid inhabitants, the primary criterion for site selection was to locate sites that vary widely in the frequency with which the soil stratum is disturbed. In addition, several relatively mature habitats of the same age but with different vegetative communities were chosen. In all, eight areas were selected to represent the major terrestrial habitat types on the inner Atlantic coastal plain, here listed in order from the youngest, most recently disturbed to the oldest, least frequently disturbed habitat. For more detailed site information, see Draney (1997a). 1). Old Field: forb-grassland with *Opuntia* and lichen. Mowed or herbicided annually. 2). Young pines: 5 year-old plantation overgrown with *Rubus* and *Prunus* spp. 3). Medium pines: 25 year-old plantation with a sparse understory. 4). Mature Pines: 40 year-old volunteer pine stand with young oak and pine understory. 5). Scrub-Oak/Pines: 50–75 year-old xeric upland oak/pine stand. 6). Upland hardwood: 50–75 year-old mesic oak-hickory stand. 7). Riparian hardwood: 50–75 year-old hydric hardwood stand. 8). Riparian old growth: ca. 200 year-old pines within riparian hardwood stand.

Sampling methods.—A study area of about 1 ha was subjectively delimited to represent each selected habitat. A 0.25 ha (50 m × 50 m) plot was randomly located within this area, and 10 pitfall traps were randomly located within each plot. Pitfalls each consisted of an 8.5 cm diameter plastic cup buried with the lip flush to the soil surface, housed under a concrete building block (39 × 19 × 9 cm) propped up at one end by a 7 cm brick. Traps contained 4% formalin with a trace of detergent to decrease surface tension.

Traps were run continuously for a year (366 days, 1–4 May 1995 to 1–4 May 1996) and emptied at approximately biweekly intervals (11–17 days; mean = 14.0). At each of 26 sampling periods, all traps were collected from each of the eight sites. Contents were washed into a jar and the trap was refilled with formalin solution. Samples were sieved through a 250 μm mesh sieve to remove the formalin, and stored in 70% ethanol for subsequent identification. Nomenclature follows Buckle et al. (1993) and Platnick (1996). Voucher specimens of all species are deposited at AMNH and UGCA.

Data analysis.—Pitfall counts from each site during each trap period were expressed as number of organisms/140 trap-days (10 traps × 14 days), to correct for variable number of days per trap period, and to correct for the 22 traps lost to animal (dog or coyote) disturbance at the old field site.

A constraint of phenological data is that

Table 1.—Phenology and habitat indices of 16 ground-dwelling linyphiids from the South Carolina inner coastal plain. *n* = Number of adults trapped. Is = Index of seasonality. Pm = proportion of adults trapped at modal sampling period. Ih = Index of habitat range. Ha = Habitat age score. See text for explanation. Species are listed by voltinism (see Draney 1997a), and then by numbers of adults trapped.

Species	*n*	Is	Pm	Ih	Ha
Winter active, univoltine					
Pelecopsidis frontalis (Banks 1904)	199	2.6	0.307	3.64	4.18
unidentified species, cf. *Walckenaeria*	191	1.7	0.351	2.04	3.59
Walckenaeria carolina Millidge 1983	110	2.1	0.355	3.66	3.90
Centromerus latidens (Emerton 1882)	110	3.8	0.200	5.20	4.35
Lepthyphantes sabulosus (Keyserling 1886)	51	3.2	0.275	3.88	3.99
Ceraticelus laetabilis (L. Pickard-Cambridge 1874)	39	2.9	0.333	1.48	5.80
Origanates rostratus (Emerton 1882)	33	3.3	0.273	2.84	3.77
Scylaceus pallidus (Emerton 1882)	33	3.3	0.242	4.35	4.73
Ceraticelus alticeps (Fox 1891)	31	1.9	0.419	2.20	4.61
Eurychronous, multivoltine					
Meioneta sp. n. #1	805	9.5	0.083	2.22	2.48
Meioneta sp. n. #3	563	4.5	0.224	1.95	5.37
Ceratinops crenatus (Emerton 1882)	230	6.3	0.161	1.00	1.00
Meioneta barrowsi Chamberlin & Ivie 1944	72	4.5	0.181	2.91	3.46
Eperigone maculata (Banks 1892)	61	4.8	0.230	3.47	4.61
Erigone autumnalis Emerton 1882	32	5.8	0.125	1.84	1.43
Meioneta micaria (Emerton 1882)	31	3.7	0.226	3.22	3.90

many parameters are dependent on sample size. As the number of individuals sampled increases, the apparent temporal span of the species will tend to increase as well. Parameters pertaining to distribution of individuals across sampling periods were only calculated on categories (species, or sexes/stages within species) when the category sample size equaled or exceeded the number of sampling periods (*n* = 26; Table 1). Thus, phenological parameters were calculated only for 16 of the 55 linyphiid species trapped during this study (Draney 1997a).

We used several indices to compare the complex temporal and spatial distribution patterns of different species and sexes (Table 1). We calculated Pm, the proportion of adults trapped during the modal sampling period (that is, the period during which the maximal number of individuals of that species was trapped) as a simple indicator of each species' temporal distribution; higher proportions indicate more stenochronous populations. We also calculated an index of seasonality (Is; Curtis 1978) for each species. This index uses the proportion of individuals of a species captured in each month to determine how evenly the species is distributed throughout the year. As our sampling periods were biweekly instead of monthly, the index was converted to a fraction and then multiplied by twelve to standardize the index to ‘‘months’’:

$$\mathrm{Is} = 12[(1/\Sigma p_j^2)/s]$$

summed over all sampling periods, where p_j = proportion caught during sampling period j, and s = total number of sampling periods (always 26 in this study). The index varies from 12/s for a highly stenochronous species found only during one sampling period, to 12, for a completely eurychronous species evenly distributed across all sampling periods.

A modified index can be used to examine the distribution of spiders across sampled habitats. This index of habitat range, Ih, can be used to categorize species as eurytopic (occurring in many habitats) or stenotopic (occurring in a narrow range of habitat types):

$$I_h = 1/\Sigma p_k^2$$

summed over all habitats sampled, where p_k = proportion caught in habitat k. This index varies from 1 for a stenotopic species found in only one habitat, to the number of habitats sampled (in this case, 8). Both of the above indices assume that each sampling period or habitat is sampled equally, an assumption met in the present study when the data are standardized to number/140 trap-days.

Because we are interested in the extent to which phenology and life history patterns may be predicted by habitat distribution, a habitat age score was calculated for each species. This score summarizes the characteristic habitat of each species with respect to habitat age, and is essentially a weighted average of a species' presence at each habitat, giving more weight to individuals found in older habitats: $P_1 = [(1n_1) + (2n_2) + (3n_3) + (4n_4) + (5n_5) + (5n_6) + (5n_7) + (6n_8)]/n_{total}$, where n_1 = Number of adults from old field, scored as 1 (disturbed yearly); n_2 = number from young pines, scored as 2 (ca. 5 years old); n_3 = number from medium pines, scored as 3 (ca. 25 years old); n_4 = number from large pines, scored as 4 (ca. 40 years old); n_5,n_6,n_7 = number from scrub-oak/pines, upland hardwoods, and riparian hardwoods, all scored as 5 (habitats were forested 40 years ago and so have been forested at least ca. 75 years); n_8 = number from old growth habitat, scored as 6 (forested for ca. 200 years); and n_{total} = sum of individuals from all sites. This species score varies from 1 to 6. For example, species found only at the most frequently disturbed habitat have a score of 1.00.

Single factor regression analyses were used to examine whether any habitat distribution indices (Ih or Ha) are related to phenological indices (Pm or Is) among the examined taxa.

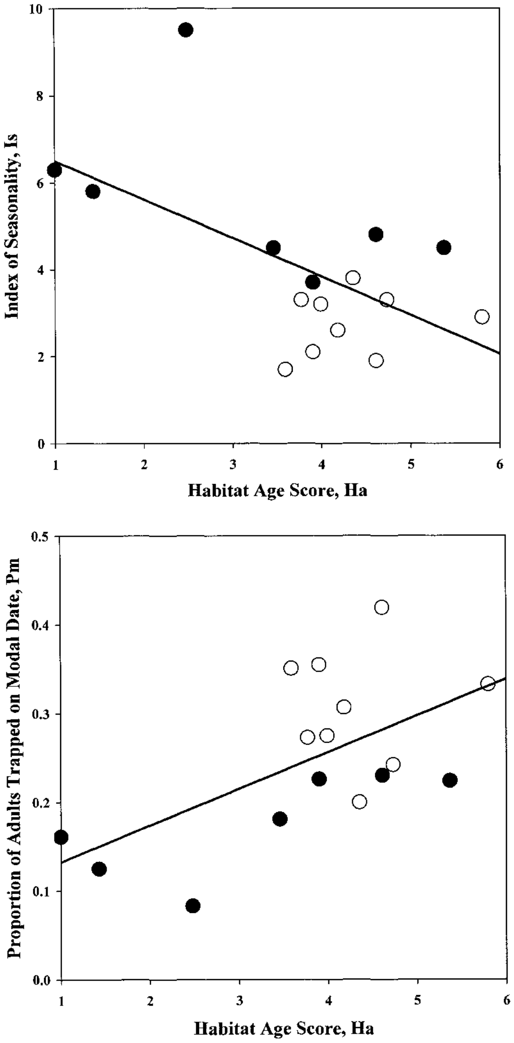
RESULTS AND DISCUSSION

Species characteristically trapped at younger habitats tended to be more eurychronous and species at older habitats tended to be more stenochronous. Species habitat range (Ih) was not correlated with phenological indices, but the age of the habitats occupied by the species was correlated with phenology. Specifically, the adult index of seasonality, Is, was negatively correlated with habitat age score, Ha ($r^2 = 0.328$, $P = 0.0204$) and percent of adults at the species' modal date, Pm, was positively correlated with Ha ($r^2 = 0.345$, $P = 0.0167$; Table 1). These trends did not hold when the sexes were examined independently. This was probably due to the decrease in number of taxa examined: sample size was adequate ($n > 25$) to examine total adults (males and females combined) of 16 species, but males of only 11 species, and females of only five species. It should be noted that Draney (1997a) found no evidence that the phenology patterns of individual taxa vary among the habitats (Draney 1997a), so it can be assumed that species are either univoltine or multivoltine within this region, regardless of the habitat they occupy.

In Figs. 1 and 2, species points in the scatterplots are labeled as multivoltine or univoltine, as determined by phenological indices, graphs of age/sex distribution over time, and other supporting evidence (Draney 1997a; Table 1). Among the species studied, those occurring mainly in younger, more frequently disturbed habitats (species with habitat age scores < 3.5) were all multivoltine, whereas species characteristically inhabiting older habitats were predominantly, but not exclusively, univoltine.

The apparent increased likelihood of finding eurychronous, multivoltine species in younger, less permanent habitats is consistent with the advantages which, we postulate, accompany this phenological strategy. Eurychronous spiders would be capable of reproducing opportunistically when the habitat is favorable or when they arrive at a favorable habitat. While the habitat remains favorable, continuous reproduction allows for individuals to maximize their instantaneous rate of reproduction (and thus, probably, their fitness). Finally, overlapping generations and the mixed age structure resulting from continuous reproduction mean that when the habitat changes, some individuals of the life history stage which is best able to survive by tolerance or dispersal should already be present. We postulate that these eurychronous species are phenological ''generalists'' with a flexible strategy that can result in successful reproduction even in unpredictable or impermanent habitats. It is interesting to note that Merrett's (1969) phenological study of 90 linyphiid species found that all eurychronous species were ''common aeronauts,'' species commonly observed or collected ballooning.

Stenochronous species, conversely, appear to be phenological ''specialists,'' finely adapted to completing various life history stages at specific times when conditions are most favorable, or to avoiding unfavorable conditions. All stenochronous species we examined are winter-reproducing, which seems to strengthen this specialization hypothesis. For



Figures 1–2.—Relationships between age of habitats in which linyphiid species were trapped, and indices of phenology. Each circle is data from all adults of one species (Table 1). Closed circles (●) are postulated to be multivoltine and open circles (○), univoltine (Draney 1997a). See text for r^2 and P values, and explanations of indices. 1, Negative correlation between habitat age score (Ha) and index of seasonality (Is); 2, Positive correlation between habitat age score (Ha) and proportion of adults trapped at modal sampling period (Pm).

three reasons, the mild southeastern US winter may be favorable for reproduction by ground-layer Linyphiidae. First, the cool, moist conditions that prevail in winter are probably more favorable both to survivorship of immatures, which are especially susceptible to desiccation (based on pers. obs., MLD), and to the longevity of adults, which is negatively correlated with temperature and positively correlated with fitness in spiders (Li & Jackson 1996). Using such a stenochronous strategy, only adults would encounter the harsher summer conditions. In contrast, a eurychronous population would include many immatures during the summer. Second, Collembola, which are a major component of the prey of ground-dwelling linyphiids (Nyffeler & Benz 1988; Nentwig 1980, 1983, 1987; Alderweireldt 1994), are most abundant during the cool season (pers. obs. MLD). Third, we believe that both predation and competition for prey resources would be lower in the winter, since most other arthropod groups (including most spiders) are more active during the warm season. For organisms from a lineage that presumably evolved at higher latitudes (linyphiids are most diverse in mid-latitude temperate regions; van Helsdingen 1983), the southeastern US winter may indeed be a temporal ''island'' of favorable conditions, which may itself select for a stenochronous life cycle.

It appears that stenochronous winter reproduction is the predominant strategy for ground-dwelling linyphiids in this region, except in the younger habitats. We hypothesize that in such frequently disturbed habitats, the advantages of multivoltinism outweigh univoltinism's postulated advantage of avoiding the harsh conditions which ground-dwelling linyphiids would encounter during the southeastern summer.

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