# Growth Ratios in Holometabolous and Hemimetabolous Insects[1]

BLAINE J. COLE

Department of Biology, Princeton University, Princeton, New Jersey, 08540

**ABSTRACT**

Ann. Entomol. Soc. Am. 73: 489–491 (1980)

Evidence from studies of 105 species of insects is presented which show that holometabolous insects grow almost twice as much in linear dimension at each molt as do hemimetabolous insects (median growth ratios of 1.52 and 1.27 respectively).

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Dyar (1890) suggested that the size of the head capsule of lepidopteran larvae increased by a factor of 1.6 per molt. His postulate has been found applicable in a wide variety of cases and inapplicable in almost an equally wide variety of cases. Przibam and Megusar (1912) suggested that size increased by a factor of 1.26 per molt. The rationale for suggesting this ratio was the postulate of a doubling of cell number in each instar resulting in a change of the cube root of two, or 1.26, in linear dimension. While Przibam's rule has also been found to agree with the observations on a number of species, it is also at odds with a number of observations. Brown and Davies (1972) show that some parts seem to obey Dyar's law, some Przibam's rule, and some are described by neither.

Although the pattern of growth of immature stages of insects has been described for many species in connection with ecological, bionomic, or developmental studies, there has been little attempt to gather together the results of such investigations. In this paper I shall present the results of studies of size change during the development of 105 species of insects. I shall show that a major difference in size change exists between holometabolous and hemimetabolous insects. The ratio of the size of one instar to the size of the previous instar, averaged over all immature molts, will be referred to in this paper as the "growth ratio." Studies which provided head width measurements, or measurements of the trophic apparatus of immature insects, were used exclusively to calculate growth ratios. This restriction was applied in order to give a similar set of data from which to draw generalizations about growth. Table 1 gives the insect species for which growth ratios were calculated.

Figure 1 shows the distribution of growth ratios for immature holometabolous (55 species) and hemimetabolous (50 species) insects. The median growth ratio for holometabolous insects is 1.52 per instar and for hemimetabolous insects is 1.27 per instar. A median test (Siegel 1956) indicates that the two medians are significantly different ($X^2 = 49.25$, $p < .001$). Only one species of hemimetabolous insect had a growth ratio as high as the median growth ration of holometabolous insects. The typical holometabolous insect grows nearly twice as much in linear dimensions at each molt as does the typical hemimetabolous insect.

There is a close correspondence of the median growth ratio of holometabolous insects (1.52) to Dyar's law (1.60) and the median growth ratio of hemimetabolous insects (1.27) to Przibam's rule (1.26). However, the variability around these figures is great enough to negate the application of a particular rule to the growth of any given species. It is significant to note that Dyar studied a group of holometabolous insects and Przibam and Megusar studied growth in a hemimetabolous insect.

The profound difference in the growth ratios of holometabolous and hemimetabolous insects suggest sharply differing selective pressures on the two groups of species which may be the result of different patterns of food or habitat use. Enders (1976) observed that some species of holometabolous insects have large growth ratios. He felt that small growth ratios were associated with high immature mobility and the necessity to move frequently in search of food. The presence of a systematic difference between holometabolous and hemimetabolous insects, regardless of foraging type, argues strongly against such an explanation.

A high growth ratio could be a key element of a developmental syndrome of rapid growth. Holometabolous insects may be adapted for exploiting ephemeral habitats which appear patchily and have a short lifetime. Such habitats would be best exploited by insects that rapidly achieve adult size, mature, and disperse before the habitat disappears. Hemimetabolous insects, on the other hand, may be adapted for exploiting habitats that are dependably present for long periods of time. Exploitation of temporally persistent habitats may not require rapid development and a high growth ratio. This explanation contrasts with the current widely favored hypothesis that the major adaptive advantage of holometaboly is a reduction of competition between adults and larvae.

[1] Received for publication Oct. 1, 1979.





0013-8746/80/0404-8903$00.75/0

**Table 1.—Growth ratio data for 105 species of insects. [1]The Body Part Measured is as described by the authority. [2]The Average Growth Ratio is, as given, the percentage size increase in the Body Part from one molt to the next averaged over all immature molts.[3] The Reference is given as: First Author, Journal, Volume:Page Number. ESA refers to the Annals of the Entomological Society of America; J. Zool. the The Journal of Zoology; J. Econ. Ent. the The Journal of Economic Entomology; Austr. J. Zool. to the Australian Journal of Zoology.**

| SPECIES | BODY PART MEASURED[1] | AVERAGE GROWTH RATIO[2] | REFERENCE[3] |
|---|---|---|---|
| DERMAPTERA | | | |
| Labiduridae | | | |
| *Labidura riparia* | Head Capsule | 25 | Sheppard ESA 66:837 |
| ORTHOPTERA | | | |
| Acrididae | | | |
| *Dendrotettix quercus* | Cranial Width | 24 | Valek ESA 65:310 |
| BLATTARIA | | | |
| Blatellidae | | | |
| *Blatella germanica* | Head Width | 19 | Murray ESA 60:10 |
| Blattidae | | | |
| *Ectobius lapponicus* | Head Width | 17 | Brown J. Zool. 166:97 |
| *E. panzeri* | Head Width | 15 | Brown J. Zool. 166:97 |
| HOMOPTERA | | | |
| Cicadellidae | | | |
| *Aceratagallia curvata* | Head Width | 34 | Nielson ESA 61:54 |
| *Acinopterus angulatus* | Head Width | 42 | Nielson ESA 61:54 |
| *Cuerna arida* | Head Width | 28 | Nielson ESA 68:346 |
| *C. balli* | Head Width | 29 | Nielson ESA 68:346 |
| *Deltocephalus sonorus* | Head Capsule Width | 21 | Gustin ESA 61:77 |
| *Draeculacephala mollipes* | Head Width | 35 | Bridges ESA 63:789 |
| *Empoasca kraemeri* | Head Width between Eyes | 30 | Wilde ESA 69:442 |
| *Graminella nigrifrons* | Head Width | 32 | Stoner ESA 60:496 |
| *Oncometopia alpha* | Head Width | 32 | Nielson ESA 68:401 |
| HETEROPTERA | | | |
| Alydidae | | | |
| *Alydus conspersus* | Head Capsule | 32 | Yonke ESA 61:526 |
| *A. eurinus* | Head Capsule | 35 | Yonke ESA 61:526 |
| *A. pilosulus* | Head Capsule | 30 | Yonke ESA 61:526 |
| *Megalotomus quinquespinosus* | Head Capsule | 35 | Yonke ESA 58:222 |
| *Riptortus* sp. | Head Width | 28 | Kumar Austr.J.Zool. 14:895 |
| Anthocoridae | | | |
| *Nidicola jaegeri* | Transocular Width | 14 | Peet ESA 72:430 |
| *N. marginata* | Head Width | 15 | Peet ESA 66:344 |
| *Xylocoris flavipes* | Rostrum | 17 | Arbogast ESA 64:1131 |
| Coreidae | | | |
| *Acanthocephala terminalis* | Head Capsule Width | 24 | Yonke ESA 62:474 |
| *Agriopocoris froggatti* | Head Width | 21 | Kumar Austr.J.Zool. 14:895 |
| *Amorbus alternatus* | Head Width | 27 | " " " " |
| *A. rubiginosus* | Head Width | 23 | " " " " |
| *Archimerus alternatua* | Head Capsule | 23 | Yonke ESA 62:477 |
| *Aulacosternum nigrogrubrum* | Head Width | 24 | Kumar Austr.J.Zool. 14:898 |
| *Euthochtha galeator* | Head Capsule | 24 | Yonke ESA 62:469 |
| *Mictis profana* | Head Width | 20 | Kumar Austr.J.Zool. 14:895 |
| *M. caja* | Head Width | 28 | " " " " |
| *Pachycolpura manca* | Head Width | 22 | " " " " |
| Hyocephalidae | | | |
| *Hyocephalus* sp. nov. | Head Width | 22 | Kumar Austr.J.Zool. 14:895 |
| Miridae | | | |
| *Plagiognathus chrysanthemi* | Head Width | 25 | Guppy ESA 56:804 |
| Pentatomidae | | | |
| *Banasa calva* | Head Width | 26 | DeCoursey ESA 56:687 |
| *B. dimidiata* | Head Width | 27 | " " " |
| *Euthyrhynchus floridanus* | Labium | 52 | Oetting ESA 68:659 |
| *Hymenarchys aequalis* | Head Width | 33 | Oetting ESA 64:1289 |
| *H. crassa* | Head Width | 41 | Oetting ESA 65:474 |
| *H. nervosa* | Head Width | 35 | Oetting ESA 64:1289 |
| *Tetyra bipunctata* | Relative Head Widths (Interocular) | 30 | Gilbert ESA 60:698 |
| Reduviidae | | | |
| *Apiomerus crassipes* | Head Width | 27 | Swadener ESA 66:188 |
| Rhopalidae | | | |
| *Harmostes reflexulus* | Outer Ocular Width | 30 | Yonke ESA 63:1749 |
| *Leptocoris mitellata* | Head Width | 32 | Kumar Austr.J.Zool. 14:895 |
| *L. tagalica* | Head Width | 28 | " " " " |
| Salididae | | | |
| *Omania samoensis* | Head Width | 8 | Kellen ESA 53:494 |
| Tessaratomidae | | | |
| *Cyclogastridea nigromarginata* | Head Width | 30 | Kumar ESA 62:681 |
| Thaumastocoridae | | | |
| *Xylastodoris luteolus* | Head Width across Eyes | 26 | Baranowski ESA 51: |
| Tingidae | | | |
| *Atheas austoparius* | Labium | 22 | Sheeley ESA 70:603 |
| *Leptophya costata* | Labium | 21 | " " " |
| Veliidae | | | |
| *Halovelia marianorum* | Head Width | 15 | Kellen ESA 52:53 |
| NEUROPTERA | | | |
| Chrysopidae | | | |
| *Chrysopa lanata* | Head Capsule | 50 | Ru ESA 68:187 |
| COLEOPTERA | | | |
| Cerambycidae | | | |
| *Deotes texanus* | Head Capsule | 31 | Hatchett ESA 68:209 |
| Chrysomelidae | | | |
| *Lema trilineata daturaphila* | Head Capsule (Relative Length) | 49 | Kegan ESA 63:537 |
| *Oulema melanopus* | Head Capsule | 35 | Hoxip ESA 67:183 |
| Colydiidae | | | |
| *Lasconotus subcostulatus* | Head Capsule | 39 | Hackwell ESA 66:62 |
| COLEOPTERA (continued) | | | |
| Curculionidae | | | |
| *Anthonomus grandis* | Head Capsule | 55 | Parrott ESA 63:1265 |
| *Ceuthorhynchidius horridus* | Head Capsule | 52 | Kok ESA 68:505 |
| *Microlarinus lareynii* | Head Capsule | 47 | Kirkland ESA 70:583 |
| *M. lypriformis* | Head Capsule | 38 | " " " |
| *Neochetina bruchi* | Head Capsule | 46 | Deloach ESA 69:643 |
| *N. eichhorniae* | Head Capsule | 53 | " " " |
| *Phrydiuchus spilmani* | Head Capsule | 52 | Rizza ESA 70:7 |
| *P. tau* | Head Capsule | 53 | " " " |
| *Pissodes approximatus* | Head Capsule | 49 | Harman ESA 63:1573 |
| *P. strobi* | Head Capsule | 45 | " " " |
| Dermestidae | | | |
| *Trogoderma glabrum* | Head Capsule | 38 | Beck ESA 64:149 |
| Nitidulidae | | | |
| *Stelidota geminata* | Head Capsule | 36 | Weber ESA 68:649 |
| Scolytidae | | | |
| *Xyleborus ferrugineus* | Head Capsule | 35 | Peleg ESA 66:180 |
| Silphidae | | | |
| *Silpha ramosa* | Head Capsule | 32 | Brewer ESA 68:786 |
| MECOPTERA | | | |
| Panorpidae | | | |
| *Panorpa nuptioalis* | Head Capsule | 46 | Byers ESA 56:142 |
| LEPIDOPTERA | | | |
| Gelechiidae | | | |
| *Dichomeris marginella* | Head Capsule | 27 | Nordin ESA 62:287 |
| *Pectinophora gossypiella* | Head Capsule | 70 | Watson ESA 67:812 |
| *Stomopteryx palpilineella* | Head Capsule | 51 | Valley ESA 69:317 |
| Geometridae | | | |
| *Ennomos subsignaris* | Head Capsule | 62 | Drooz J.Econ.Ent. 58:629 |
| *Phaeoura mexicanaria* | Head Capsule | 62 | Dewey ESA 65:306 |
| *Rheumaptera Hastata* | Head Width | 67 | Werner ESA 70:328 |
| Gracillariidae | | | |
| *Marmara fraxinicola* | Head Capsule | 22 | Fitzgerald ESA 64:765 |
| Noctuidae | | | |
| *Bellura gortynoides* | Head Capsule | 47 | Levine ESA 69:405 |
| *Elasmopalpus lignosellus* | Head Capsule | 69 | Dupree J.Econ.Ent. 58:1156 |
| *Tarachidia candefacta* | Head Capsule | 62 | Gilstrap ESA 67:265 |
| Notodontidae | | | |
| *Heterocampa manteo* | Head Capsule | 59 | Surgeoner ESA 68:1061 |
| Olethreutidae | | | |
| *Rhyacionia neomexicana* | Head Capsule | 52 | Jennings ESA 68:597 |
| Saturniidae | | | |
| *Dryocampa rubicunda* | Head Capsule | 48 | Allen ESA 69:857 |
| Tortricidae | | | |
| *Archips rosanus* | Head Capsule | 56 | AliNiazee ESA 70:391 |
| *A. semiferanus* | Head Capsule | 60 | Mumm ESA 70:641 |
| *Choristoneura occidentalis* | Head Capsule | 55 | Schmidt ESA 70:112 |
| *C. viridis* | Head Capsule | 50 | Schmidt ESA 70:112 |
| DIPTERA | | | |
| Chironomidae | | | |
| *Chironomus plumosus* | Head Capsule | 94 | Wilsenhoff ESA 59:465 |
| Culicidae | | | |
| *Orthopodymia alba* | Siphon Length | 97 | Eddleman ESA 61:1372 |
| *O. signifera* | Siphon Length | 137 | Eddleman ESA 61:1372 |
| Lonchaeidae | | | |
| *Lonchaea corticis* | Cephalopharyngeal Skeleton | 100 | Harman ESA 64:1221 |
| Otitidae | | | |
| *Eumetopiella rufipes* | Cephalopharyngeal Skeleton | 97 | Valley ESA 62:227 |
| Sarcophagidae | | | |
| *Tricholioproctia impatiens* | Length of Mouthhooks | 43 | Roberts ESA 69:158 |
| Sciaridae | | | |
| *Bradysia impatiens* | Head Capsule | 59 | Wikinson ESA 63:656 |
| Sciomyzidae | | | |
| *Hedria mixta* | Cephalopharyngeal Skeleton | 39 | Foote ESA 64:931 |
| *Pteromicra angustipennis* | Cephalopharyngeal Skeleton | 70 | Rozkosny ESA 63:1434 |
| *P. glabricula* | Cephalopharyngeal Skeleton | 58 | Rozkosny ESA 63:1434 |
| *P. pectorosa* | Cephalopharyngeal Skeleton | 74 | Rozkosny ESA 63:1434 |
| Tanypezidae | | | |
| *Tanypeza longimana* | Cephalopharyngeal Skeleton | 29 | Foote ESA 63:235 |
| HYMENOPTERA | | | |
| Braconidae | | | |
| *Microplitis fettiae* | Head Width | 133 | Puttler ESA 63:645 |
| Diprionidae | | | |
| *Neodiprion merkeli* | Head Capsule | 26 | Wilkinson ESA 64:241 |
| Ichneumonidae | | | |
| *Mesochorus nigripes* | Head Capsule Width | 35 | Coseglia ESA 70:695 |
| Pteromalidae | | | |
| *Dinarmus acutus* | Head Capsule | 104 | Leong ESA 68:943 |
| *Eupteromales americanus* | Head Capsule | 33 | Best ESA 68:1117 |
| Tenthredinidae | | | |
| *Schizocerella pilicornis* | Head Capsule | 30 | Gorske ESA 70:107 |

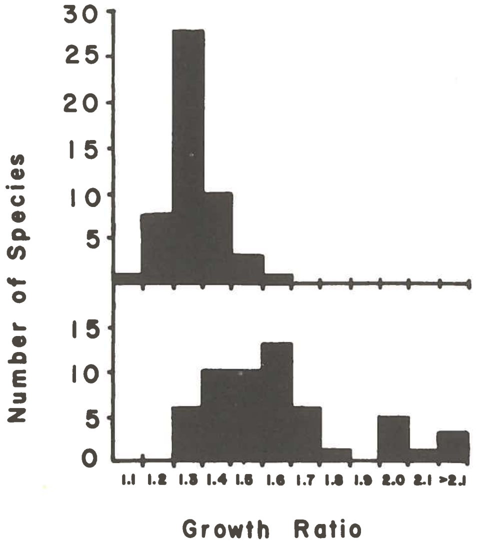


FIG. 1.—The growth ratios of hemimetabolous insects (upper portion of figure) and of holometabolous insects (lower portion of figure). A growth ratio class of 1.2 indicates a growth ratio of 1.11–1.20. The median growth ratio for hemimetabolous insects is 1.27 and for holometabolous insects is 1.52.


## Acknowledgements

I would like to thank Diane Wiernasz, David Tonkyn, Catherine Bristow, John Schneider, Douglas Green, Anthony Janetos, Robert May, John Endler, and Henry Horn for helpful comments, suggestions and for patiently listening to me expound on the differences between holometabolous and hemimetabolous insects.


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