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TWO-YEAR LIFE CYCLE AND LOW PALPAL CHARACTER VARIANCE IN A GREAT SMOKY MOUNTAIN POPULATION OF THE LAMP-SHADE SPIDER (ARANEAE, HYPOCHILIDAE, *HYPOCHILUS*)

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ABSTRACT

Size-frequency histograms and other data generated from four samples (totaling 926 specimens) collected during a complete year show that a *Hypochilus* population in the Great Smoky Mountains has a two-year life cycle with the following schedule: spiderlings emerge from egg sacs and construct their first webs in late May; 15 to 18 months later, during their second autumn, these spiders mature, mate, and lay eggs. The growth rate and adult body size variances of this population are very large. The coefficients of variation of three palpal dimensions in a sample of 38 males are significantly smaller than those of tibia I length or carapace length. Such relative constancy of palpal characters within a population may be common in spiders and may result from stabilizing selection in one or both of the following forms: selection for the mechanical compatibility necessary for effective sperm placement during copulation, and sexual selection by female choice.

INTRODUCTION

In his study of several populations of the lamp-shade spider, *Hypochilus*, Fergusson (1972) concluded, chiefly from the frequency distribution of tibia I lengths of 164 individuals collected in late October, that this species has a two-year life cycle. The current study was undertaken primarily to rigorously test this life-cycle hypothesis and, secondarily, to determine whether the coefficients of variation (standard deviation x 100/ mean) of palpal dimensions are less than the large coefficients of variation of male body dimensions in this population. Even though the relative constancy of genital characters is often noted in taxonomic revisions (for example Reiskind 1969, Levi 1981) and may be one of the reasons taxonomists rely so heavily on genital characters to diagnose species of spiders and many other animals (Mayr 1969), I am not aware of any rigorous statistical attempt to confirm its occurrence in any species of spider. It is important to note that Hoffman (1982, pers. comm.) recently concluded that the southern Blue Ridge Province populations of *Hypochilus* which Fergusson (1972) and I have studied represent a new species (as yet undescribed) that is distinct from the Appalachian Plateau populations of *Hypochilus thorelli*.

METHODS

Life History.—Four collections of individuals from a single, dense *Hypochilus* population living on rock outcrops along Little River Road on the Tennessee side of the Great Smoky Mountain National Park were made between 1.5 miles upriver and 1.5 miles downriver from The Sinks on the following days (sample size in parentheses): 1 October 1982 (207), 8 May 1983 (134), 1 June 1983 (287), and 30 September 1983 (298). For each collection an attempt was made to carefully examine entire areas of rock outcrop surface (different for each collection) and collect every *Hypochilus* individual within reach. However, during the October 1 collection a number of adult males and females that were spotted were not collected, and during the June 1 collection it was possible that not all reachable spiderlings were collected since these are very small and difficult to see.

All specimens were preserved in 70% ethanol. The length of the first tibia of each specimen was measured by me with a Wild M5 stereomicroscope fitted with 20x eyepiece lenses with a 100-unit eyepiece reticle scale. Tibia I length was selected as an indicator of body size because measuring carapace or sternum dimensions would have required the removal of all legs. Tibia I length is defined as the straight line distance between the proximal and distal ends of the article in lateral view with the article on the horizontal plane. In order to avoid using a value for a regenerating leg, both the left and right tibia I were measured and the value for the left recorded unless it was more than three scale units shorter than the right tibia. Measurements were recorded to the nearest half unit and repeated measurements of two specimens indicated that measurements were precise to within 0.04 mm for the smallest specimens and 0.23 mm for the largest ones. If a specimen belonged in any of the following categories, such was noted: adult female (any female with developing or fully developed eggs and a markedly hirsute area just anterior to the genital groove); adult male; penultimate male (identified by swollen pedipalp tarsi); about to molt (any individual with dark setae of new exoskeleton visible under old exoskeleton).

Palpal Character Variance.—Measurements were recorded for two non-genital characters that are frequently used as indicators of body size and three palpal characters on each of the 38 adult *Hypochilus* males collected on September 30. Extreme care was taken to minimize measurement imprecision, an especially important goal when generating coefficients of variation (Rohlf, Gilmartin, and Hart 1983). Structures were selected which can be consistently positioned, and whose linear dimension has well-defined end points. The two non-genital characters are defined as follows: ITL = tibia I length as defined above; CL = distance along median longitudinal line connecting anterior edge of carapace to median indented posterior edge of carapace with all legs removed and carapace horizontal. The three palpal characters were measured on the left pedipalp after it was removed from the body and are defined as follows: PTC = width of palpal tarsus "clasper" in retrolateral view (Fig. 1); PL = length of palpus in retrolateral view (Fig. 1); CdL = length of palpal conductor in prolateral view (Fig. 2). The measurements were performed by me with the optical equipment described above. ITL was measured to the nearest end point of a scale-unit 0.077 mm long, CL to the nearest 0.037 mm scale-unit end point, and the palpal characters to the nearest 0.009 mm scale-unit end point. In order to determine the imprecision involved in making these measurements, one specimen was remeasured ten times

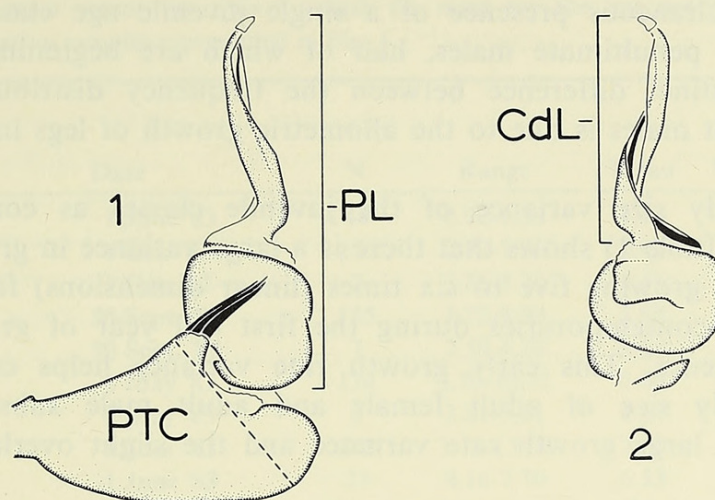


Fig. 1-2.—Left palpal tarsus and palpus of *Hypochilus* male showing three palpal measurements as defined in text: 1, retrolateral view; 2, prolateral view.

over the period of a week (after each set of five measurements was recorded the examining dish was swirled so that each part would have to be repositioned during the next set of measurements), and the coefficient of variation was calculated for each of the five measurement characters for that sample of ten remeasurements.

RESULTS

Life History.—Frequency distribution histograms of tibia I length for each of the four collections are presented in Fig. 3, and statistical values for the age, sex, and molting classes represented in these histograms are presented in Table 1. The May 8 collection histogram indicates that there is only a single age class—all juveniles—present at that time. Although the size range is large, the distribution is monomodal and is not skewed markedly to the right, indicating that it does not comprise two or more age classes. The relatively small size of individuals about to molt also supports this conclusion because, in a homogeneous and relatively young age class with non-synchronous molting, small individuals should be further in time than large individuals from their last molt, and thus more likely to molt than large individuals. The June 1 collection reveals two age classes, a class of spiderlings recently emerged from egg sacs and a class of older juveniles. The latter class, despite its large size range, exhibits those characteristics (non-skewed shape and restriction of molting to smaller individuals) which indicate that it is one age class.

The age class patterns of the histograms for both fall collections are similar to each other. In each there is a single juvenile class with large size variance but with the non-skewed size distribution and molting activity pattern which indicate age homogeneity. In addition, each collection contains an adult age class with an extremely large size variance but with only a slight size overlap with the juvenile class. That this adult class is made up of same aged individuals in their second autumn is indicated by the absence of adults during the spring and early summer

and by the simultaneous presence of a single juvenile age class. In both fall collections some penultimate males, half of which are beginning to molt, are present. The distinct difference between the frequency distributions of adult females and adult males is due to the allometric growth of legs in the final male molt.

The large body size variance of the juvenile classes as compared to the spiderling class (Table 1) shows that there is a large variance in growth rate, with some individuals growing five to six times (linear dimensions) faster than their slowest growing contemporaries during the first full year of growth following spiderling emergence. This early growth rate variance helps create the large variance in body size of adult female and adult male subsamples of the population. This large growth rate variance and the slight overlap between the

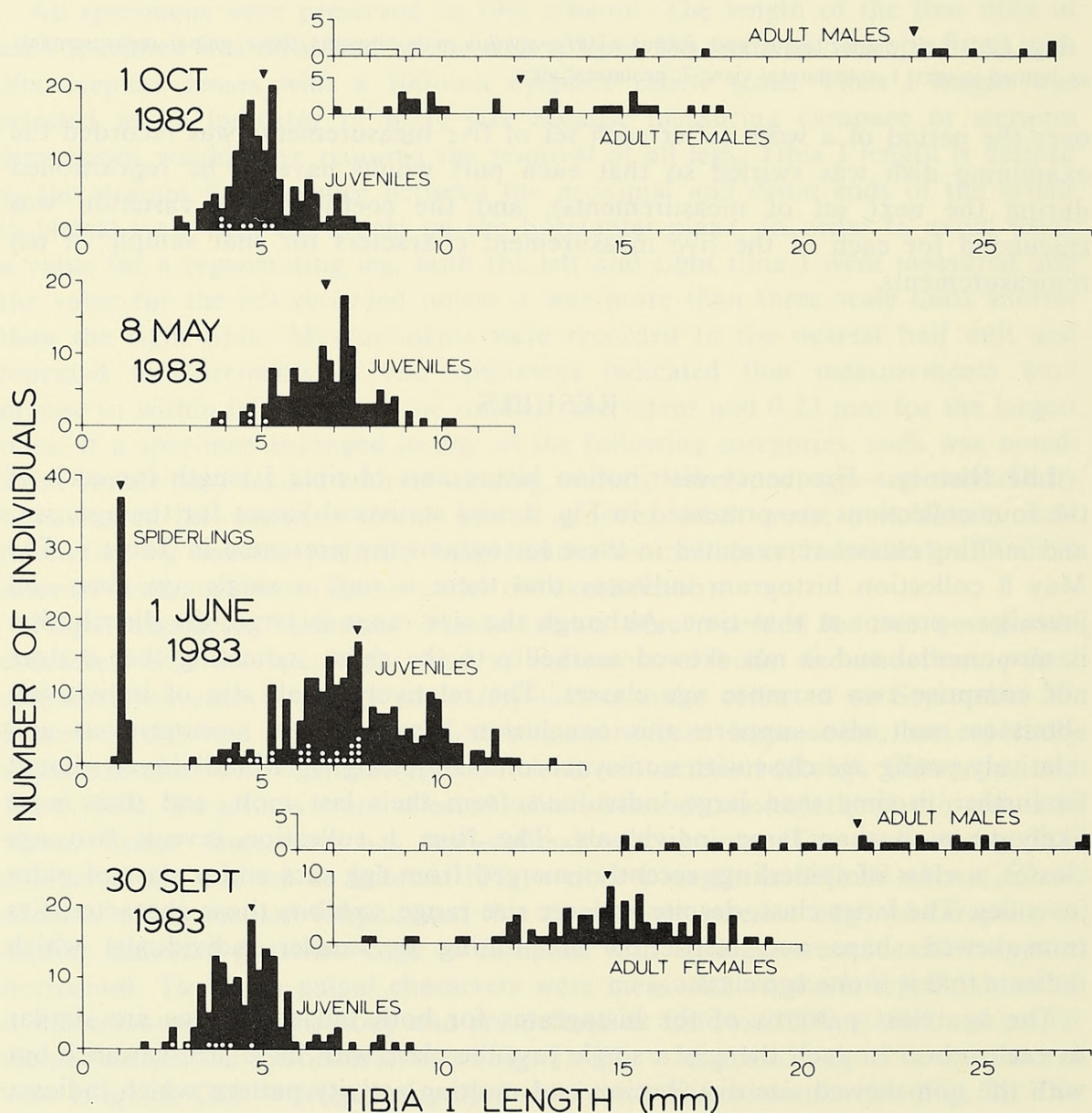


Fig. 3.—Frequency distributions of tibia I lengths for four collections from a *Hypochilus* population. Adults of each sex grouped on separate scale lines. Each square represents one specimen. White squares represent penultimate males. White circles represent individuals ready to molt. Triangles mark means of each age/sex class sample.

Table 1.—Statistical values for tibia I length (in mm) for the age/sex/molting classes of the *Hypochilus* population samples represented in Fig. 1.

Class	Date	N	Range	Mean	Variance	Coefficient of Variation
Spiderlings	1 June '83	44	0.92-1.30	1.13	0.004	5.60
Juveniles (Year 1)	1 Oct. '82	156	2.72-7.85	5.09	1.07	20.32
About to Molt	1 Oct. '82	7	3.85-5.39	4.48	0.31	12.43
Juveniles (Year 1)	30 Sept. '83	155	1.72-9.09	4.68	1.48	26.00
About to Molt	30 Sept. '83	7	2.59-4.70	3.61	0.44	18.37
Juveniles (Year 2)	8 May '83	134	3.70-10.32	6.80	1.49	17.95
About to Molt	8 May '83	4	3.81-5.01	4.57	0.20	9.79
Juveniles (Year 2)	1 June '83	243	3.18-13.09	7.66	3.23	23.46
About to Molt	1 June '83	23	4.16-7.70	6.53	1.03	15.54
Adult Females	1 Oct. '82	34	7.16-17.79	12.20	9.74	25.58
Adult Females	30 Sept. '83	103	7.85-19.02	14.63	4.92	15.16
Adult Males	1 Oct. '82	9	15.40-26.80	23.09	14.66	16.58
Adult Males	30 Sept. '83	38	15.02-27.87	21.56	12.49	16.39

juvenile and adult classes in tibia I length in the fall raise the possibility, albeit very remote, that a very fast growing individual might occasionally mature in its first fall and that a very slow growing individual might, on occasion, fail to mature until its third fall.

Each of the ten egg sacs collected on October 1 and September 30 contained eggs, many of which contained embryos with appendage buds readily visible. Of the eight egg sacs collected on May 8, five were preserved and contained faintly pigmented spiderlings, whereas the remaining three were kept in the laboratory until spiderlings emerged on 13, 22, and 24 May. These spiderlings had longer legs, more hair, and more pigment than those preserved on May 8, and had the same tibia I lengths as those collected in their webs on 1 June. They spun silk in the glass vial within which they emerged and, when disturbed, bounced on this webbing. Each of the 12 egg sacs collected on June 1 had been vacated. Apparently the great majority of spiderlings in this population had emerged from their egg sacs between May 8 and June 1. In spite of diligent searching on June 1, fewer of these spiderlings were found than expected. These newly emerged spiderlings were found (in their webs) only on the more sheltered outcrop surfaces where the light intensity was lowest (and probably the humidity was highest). On the more exposed outcrop surfaces these spiders and their webs were absent or only the bases of their abandoned webs were present, even though older spiders were common. Perhaps these spiderlings tend to hide in crevices during dry periods and build capture webs only at night and/or during humid days.

In summary, the size/age frequency distribution, egg sac, and spiderling data show that this *Hypochilus* population has a two-year life cycle with the following schedule: eggs are deposited in the fall, spiderlings emerged from egg sacs and construct their first webs during the second half of May, these spiderlings then eventually mature, mate, and lay eggs 15 to 18 months later in their second fall, and adults seldom, if ever, survive to reproduce for more than one breeding season.

Palpal Character Variance.—For the sample of 38 males the coefficient of variation of each palpal character (PTC, PL, CdL; Table 2) is significantly less (using Lewontin's (1966) method, $P < 0.01$) than the coefficient of variation of either non-genital character (ITL, CL). Since the measurement imprecision indices (Table 2) indicate that the three palpal characters are more difficult to measure accurately than are the non-genital characters, factoring out the effect of measurement imprecision on the coefficient of variation of the sample should not reduce (indeed, it would increase) the significance of these differences. It is important to point out that the difference between the coefficients of variation of ITL and CL is largely due to the allometric increase of leg length during the final molt.

DISCUSSION

Life History.—These results strengthen Fergusson's (1972) hypothesis that *Hypochilus* populations in the southern Blue Ridge Province have a two-year life cycle, with adult females rarely, if ever, surviving to a second year of reproduction. Although spiders generally exhibit large intrapopulation size variation as adults (Jocqué 1981), the very large variation in growth rate and, consequently, adult body size observed in this *Hypochilus* population and in some araneid populations (Crome and Crome 1961, Vollrath 1980, Levi 1981) appears to surpass that of most other spiders investigated (for example Dondale 1961, Reiskind 1969, Vogel 1970, Brady 1979, Jocqué 1981). It seems reasonable to postulate that the most probable primary cause of this especially large growth rate variance in *Hypochilus* and some other spiders is a large variance in prey capture success. Whether this prey capture variance results mainly from a patchy prey distribution and an inability to move webs quickly to more profitable sites, or from other factors, remains to be investigated. Riechert and Cady (1983) present evidence suggesting that the spiders *Achaearanea tepidariorum* and *Coelotes montanus*, both common inhabitants of the rock outcrops where *Hypochilus* lives, may have an important impact on *Hypochilus* foraging success by serving as a source of food (*A. tepidariorum*) or by competing for space (*C.*

Table 2.—Statistics for five measurement (mm) characters for a population sample of 38 adult male *Hypochilus*. Measurement imprecision index is the coefficient of variation of a sample of ten remeasurements of a single specimen. Characters are defined in text. The coefficient of variation for each a palpal character is significantly less ($P < 0.01$) than that of either non-genital character.

Character	Range	Mean	Variance	Coefficient of Variation	Measurement Imprecision Index
<i>Non-Genital</i>					
ITL	15.02-27.87	21.56	12.49	16.40	0.348
CL	2.73-4.54	3.69	0.23	12.85	0.293
<i>Palpal</i>					
PTC	0.52-0.70	0.61	0.002	8.15	1.149
PL	1.07-1.37	1.25	0.006	6.39	0.362
CdL	0.65-0.82	0.75	0.002	6.37	1.005

montanus). It is therefore possible that a patchy distribution of these species over the outcrop surfaces inhabited by *Hypochilus* might help create a large variance in *Hypochilus* foraging success.

Palpal Character Variance.—The widespread reliance of spider systematists upon genital characters to diagnose species is presumably due primarily to the tendency of these characters to evolve more rapidly and divergently than other characters. However, the analysis of variance in this sample of *Hypochilus* males suggests that the usefulness of genital characters for diagnosing species may also be due to a tendency for genitalia to vary less than other characters within populations and groups of freely interbreeding populations. Such genital character constancy is frequently implied or demonstrated indirectly in taxonomic papers (for example McCrone 1963, Reiskind 1969). Vollrath's (1980) data for a sample of 38 *Nephila clavipes* males indicate relatively low variance in palpal conductor length. With a sample of only two *Tetragnatha elongata* males, Levi (1981) has illustrated the same phenomenon of relative palpal character constancy. Whether this phenomenon is widespread in spiders awaits analyses of variance in other taxa, but it seems heuristic to suggest two possible causes for such a phenomenon.

If, as seems likely, there is some optimal range of palpus size and shape required for quick and accurate insertion into the copulatory bursae and spermathecae of the females of this *Hypochilus* population in order to achieve effective semen transfer, there should then be selection for a developmental mechanism that insures that a male's palpus will approach that optimum form independent of his body size. In other words, although there is no evidence to suggest that the species-specific shape of *Hypochilus* genitalia (Gertsch 1958, 1964, Hoffman 1963) is a mechanical (lock and key) reproductive isolating mechanism (indeed the unsclerotized nature of the female genital region, bursa, and spermathecae [Coyle et al. 1983] argue against such a function), selection could be acting to maintain some degree of mechanical compatibility in these copulatory structures.

Sexual selection by female choice acting late in courtship or during copulation may be another cause for relatively low intrapopulation variance in palpal characters. As suggested by Eberhard (in press), the tactile information produced by the male palpus during copulation may affect the behavior and/or physiology of the female in a way that affects the male's success in fertilizing her eggs. That is, the female may be selecting mates partly on the basis of her tactile perception of palpus form. Once a preference is established by a proportion of the population's females, there may be strong stabilizing selection for that palpus size and shape and, consequently, a developmental mechanism that regulates palpus size independent of body size. Although West-Eberhard (1983) has justifiably emphasized the probable importance of sexual selection in causing rapid evolution that may accelerate speciation, it is also important to recognize that under some circumstances sexual selection may instead have a stabilizing effect.

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