Dyar's rule and multivariate allometric growth in nine species of waterstriders (Heteroptera: Gerridae)

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(With 3 figures in the text)

The constancy of postmoult/premoult ratios of measures of linear size during ontogeny in insects and other arthropods is widely known as Dyar's rule. We tested this rule in nine species of the waterstrider genera *Gerris* and *Aquarius* (Heteroptera: Gerridae), using two size variables: head width and a multivariate measure derived from the pattern of multivariate allometry common to the species considered. Allometric patterns were similar in two independent datasets of laboratory-reared and field-caught specimens. Although our data strictly followed Dyar's rule in just a few instances, all growth ratios varied within a limited range only. Growth ratios for head width differed more between moults than those for multivariate size. The relationship between growth ratios for the two size measures conformed to the predictions based on allometry. We discuss hypotheses of the possible adaptive significance of growth ratios, such as their relation to mobility and systematic differences between hemimetabolous and holometabolous insects, and emphasize the importance of allometry. Since Dyar's rule is consistent with available evidence of physiological mechanisms underlying growth and moulting control of insects and crustaceans, it can be used as a general frame of reference to test alternative growth models.

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Introduction

Arthropods are covered by a cuticle which mainly functions as an exoskeleton (Hadley, 1986). In most arthropod species at least some parts of this exoskeleton are strongly sclerotized and unable to expand (Teissier, 1960; Nijhout, 1981; Sehnal, 1985). This rigidity prevents continuous growth, and such structures therefore grow in a stepwise manner. The stepwise growth results from moulting, i.e. the replacement of the old cuticle by a new one which was formed during the intermoult cycle prior to ecdysis (Sehnal, 1985). Growth of sclerotized parts can easily be analysed by assessing their size in successive instars. Many authors studied growth of immature insects (e.g. Dyar, 1890; Gaines & Campbell, 1935; reviews by Nijhout, 1981; Daly, 1985; Sehnal, 1985). Similar studies of other arthropods include Enders (1976) on spiders, Teissier (1960) and Freeman (1990) on crustaceans, and Albert (1982) on centipedes.

Several mathematical models have been used to describe linear measurements of sclerotized parts in successive instars. Two frequently used models are the linear progression $y = a + bx$, and the geometric progression $y = ab^x$, termed Dyar's rule (Dyar, 1890), or equivalently its log-transformed version $\log y = \log a + (\log b)x$, where y is a measure of size, x is the instar number, and a and b are constants. This relation has also been termed Brooks-Dyar rule (Hutchinson & Tongring, 1984). Despite their simplicity, these models have sometimes been confounded (e.g. Richards, 1949; Savopoulou-Soultani & Tzanakakis, 1990). The linear progression model is appropriate if there is a straight-line relation between untransformed size measures and instar number, i.e. if *absolute growth increments* are the same in all moults. Reports of linear increase include Richards (1949) and Ghent (1956). In contrast, Dyar's rule assumes a geometric progression of size measures, where succeeding *growth ratios* (i.e. postmoult size/premoult size; also termed Dyar's coefficient) or *percentage increments*, but not the absolute increments, are constant (Dyar, 1890; Hutchinson & Tongring, 1984; Sehnal, 1985). Therefore, a plot of log-transformed size measurements against instar number reveals a straight-line relation. Larval growth according to Dyar's Rule was reported among others by Hemmingsen (1965), Brown & Davies (1972), Peters (1972) and Loudon (1988). However, there can be considerable differences between various body parts (Brown & Davies, 1972).

Originally, such relations were used to determine the number of instars (e.g. Dyar, 1890; Gaines & Campbell, 1935). In most of these studies, the width of the head capsule was taken as a measure of larval size (see Cole, 1980, and references therein). However, head capsule width can increase slightly, but significantly, within stadia (Bliss & Beard, 1954) or even exhibit apparently continuous growth (Hemmingsen, 1965). Therefore, some authors included a variety of measurements of rigidly sclerotized structures which lack significant growth within stadia (e.g. Hemmingsen, 1965; Brown & Davies, 1972).

More recently, Enders (1976), Cole (1980) and Hutchinson & Tongring (1984) emphasized the possible adaptive importance of Dyar's rule. However, in such a context, it seems important to use a general measure of size representative of all the body parts involved in a functional hypothesis, e.g. feeding parts and appendages used in locomotion. Because animal size and shape are intrinsically multivariate concepts, we prefer to use a synthetic variable expressing multivariate size, instead of an arbitrarily chosen single character (see Bookstein *et al.*, 1985; Bookstein, 1989). A rigorous mathematical concept of multivariate size and shape within the framework of geometric similarity was presented by Mosimann (1970) and exemplified by the study of Mosimann & James (1979).

Several authors already mentioned the relation between Dyar's rule and allometry (Teissier,

1960; Matsuda, 1964; Hemmingsen, 1965; Brown & Davies, 1972). However, it should be noted that Dyar's rule is not simply a special case of allometry (*contra* Matsuda, 1964), but covers an entirely different aspect of growth. Allometry pertains to the relations between different body parts, whereas Dyar's rule describes the stepwise growth of any single part in successive moults (or, alternatively, of a multivariate measure of general size). In other words, allometry indicates the ontogenetic trajectory, i.e. the path in morphospace along which an organism moves during ontogeny, whereas Dyar's rule is concerned with the discrete steps of growth along that path. However, there is a relation between allometry and Dyar's rule: if two characters x_1 and x_2 follow the allometric equation $x_1 = bx_2^k$, then either both characters grow according to Dyar's rule (with the corresponding postmoult/premoult ratios r_1 and r_2 satisfying $r_1 = r_2^k$) or neither of them does.

In this study we evaluate Dyar's rule in all five larval instars of nine species of the waterstrider genera *Gerris* and *Aquarius*, and discuss it in relation to allometric growth and the physiology of moulting. Patterns of multivariate allometry were compared by Klingenberg & Zimmermann (In press) using the same data. Here, we use Mosimann's (1970) definition of size variables to extend Dyar's rule in the context of multivariate allometry.

Materials and methods

Materials and measurements

The present study includes all 5 larval instars (denoted L1 to L5, respectively) of 9 species of waterstriders: *Gerris argentatus*, *G. costae*, *G. gibbifer*, *G. lacustris*, *G. lateralis*, *G. odontogaster*, *G. thoracicus*, *Aquarius najas* and *A. paludum*.

We performed parallel analyses on 2 separate datasets of larvae collected either in the field or reared in the laboratory (for details, see Zimmermann, 1987). Sample sizes for each instar and species were 20 in both datasets, except for L1 of all species from the field ($n = 10$), L2 of *G. lateralis* from the field ($n = 12$), and L5 of *A. paludum* reared in the laboratory ($n = 19$). Thus, the total number of larvae was 899 for laboratory rearings and 802 for the field samples. All specimens were preserved in 70% ethanol.

Eleven measurements were taken on each specimen by means of a dissecting microscope fitted with an eyepiece micrometer for the laboratory-reared specimens, and with a Wild MMS 235 digital length measuring equipment for the larvae from the field. Characters measured are head width (HEAD), lengths of the 4 antennal segments (ANTSEG1 to ANTSEG4, respectively), and lengths of femora, tibiae and tarsi of the middle (MIDFEM, MIDTIB and MIDTARS) and hind legs (HINDFEM, HINDTIB and HINDTARS). Details of measurement and univariate statistics are given by Zimmermann (1987).

Statistical analysis

Ontogenetic allometry pertains to the character covariation within species over the 5 larval instars considered. We apply Jolicoeur's (1963) concept of multivariate allometry, using the first principal component (PC) of the covariance matrix of log-transformed variables to characterize patterns of allometric variation. The first PC is the normalized linear combination of the log-transformed variables which maximizes the proportion of total variance accounted for, and can therefore be seen as a line of best fit to the data points (Pimentel, 1979). The first PC score of an individual indicates its position along that line.

Since both our datasets are composed of 9 closely related species, we use a model specifically designed for such a multigroup situation instead of analysing each species separately. The common principal component (CPC) model assumes that the eigenvectors (PCs) of the covariance matrices in all species are identical (Airoldi & Flury, 1988; Flury, 1988), i.e. the species share a common allometric pattern. In a previous study, we applied this model to the present dataset for 8 variables (Klingenberg & Zimmermann, In press). First

ontogenetic CPCs were closely similar in their coefficients to first PCs estimated for each group separately, and also accounted for a similar proportion of total variance, thus demonstrating the good fit of the CPC model (Klingenberg & Zimmermann, In press). We therefore consider the CPC model as an extension of Jolicoeur's (1963) approach, characterizing a common pattern of multivariate ontogenetic allometry in all 9 species studied. Two parallel analyses were performed for the specimens reared in the laboratory and those collected in the field. The bootstrap technique (Efron & Tibshirani, 1986), with 250 bootstrap iterations for each dataset, was used to determine standard errors of ontogenetic CPC coefficients (for details see Klingenberg & Zimmermann, In press).

We use the mathematical concept of size variables presented by Mosimann (1970). Let $\mathbf{x} = (x_1, \ldots, x_p)$ be a vector of p linear measurements. A positive real-valued function $G(\mathbf{x})$ is a standard size variable if $G(a\mathbf{x}) = aG(\mathbf{x})$, where a is any positive real number. A log-transformed size variable is termed a log-size variable. An important group of log-size variables can be written as linear combinations of log-transformed measurements, i.e. $\log G(\mathbf{x}) = \Sigma b_i(\log x_i)$. Since G is a standard size variable, it can be shown that the coefficients b_i must satisfy $\Sigma b_i = 1$ (Mosimann & James, 1979). Note that any single character also conforms to this definition [i.e. $\log G(\mathbf{x}) = \log x_i$], by setting $b_i = 1$ and $b_j = 0$ for any $j \neq i$ in the above linear combination.

We defined a multivariate measure of size by rescaling the first ontogenetic CPC so that the coefficients sum up to unity. This was achieved by dividing each coefficient by the sum of all coefficients. The rescaled component therefore fulfils the criteria for a standard size variable *sensu* Mosimann (1970), and it simultaneously reflects the main allometric pattern of ontogenetic change in the characters included in the analysis. For comparison, we used log-transformed head width as another log-size variable.

The geometric-mean growth ratio of both standard size variables at each moult was determined as the antilogarithm of the difference between mean values of the respective log-size variable for 2 successive instars. It therefore corresponds to the ratio of the geometric means of the size variable in successive instars.

Confidence intervals of geometric-mean growth ratios were established using the bootstrap technique (Efron & Tibshirani, 1986). In each bootstrap iteration, bootstrap samples were drawn at random, with replacement, from the original samples. A bootstrap estimate of the geometric-mean growth ratio was then determined as the antilogarithm of the difference in mean scores of the respective size variable in the bootstrap samples of successive instars. One thousand bootstrap iterations were performed for each moult and for both standard size variables. The percentile method (Efron & Tibshirani, 1986) was used to determine central 95% confidence intervals, i.e. the confidence limits are the 2·5% and 97·5% quantiles of the empirical distribution of bootstrap estimates.

Tests for equality of size ratios using null hypotheses with log-uniform (Simberloff & Boecklen, 1981) or log-normal (Boecklen & NeSmith, 1985) distributions of size measures cannot be applied here, since the sizes of successive instars cannot be assumed to be independent of each other (see also Tonkyn & Cole, 1986). Therefore, we interpret confidence intervals of geometric-mean growth ratios which include a common value or interval in all successive moults as supporting the hypothesis of constant growth ratios.

Computations were done on DEC/VAX systems at the computing centres of the Institut für Meereskunde an der Universität Kiel and of Kiel University. CPCs were estimated using the FORTRAN subroutine FGALG of Flury (1988). FGALG was run in REAL*16 precision, while all other computations were performed in double precision (REAL*8).

Results

Multivariate allometry

The first ontogenetic CPCs accounted for most of the total variance in all nine species. In the dataset of laboratory cultures, the amount of total variance explained by the first CPC ranged from 97·55% (*A. najas*) to 99·22% (*G. gibbifer*), and from 97·04% (*A. najas*) to 99·51% (*G. thoracicus*) in the field data. Therefore, almost the entire ontogenetic variation is represented by first ontogenetic CPCs.

TABLE I

Estimates of first ontogenetic common principal component coefficients and their bootstrapped standard errors

Character	Laboratory		Field	
	Coeff.	S.E.	Coeff.	S.E.
HEAD	0·210	0·0009	0·201	0·0008
ANTSEG1	0·371	0·0034	0·350	0·0010
ANTSEG2	0·331	0·0018	0·321	0·0013
ANTSEG3	0·294	0·0018	0·279	0·0014
ANTSEG4	0·171	0·0012	0·167	0·0012
MIDFEM	0·377	0·0011	0·384	0·0008
MIDTIB	0·289	0·0010	0·297	0·0007
MIDTARS	0·252	0·0014	0·259	0·0009
HINDFEM	0·390	0·0010	0·397	0·0007
HINDTIB	0·318	0·0019	0·332	0·0009
HINDTARS	0·225	0·0022	0·243	0·0010
Σ	3·228		3·230	

The estimates of CPC coefficients are fairly stable, as can be seen from their small standard errors (Table I). Most of the first CPC coefficients are similar in the separate analyses for laboratory and field samples, and clearly differ from the coefficient value for isometry, which is 0·302. Head width shows negative allometric growth. In the antennae, there is a clear gradient from the first segment with clearly positive allometry, to the fourth segment with strongly negative allometry. A similar gradient with decreasing allometric coefficients from proximal to distal segments also pertains to the middle and hind legs. Tibiae and femora have higher coefficients in the hind legs than in the middle legs, whereas the reverse is true for the tarsi. The multivariate allometric coefficients of head width are equal in both datasets, while coefficients of antennal segments are somewhat higher in the laboratory samples than in the field, and the reverse occurs in leg segments. Overall, however, allometric patterns in both datasets are very similar, as indicated by the very narrow angle between the first ontogenetic CPCs, which amounts to only 2·24°.

Dyar's rule

There is significant variation in growth ratios among species and the four larval moults considered, both for head width (Fig. 1) and for the multivariate size measure (Fig. 2). Values of the growth ratio for head width, where the confidence intervals of all four moults intersect, are found only in the field samples of *A. paludum*. Therefore, Dyar's rule does not apply in a strict sense to the growth of the head width in most of the material considered here. However, for multivariate size there are more instances where all four confidence intervals overlap: in the field samples of *G. argentatus*, *G. thoracicus*, *A. najas* and *A. paludum*, as well as in both field and laboratory samples of *G. gibbifer* and *G. lateralis*.

Despite considerable differences between the two datasets, growth ratios of head width tend to decrease during larval development, most clearly for the samples from the field. In the laboratory material, a remarkably similar pattern of growth ratios (L1–L2 > L2–L3 < L3–L4 > L4–L5) is seen
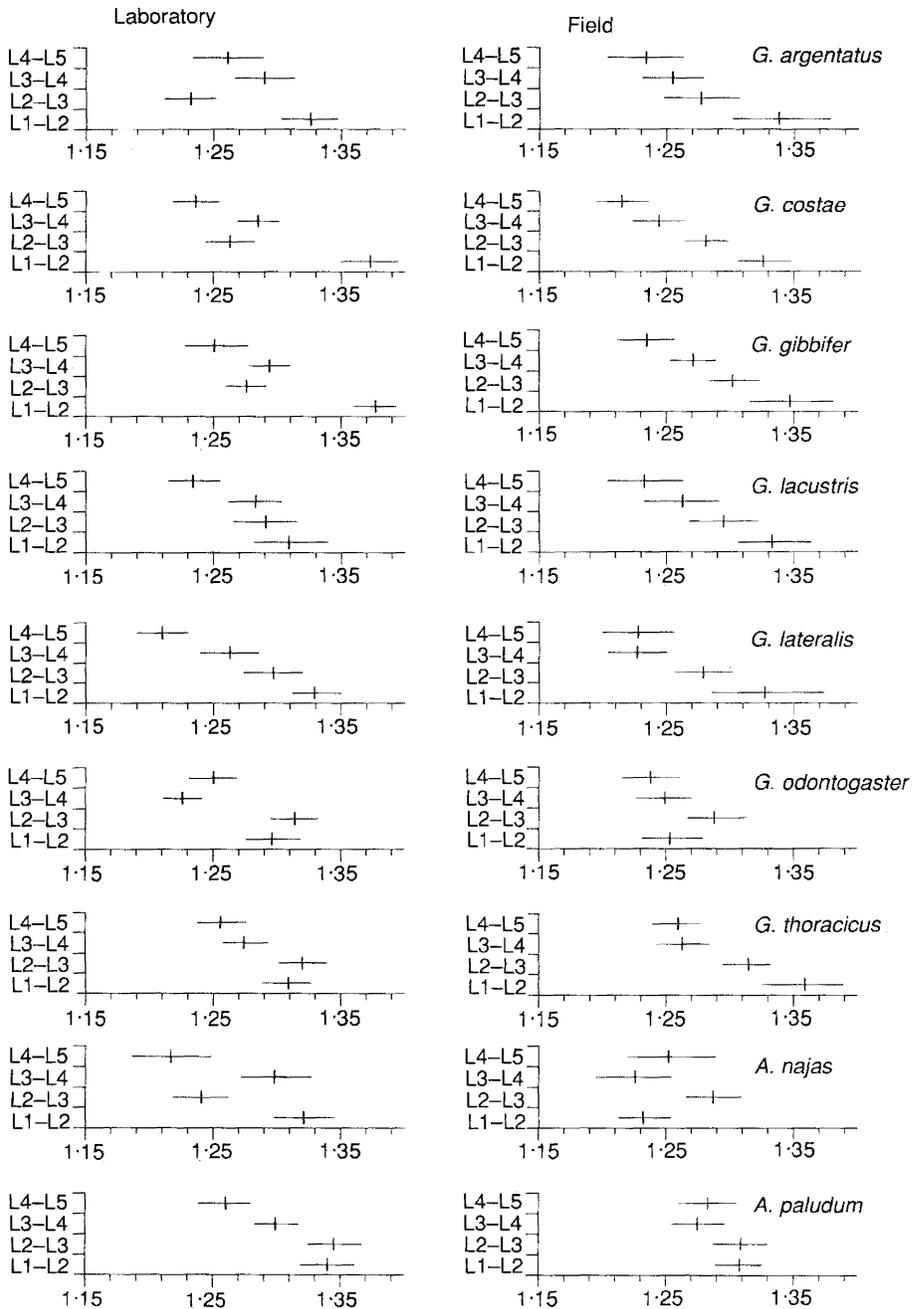
FIG. 1. Geometric-mean growth ratios of head width in nine species of *Gerris* and *Aquarius* for samples from laboratory cultures and from the field. Bars indicate bootstrapped central 95% confidence intervals of the estimates (for details see text).
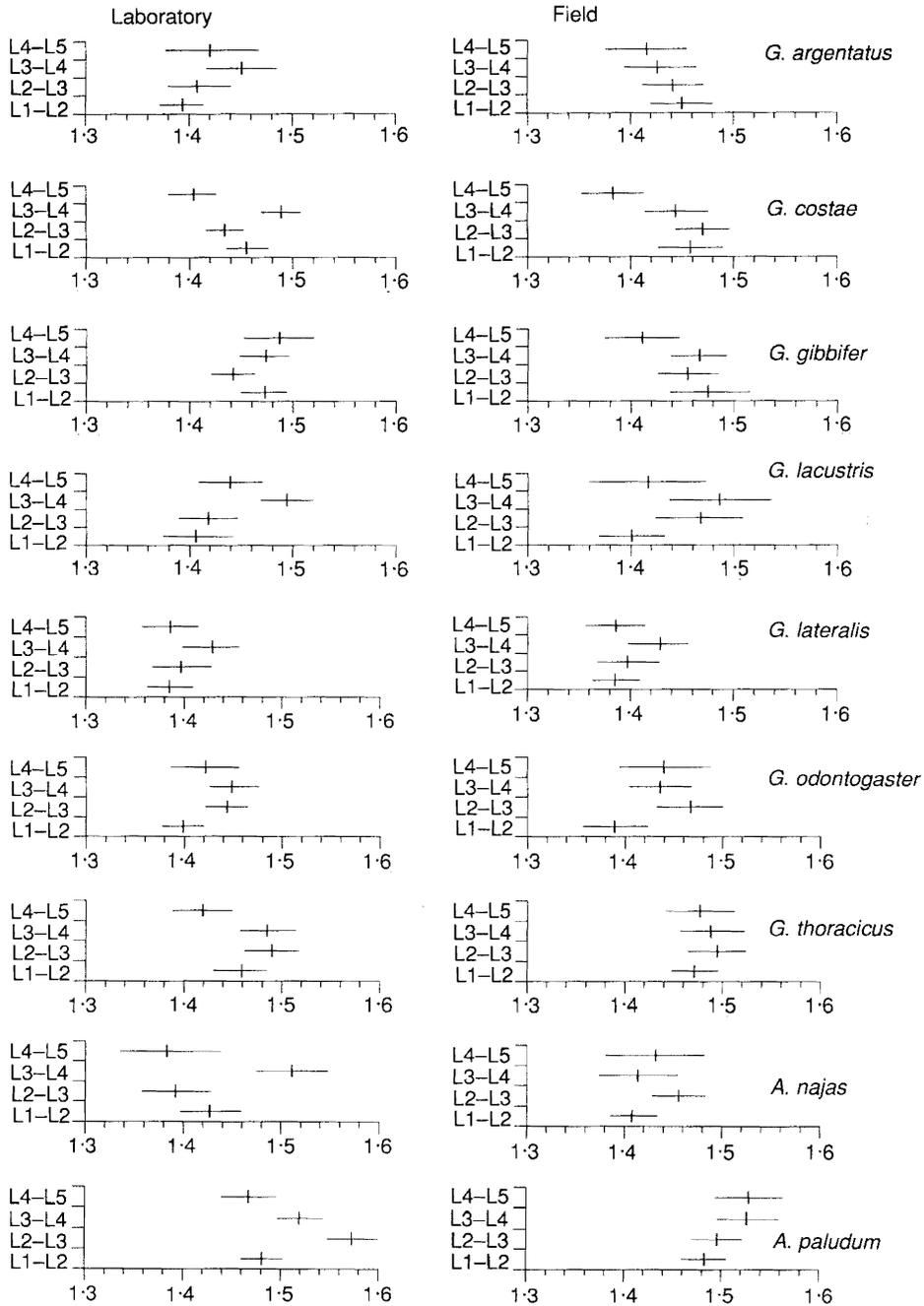
FIG. 2. Geometric-mean growth ratios of the multivariate size variable, i.e. the rescaled scores of the first ontogenetic common principal component. Bars indicate bootstrapped central 95% confidence intervals of the estimates (for details see text).
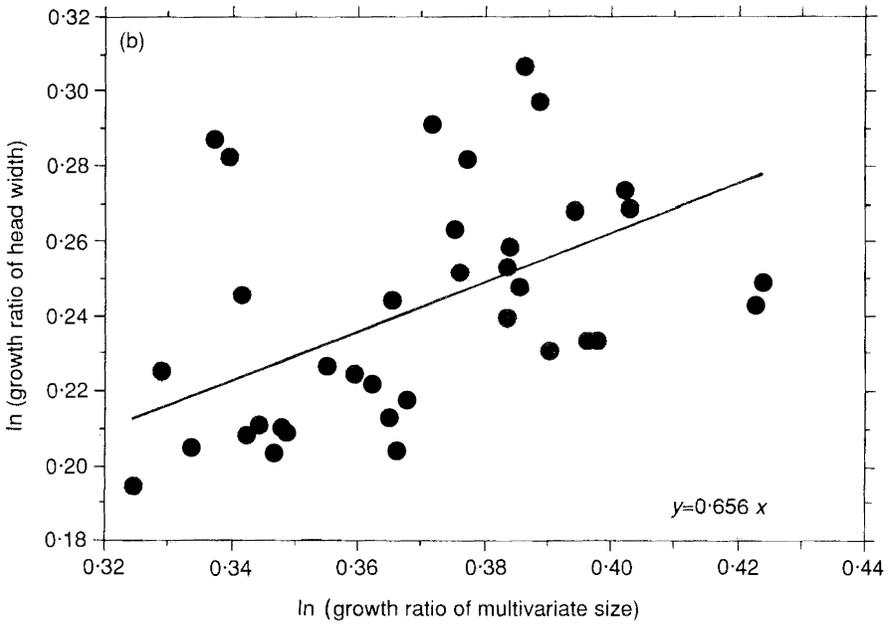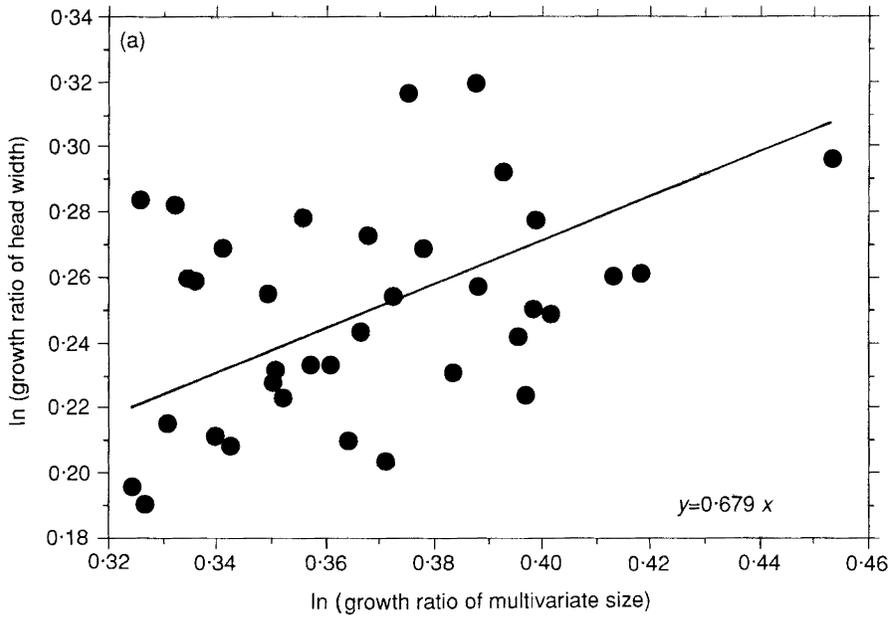
FIG. 3. Relations between geometric-mean growth ratios of the multivariate size and those of head width. (a) Laboratory cultures. (b) Field samples.

in *G. argentatus*, *G. costae*, *G. gibbifer* and *A. najas*. The same pattern was not found in the field data. Except for the laboratory samples of *A. najas* and *A. paludum*, the growth ratios of multivariate size seem to vary less within species than those of head width. Depending on the species considered, growth ratios can increase as well as decrease from younger to older instars.

Interestingly, confidence intervals are fairly narrow even at the L1–L2 transition in the field data, where small samples ($n = 10$ in L1) are used to estimate growth ratios. For multivariate size, confidence intervals are even considerably wider in later moults, related to increased individual size variation in older instars.

Growth ratios of head width are consistently smaller than corresponding growth ratios of the multivariate size measure (Figs 1 & 2). The theoretical relation between the two kinds of growth ratios is $r_{HEAD} = r_{CPC}^{k}$, or equivalently $\log r_{HEAD} = k \log r_{CPC}$, where r_{HEAD} and r_{CPC} are the growth ratios of head width and the rescaled CPC, respectively, and k is the allometric coefficient of head width with respect to the multivariate size measure. Because the coefficient of head width on the first ontogenetic CPC is also the allometric coefficient with respect to the CPC score, and since we rescaled the CPC by dividing scores by the sum of all coefficients (Table I), the theoretical value of k equals the first CPC coefficient of head width multiplied by the sum of all first ontogenetic CPC coefficients. Despite the substantial amount of variation (Fig. 3), the regressions of $\log r_{HEAD}$ on $\log r_{CPC}$ were significant for both datasets. The intercept did not differ significantly from zero, and there were no significant differences between slopes observed and expected from multivariate allometry. In a regression model without an intercept, regression estimates of k values of 0·679 for laboratory rearings and 0·656 for field samples did not differ significantly from the expected values of 0·678 and 0·649, respectively (*t*-test, Sokal & Rohlf, 1981).

Discussion

Dyar's rule, the constancy of the ratios of postmoult/premoult size measures in successive larval ecdyses, was not strictly fulfilled for most species in our datasets, although growth ratios varied only within a limited range. Similar results were reported in earlier studies on various insects (Hemmingsen, 1965; Brown & Davies, 1972; Sehnal, 1985; Loudon, 1988; Savopoulou-Soultani & Tzanakakis, 1990), and also in other arthropods such as spiders (Enders, 1976), centipedes (Albert, 1982), and crustaceans (Freeman, 1990).

Our study is based on a cross-sectional design, i.e. different specimens were measured for each instar, assuming that samples are representative of the respective instars. Therefore, we cannot assess individual growth ratios, as in a longitudial design using the same individuals in subsequent instars (Kowalski & Guire, 1974). However, this does not affect our estimates of geometric-mean growth ratios, since the geometric mean of ratios in two paired samples equals the ratio of geometric means of the samples [in log-transformed notation: $\log r = \Sigma \log(x_2/x_1)/n = \Sigma(\log x_2 - \log x_1)/n = \Sigma \log x_2/n - \Sigma \log x_1/n$, where r is the geometric-mean growth ratio, x_1 and x_2 are the values of a size variable in two successive instars, and n is sample size]. When considering the confidence intervals of the estimates of geometric-mean growth ratios, however, it is important to keep in mind that our estimates of variability were obtained by randomly drawing specimens from two independent samples of successive instars, thereby ignoring any correlation of individual size between instars, and thus including the possibility that the largest individuals in the previous instar might be the smallest after moulting, or vice versa. Since this seems rather unlikely, we presume that a longitudinal study would reveal even narrower confidence intervals. Regulatory phenomena resulting in targeted growth (e.g. Atchley, 1984), as reported for cockroaches by Tanaka (1981)

and for crustaceans by Hartnoll & Dalley (1981), would also tend to reduce the range of individual variability in growth ratios.

Variation in growth ratios between succeeding ecdyses was generally less important for our multivariate size variable than for head width. There seems to be some unique variation in the growth of the head, since growth ratios of head width have a general tendency to decrease during development (Fig. 1). A slight decrease in growth ratios of head width has often been observed, e.g. in the milkweed bug *Oncopeltus fasciatus* (Bliss & Beard, 1954) and in later instars of the mealworm *Tenebrio molitor* (Loudon, 1988). However, such a decrease in growth ratios is not seen for the multivariate size measure (Fig. 2). The decelerating growth of the head apparently is outweighed by the faster development of proximal appendage segments, most of which have considerably higher allometric coefficients than head width (Table I).

Enders (1976) stated that growth ratios of head and body dimensions in spiders and insects are inversely related to locomotory activity, since the energetic costs of transport of nutrients stored for growth increase with growth ratios. In a comparison of published data of 105 insect species, Cole (1980) found generally higher growth ratios of head measurements in holometabolous (median: 1·52) than in hemimetabolous (median: 1·27) insects. Cole interpreted this difference as evidence against Enders' hypothesis, and argued that it might reflect a general divergence in habitats and resource use. The hypotheses of Cole and Enders are not mutually exclusive, however, since larvae of hemimetabolous insects are often more mobile than holometabolous larvae; specific tests of both hypotheses will be needed. Furthermore, it should be noted that most previous studies considered only measurements of the head capsule. Our estimates of growth ratios of head width are close to typical values reported for hemimetabolous insects by Cole (1980), whereas those for the multivariate size measure are higher due to allometry. Therefore, another important difference between hemimetabolous and holometabolous insects might be that the former allocate more resources to the growth of larval locomotory structures than the latter (i.e. the two groups differ in their allometric patterns), although they might be fairly similar in 'overall growth'. Unfortunately, most studies of allometric growth in insects focused on hemimetabolous insects (e.g. Matsuda, 1960, 1961*a*, *b*, 1962; Matsuda & Rohlf, 1961; Blackith, Davies & Moy, 1963; Davies & Brown, 1972; Cuzin-Roudy & Laval, 1975), and we are not aware of any similar investigations in holometabolous insects, except Hemmingsen (1965) who only considered dimensions of the head capsule and spiracle diameter.

Hutchinson & Tongring (1984) argued that Dyar's rule might result from a maximization of growth efficiency, assuming that the size of the first instar, the number of instars, and the arithmetic mean of growth ratios are predetermined. However, the approximate constancy of growth ratios can as well be seen as resulting from the physiological base of moulting (e.g. Nijhout, 1981; Sehnal, 1985). In a series of experiments on the bug *Rhodnius prolixus*, Bennet-Clark (1971) showed that the old cuticle plays an important role in determining the size of the successive instar, and he argued that the cuticle works as a template for the formation of the epicuticle of the following instar (see Freeman, 1990, for a similar study of a crustacean). If successive moults are controlled by the same physiological mechanism, constancy of growth ratios will result. Therefore, we prefer to view Dyar's rule as a base of comparison against which specific adaptive hypotheses can be tested, rather than to search for an adaptive explanation for the rule itself, as Hutchinson & Tongring (1984) attempted to do.

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