

Morphology, Ontogeny, and Adaptation of *Ambrysus mormon* (Hemiptera: Naucoridae): Quantitative Comparisons Among Populations in Different Thermal Environments

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ABSTRACT Specimens of *Ambrysus mormon* Montandon were collected from each of 3 widely separated populations that differed in thermal environment. For each population, 15 characters were measured from each of 10 individuals—for each of the 5 instars, adult males, and adult females—to determine if interdemographic differences exist in allometric development. All 3 populations can be distinguished at each instar based on multivariate analyses, and all instars and both sexes of adult are morphometrically distinct within each population. Nonetheless, the magnitude of difference among populations depended on instar. Most of the variation among individuals (>99.0%) was related to size and could be associated with differences among instars or between sexes of adult. In most cases (40 of 42 analyses), growth was allometric rather than isometric, and regardless of population, the direction of allometry was consistent for a particular character (body width and profemur length are exceptions). Although the magnitude of size variation from 1st to 5th instars and adults was similar in all populations, interpopulational differences in allometric development occurred as well. Specifically, the rate of increase in size of 6 characters (head width, pronotum length, profemur length, mesotibia length, metatibia length, and metatarsus length) with respect to the rate of increase in body length differed among populations developing at different temperatures. Thus, overall shape differences existed among populations, and these differences changed through ontogeny. Because allometric relations consistently accounted for a significant and large portion of interindividual variation, we suggest that autadaptation rather than exadaptation has played a predominant role in the morphological evolution of *A. mormon*.

KEY WORDS Naucoridae, *Ambrysus*, ontogeny, allometry, temperature

DEVELOPMENT, SYSTEMATICS, AND evolution have endured a long and sometimes tumultuous association. Nonetheless, it is increasingly clear that ontogenetic trajectories of morphology (Alberch et al. 1979, Alberch 1980, Sites and Willig 1994a) can provide incisive information about evolution and systematic relationships (Kluge and Strauss 1985). Although Blackstone (1987) recently presented conceptual shortcomings of morphometric studies that were based on Huxley's (1932) allometric relation, such critiques have been shown to be an oversimplification or to be of minor importance (Bookstein et al. 1985, Strauss 1987, Sites and Willig 1994a).

Conceptual Overview

Allometry can be conceptualized at 3 hierarchical levels: static, ontogenetic, and phylogenetic (Cock 1966, Gould 1966). Static allometry refers

to patterns of variation or covariation in morphology among individuals at the same ontogenetic stage; ontogenetic allometry pertains to patterns of covariation among instars or stages, or throughout a trajectory of continuous growth; phylogenetic allometry focuses on character covariation among groups at the same ontogenetic stage but representing different taxa. All 3 types of allometry are inextricably interrelated (Rieppel 1990).

Until relatively recently, the field of morphometrics, or morphometry, primarily has focused on univariate or multivariate analyses of characters associated with particular structures in adults, with little attention to variation associated with life history. Nonetheless, adult morphology is clearly a product of developmental changes orchestrated by an interaction between the genome and the environment (Raff and Kaufman 1983). The processes that give rise to morphological variation in adults, as well as the structural changes that transpire during development, are subject to selection, and thus should contain useful systematic information (Kluge and Strauss 1985, Willig and Hollander 1995).

Organisms that undergo discrete development with fixed numbers of instars are ideal subjects for morphometric analyses of all 3 types of allometry

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(Sehnal 1985, Klingenberg and Zimmermann 1992). Instars and adult states represent a priori landmarks during development that obtain as a consequence of orchestrated physiological, biochemical, and anatomical dynamics, even if the stadia that precede them are of different durations. Moreover, after initial cuticle hardening, changes in size or shape during a particular stadium are minor and restricted by cuticular inflexibility. Hence, morphometric comparisons of instars (including adult males and females separately), as well as the size and shape changes that generate them, should be of considerable evolutionary significance. Finally, allometric variation can arise in a number of ways (Fairbairn 1992). For example, ontogenetic allometry can result as a consequence of selection acting primarily on overall size, with attendant changes in shape resulting because of physiological and mechanical constraints or as a consequence of differential responses of different structures to the same environmental pressures. Alternatively, selection acting on body shape may be associated with overall changes in size because of pleiotropism and genetic correlations.

Entomological Overview

Most research concerning allometric growth has focused on vertebrates; consequently, insects have been somewhat neglected (Jander and Jander 1994). Studies of morphometric variation during development in insects was pioneered by Matsuda in a series of contributions concerning gerrids (Matsuda 1961a, b, 1962a; Matsuda and Rohlf 1961) as well as belostomatids and reduviids (Matsuda 1962b). Although intraspecific differences in relative growth rates of mensural characters is well understood for certain structures (for example, head versus body size), details concerning morphogenesis (allometric relationships and developmental trajectories) and the magnitude of morphological differences among populations of conspecifics have not been addressed for members of many hemipteran families, including Naucoridae. Since Matsuda's allometric studies, work concerning static, ontogenetic, and intra- and interspecific phylogenetic allometry has been reported for some hemipteran taxa. For example, in studies of ontogenetic allometry, Cuzin-Roudy and Laval (1975) used multivariate statistical procedures to examine growth pattern in *Notonecta maculata* F. (Notonectidae). More recently, Sites and Willig (1994a) examined differences in developmental relationships among 8 taxa of Naucoridae and proposed use of principal components analysis to illuminate ontogenetic trajectories as a means to infer evolutionary relationships in systematic studies. In studies of phylogenetic allometry examining intraspecific morphometric variation, Jansson and Pajunen (1978) found that populations of *Arctocoris carinata* (Sahlberg) (Corixidae) formed distinct groups corresponding to either gross habitat type

or geographic distribution. In a taxonomic contribution, morphometric analysis of 10 populations of *Gerris costae* (Herrich-Schaeffer) (Gerridae) supported the continued recognition of 3 previously delineated subspecies (Klingenberg 1992). In an analogous interspecific study of phylogenetic allometry, Sites and Willig (1994b) determined that shape-related variation among 22 species of *Ambrysus* (Naucoridae) did not support the continued recognition of established subgenera. A modicum of other reports exist comparing allometric attributes of different species of Hemiptera.

Although it has been well documented that temperature affects developmental rates, few studies have addressed variation in allometry among populations of conspecific insects from different thermal environments. Herein, we define ontogenetic allometries for each of 3 populations of *Ambrysus mormon* Montandon, and compare aspects of size and shape among populations for each instar.

Materials and Methods

Ambrysus mormon is the most widespread species of the genus in the United States, occurring from southern Oregon and Idaho, south through the western states to Mexico. Three currently recognized subspecies occur within the United States. Two are local, geographic isolates, whereas the nominate subspecies occupies an extensive range through much of the western United States. Subspecific designations of the U.S. fauna are equivocal, as R.W.S. demonstrated (unpublished data) a lack of correspondence between shape and currently accepted subspecific affiliations in 13 populations of *A. mormon*.

Three geographically disparate populations were collected from streams that were characterized by widely different ($\approx 10^\circ\text{C}$) mean water temperatures (NEW MEXICO population, Lincoln County, Rio Hondo [12.0°C]; IDAHO population, Owyhee County, Bruneau River [22.5°C]; and NEVADA population, Clark County, Warm Springs [32°C]). Each population comprised specimens of the nominate subspecies. For analytical purposes, we recognized 7 groups within each population: instars 1 through 5, adult males, and adult females. Morphological characters were measured on 10 individuals per group, although for some instars of the Nevada and New Mexico populations, fewer than 10 specimens were available. Morphological characters assessed both size and shape by including length and width of the body and head, as well as length of leg segments; elsewhere, these 15 characters provided effective interspecific discrimination among a variety of naucorid taxa as well as intraspecific discrimination among groups (Sites and Willig 1994a, b). All measurements were ln-transformed to facilitate correspondence with assumptions for multivariate assessment of geographic variation or to provide variables for allometric regressions. All analyses were performed using SPSS

statistical software (SPSS 1986). Voucher specimens are deposited in the Wilbur R. Enns Entomology Museum, University of Missouri-Columbia.

Populational and Age-Specific Variation in Mensural Characters. Two-way multivariate analysis of variance (MANOVA) was performed to determine if significant differences existed among groups or populations (Willig et al. 1986, Willig and Owen 1987). Discriminant function analysis (DFA) maximizes intergroup differences, while simultaneously minimizing intragroup dispersion, by constructing a linear combination of variables on each of a number of orthogonal axes. Multivariate *F*-tests associated with DFA were used to assess significance between all possible pairwise comparisons of groups within populations. The subsequent classificatory phase of DFA then assigned each individual to a group based on its position in discriminant space. Percent of correct assignments was used as an additional measure of morphometric distinction for that group.

Allometry and Ontogenetic Trajectories. Allometry represents the manner in which 1 character (*Y*) changes with respect to variation in another character (*X*). The general form of the relationship (Huxley 1932) is

$$Y = CX^z$$

in which *C* and *z* are constants fitted by least-squares analysis. Its logarithmic form gives rise to a linear relation

$$\ln Y = \ln C + z \ln X$$

in which $\ln C$ and *z* are the *y*-intercept and slope, respectively (Sneath and Sokal 1973). A value of *z* that is indistinguishable from 1 indicates isometry, whereas values of *z* statistically different than 1 represent allometry.

For each population, we performed least-squares and linear regression analysis of the natural logarithm of each mensural character and the \ln of body length. These parameter estimates, along with their 95% CL, were used to assess if a character changes in an isometric or allometric fashion with body length ($H_0: z = 1; H_a: z \neq 1$), and compare allometric growth of populations subjected to different temperature regimes ($H_0: z_1 = z_2 = z_3; H_a: \text{at least 1 inequality}$). Because only a single population was examined at each temperature regime, effects of geography and temperature cannot be disassociated in an incontrovertible manner.

We used the dimensionality reduction capabilities of principal components analysis (PCA) to decompose the total variation among individuals into size (PC 1) and shape (other PC axes) components. Nonetheless, we recognize that size can assume a variety of meanings depending on the variable or variables used to represent it (Somers 1986, 1989; Bookstein 1989; Sundberg 1989; Rohlf 1990; Atchley et al. 1992). To the extent that the total variation among individuals in our analyses is size

associated, and not the consequence of outliers, polymorphisms, or the inadvertent inclusion of >1 taxon, our analytical approach should be fairly robust, even if it does incorporate some variation that does not reflect size alone. In addition, the literature is replete with controversies and inconsistencies surrounding the definition of shape (Bookstein 1989, Somers 1989). Rather than contribute to that morass, we provide an operational definition for use here. Shape is considered to be those linear combinations of variables that account for morphometric variation after PC 1 (size) has been extracted from the data. Principal components were derived from the covariance matrix of \ln -transformed measurements, thereby maintaining allometries and ensuring that the covariance matrix is independent of scale (Jolicœur 1963). Changes in size or shape during ontogeny can be visualized in PC space by connecting the centroids of each group in proper temporal sequence to produce an ontogenetic trajectory (Sites and Willig 1994a). Comparisons of morphometric trajectories during ontogeny are facilitated by simultaneous graphical representation of all taxa in morphological space defined by pairs of PC axes.

Results and Discussion

The size of aquatic insects at maturity depends largely on 2 temperature-related phenomena: duration of development and growth rate (Sweeney 1984). Nonetheless, size also may be affected by metabolic state and environmental factors such as food quality and quantity (Ursin 1979, Taylor 1981) which themselves may differ in alternative thermal environments. Because of its wide geographic range, *A. mormon* is subject to a diversity of environmental conditions, and manifests a variety of body sizes in response to temperature during ontogeny. The relationship between size and temperature is strongly evident in a variety of naucorids (especially *A. thermarum* La Rivers), as well as in other aquatic insects, including Ephemeroptera (Brittain 1976, 1983; Obrdlík et al. 1979), Plecoptera (Sweeney and Vannote 1986), Trichoptera (Oemke 1987), and Diptera (Konstantinov 1958, Heuvel 1963, Brust 1967, Hagstrum and Workman 1971, Mackey 1977). Few studies have addressed the effect of temperature on shape development.

Populational and Age-Specific Variation in Mensural Characters. A very highly significant interaction (MANOVA, $P < 0.001$) was detected between groups and populations. Nonetheless, 2 phenomena suggest that the interaction is one of magnitude rather than direction. The main effects (group and population) were each significant in the MANOVA, and the means for each morphometric character increased with increasing age within each population. In concert, this suggests that at least for some characters, increases in absolute size with age are more pronounced in 1 or more of the populations than in others. Alternatively, this could

Table 1. Results of least-squares and linear regression analysis (ln C is the y-intercept, z is the slope) between ln of each mensural character and ln of total length for each of 3 populations of *A. mormon* that differ in thermal environment ($P < 0.05$ in all regressions)

Dependent variable	New Mexico			Idaho			Nevada			Isometry
	ln C	Z	r ²	ln C	Z	r ²	ln C	Z	r ²	
Body width	-0.434	1.030a	0.997	-0.469	1.029a	0.994	-0.496	1.008a	0.990	>, >, =
Head length	-0.995	0.687a	0.994	-1.010	0.690a	0.995	-1.043	0.695a	0.993	<, <, <
Head width	-0.873	0.803a	0.992	-0.933	0.832a	0.997	-1.000	0.866b	0.994	<, <, <
Synthlipsis	-1.583	0.784a	0.980	-1.604	0.792a	0.985	-1.698	0.826a	0.982	<, <, <
Pronotum length	-2.631	1.308a	0.987	-2.607	1.306a	0.986	-2.796	1.436b	0.983	>, >, >
Profemur length	-1.420	0.973a	0.990	-1.495	0.993ab	0.992	-1.502	1.026b	0.993	<, =, >
Protibia length	-1.847	1.065a	0.991	-1.935	1.092a	0.991	-1.974	1.126a	0.994	>, >, >
Protarsus length	-1.777	0.511a	0.943	-1.872	0.541a	0.974	-1.942	0.554a	0.953	<, <, <
Mesofemur length	-1.581	1.078a	0.996	-1.654	1.100a	0.996	-1.661	1.105a	0.995	>, >, >
Mesotibia length	-1.761	1.086a	0.995	-1.856	1.124ab	0.994	-1.919	1.156b	0.994	>, >, >
Mesotarsus length	-2.167	0.889a	0.984	-2.196	0.903a	0.988	-2.312	0.938a	0.977	<, <, <
Metafemur length	-1.257	1.051a	0.995	-1.355	1.085a	0.996	1.410	1.087a	0.997	>, >, >
Metatibia length	-1.142	1.056a	0.997	-1.246	1.095b	0.997	-1.286	1.095b	0.996	>, >, >
Metatarsus length	-1.640	0.851a	0.988	-1.706	0.879a	0.993	-1.883	0.928b	0.987	<, <, <

For each dependent variable, indistinguishable slopes share a common alphabetic superscript, based on overlapping 95% CL. Codes for isometry (H_0 : slope = 1) relate in sequence to New Mexico, Idaho, and Nevada populations. <, slope is statistically < 1; =, slope is statistically indistinguishable from 1; and >, slope is statistically > 1.

be viewed as constant size rankings among populations within instars, with the size differential among populations changing throughout ontogeny.

Multivariate *F*-tests (DFA) between all possible pairs of groups within populations and between all possible pairs of populations within groups resulted in very highly significant differences ($P < 0.001$) for all contrasts. Clearly, populations can be distinguished at each instar and each instar is distinguishable within a population based on the selected suite of morphometric characters. The subsequent classificatory phase of DFA appropriately assigned each individual to the correct group (instar and sex) and population for 98.9% of the cases. The 2 classificatory errors involved an incorrect assignment of sex within adults of the correct population. Not only are group centroids distinguishable, but the multidimensional dispersion of the group clusters are essentially nonoverlapping, with the 2 minor exceptions involving misclassifications with respect to sex.

Allometry. The allometric growth equation significantly accounted for at least 94% of the variation in linear dimensions regardless of morphometric character or population (Table 1). Isometric relationships were detected in only 2 of 42 regression analyses (body width in the Nevada population, profemur length in the Idaho population); moreover, when allometry was exhibited consistently, all 3 populations deviated from isometry in the same direction for corresponding characters (Table 1). In general, linear attributes of the head and tarsi increase less rapidly, whereas the pronotum and components of the femora and tibiae increase more rapidly, than does body length. More specifically, head length, head width, synthlipsis, protarsus length, mesotarsus length, and metatarsus length each increase more slowly than does body length during ontogeny. In contrast, pronotum length, protibia length, mesotibia length, me-

sofemur length, and metafemur length each increases more rapidly during ontogeny than does body length.

For 8 of the 14 characters, no interpopulational differences in allometry (slope) were detected (Table 1). In cases where significant differences in slope existed among populations (head width, pronotum length, profemur length, mesotibia length, metatibia length, and metatarsus length), differential growth of characters with respect to body length was greater in the Nevada population than in the New Mexico population. The Idaho population differed from the New Mexico population for only a single character: metatibia length increased more rapidly in the Idaho population than in the New Mexico population.

Because slopes differed from 1 for most morphometric characters within a population, shape as well as size changed during ontogeny. Moreover, temperature or geographic correlates had a selective effect on shape in that only a subset of all characters experienced accelerated allometric growth in different populations. We hypothesize that temperature responses may exhibit a threshold below which developmental effects are not manifested, perhaps because of homeostatic buffering or because the effects are too small to be detected by our analyses.

Autadaptations Versus Exadaptations. Changes in the linear dimension of a trait with respect to some general measure of size (for example, body length) may be a consequence of autadaptations or exadaptations. Autadaptations represent changes in the trait that are coupled to changes in size per se (trait-to-size adaptations), whereas exadaptations represent externally driven changes in the trait associated with the environment (trait-to-environment adaptations) (Gould 1977, Parker and Larkin 1959). This adaptive framework was used by Jander and Jander (1994) to elucidate the significance

Table 2. Factor loadings for each principal component

Character	Principal component factor					
	1	2	3	4	5	6
Body length	0.998	-0.032	-0.022	0.014	-0.014	-0.007
Body width	0.996	0.040	-0.062	-0.007	-0.031	0.017
Head length	0.997	0.004	-0.027	0.002	-0.024	-0.031
Head width	0.997	-0.015	-0.028	0.037	-0.007	-0.034
Synthlipsis	0.993	0.015	-0.070	0.029	-0.091	0.003
Pronotum length	0.991	-0.106	0.053	0.009	0.031	0.020
Profemur length	0.996	-0.061	0.046	0.020	0.002	0.008
Protibia length	0.997	-0.038	0.035	0.018	-0.015	0.000
Protarsus length	0.980	0.178	0.072	0.046	0.007	0.002
Mesofemur length	0.999	-0.027	0.000	0.008	-0.016	0.014
Mesotibia length	0.999	-0.025	0.007	0.007	-0.019	-0.001
Mesotarsus length	0.995	0.002	0.037	-0.077	0.024	-0.046
Metafemur length	0.999	0.014	-0.019	-0.013	-0.024	0.015
Metatibia length	0.999	0.092	-0.018	-0.006	0.018	0.012
Metatarsus length	0.994	0.044	-0.001	-0.086	0.012	0.027
% variance (total)	99.13	0.36	0.16	0.13	0.09	0.04
% variance (shape)	—	41.38	18.39	14.94	10.34	4.60

of morphometric growth patterns in the greater milkweed bug, *Oncopeltus fasciatus* Dallas (Lygaeidae), especially with regard to differences between observed traits of adults and those extrapolated from allometric equations developed for instars and adult females. Inherent in their approach was the assumption that the ecological and physiological demands associated with adulthood (for example, reproduction and dispersal) require niche-shifts beyond those generated by autadaptations. Indeed, they documented that some traits (for example, number of sensillae on the 3rd and 4th antennal segments) are markedly different from those expected based on nymphal allometries. For methodological reasons, we included adult males and adult females in the elucidation of trait-size allometries and consider the coefficient of determination (r^2) and significance (P) of the regression to be measures of autadaptation. The deviation between the value of a trait for any particular instar and that predicted by the allometric equation represents unique instar-specific niche adaptation (exadaptation).

The situation in *A. mormon* is different from that in *O. fasciatus*. Consistent significance and high coefficients of determination suggest that in all 3 populations of *A. mormon*, none of the instars, as well as adult males and adult females, experience sufficiently novel ecological demands beyond those for which size-driven changes in morphology provide adaptive success. Exadaptation is not an obvious or predominant evolutionary force molding the morphology of *A. mormon*.

Ontogenetic Trajectories. The first 6 PCs accounted for 99.8% of the morphometric variation among individuals regardless of population, instar, or sex (Table 2). The 1st PC may be considered to be a size component (all character loadings are positive, and between 0.98 and 1.00) that accounts for most (99.1%) of the interindividual variation; whereas the subsequent 5 axes embody aspects of

shape (each contains positive and negative character loadings) and account for a small proportion of the total variation among individuals (0.9%). Nonetheless, PCs 2 through 6 account for at least 89% of the shape variation.

When viewed from the perspective of ontogeny (Fig. 1), PC 1 scores gradually increase with each molt for each population, adult females in each population having slightly higher scores than do corresponding adult males. Because PC 1 accounts for size-related variation, the relationship among instars and populations is clear: specimens for each instar of the New Mexico (cold water) population are larger than corresponding instars of each of the other 2 populations. The size (PC 1) of Idaho specimens is intermediate between those of the New Mexico and Nevada populations (Fig. 1). In general, this is true of C , the hypothetical linear dimension of a character when body length equals zero in the allometric equation. Specimens from Nevada (warm water) exhibit the smallest overall size, consistent with thermal effects found in other aquatic organisms. Nonetheless, morphological trajectories during ontogeny are not parallel for the three populations (Fig. 1), a fact corroborating the significant interaction between group and population detected by the MANOVA.

Principal component 2 accounts for 46.4% of the shape-related variation among individuals. Within groups, scores on PC 2 were consistently largest for the New Mexico population and lowest for Nevada, whereas Idaho was intermediate (Fig. 1). Among the 5th instars, the relationship between the Idaho and New Mexico populations was reversed. The largest loadings on PC 2 were associated with pronotum length (-0.106) and protarsus length (0.178); hence, individuals with relatively long protarsi and a short pronotum exhibit high scores. Because ln-transformed characters were analyzed, this relationship may be viewed as ln of the ratio of protarsus to pronotum length (ln

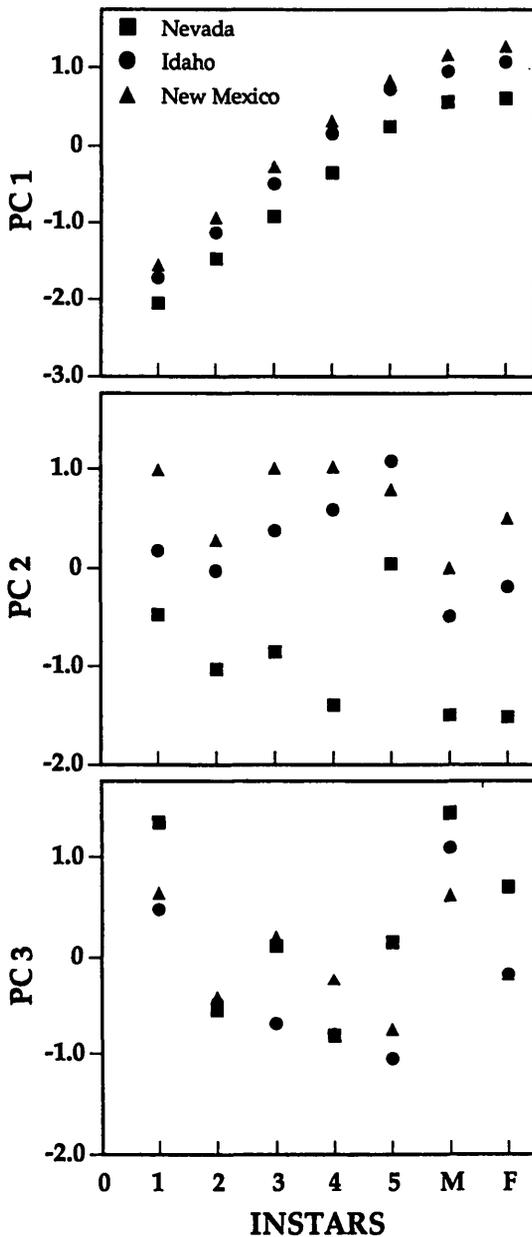


Fig. 1. Ontogenetic variation in size (PC 1) and shape (PC 2 and PC 3) for each of 3 populations of *A. mormon*. A consistent size pattern among populations (New Mexico > Idaho > Nevada) for each instar corresponded to differences among streams in water temperature (New Mexico < Idaho < Nevada); a similar pattern did not obtain for aspects of shape.

$A + \ln B = \ln[A/B]$. Principal component 3 accounts for 20.6% of the shape-related variation among individuals; high scores are associated with body width (-0.062), synthlipsis (-0.070), pronotum length (0.053), and protarsus length (0.072). This relationship may be viewed as the ln of the ratio of the product of protarsus and pronotum to the product of body width and synthlipsis. The re-

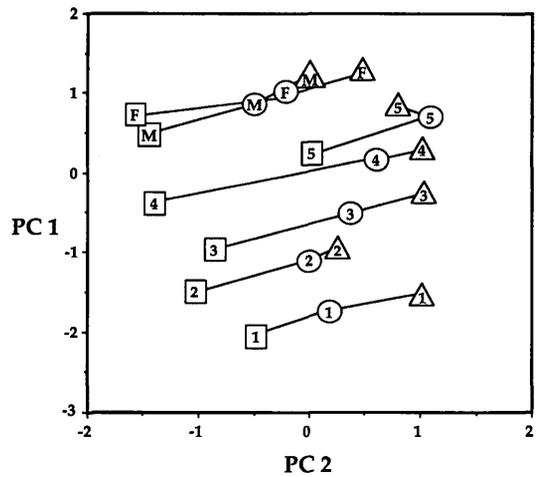


Fig. 2. Morphological relationships among populations (squares, Nevada; circles, Idaho; triangles, New Mexico) and groups (numbers refer to corresponding instars, M and F to adult males and females, respectively) based on size (PC 1) and shape (PC 2). For each group (instars 1 through 5, adult males, and adult females), lines connect centroids of the different populations.

relationships among populations differed depending on instar, the Nevada or New Mexico populations exhibiting the highest scores and Idaho usually exhibiting the lowest scores.

Finally, the changes in shape that accompany ontogeny do not produce trajectories that consistently change in a particular direction, like those that result from changes in size (Figs. 1 and 2). In part, this is a product of the dissimilar allometries that typify many of the morphometric characters. Two characters could consistently increase between instars, but if the amount of increase in a negatively loaded character was greater than that of the positively loaded character, the overall PC score could decrease. Hence, cyclic or semicyclic changes in the magnitude of PCs 2-6 with instar number could be obtained even with continual increases in all characters.

Because intraspecific differences in allometric development (z) were detected, morphometric differences among populations (or species) could result from phenotypic plasticity or modulated ontogeny rather than from genetic-based differences, per se. Further, if intraspecific variation is significantly less than interspecific variation, then developmental trajectories may be valuable as specific descriptors.

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