CHARACTERIZATION OF THE LARVAL STAGES OF *Alphitobius diaperinus* (PANZER) (COLEOPTERA: TENEBRIONIDAE) USING HEAD CAPSULE WIDTH

FRANCISCO, O.[1] and PRADO, A. P. do[2]

[1]Programa de Pós-graduação em Parasitologia, Instituto de Biologia, Unicamp, C.P. 6109, CEP 13083-970, Campinas, SP, Brazil

[2]Departamento de Parasitologia, Instituto de Biologia, Unicamp, C.P. 6109, CEP 13083-970, Campinas, SP, Brazil

Correspondence to: Angelo Pires do Prado, Departamento de Parasitologia, Instituto de Biologia, Unicamp, C.P. 6109, CEP 13083-970, Campinas, SP, Brazil, e-mail: odpret@obelix.unicamp.br

Received October 5, 1999 – Accepted April 29, 2000 – Distributed February 28, 2001

(With 1 figure)

ABSTRACT

The mean width (n = 5) of the cephalic capsule instar of *Alphitobius diaperinus* was determined. The larvae were reared at 27ºC (± 0.1ºC). The result showed that *A. diaperinus* has eight larval instars. The head capsule of the 1st instar larvae measured $\bar{x}$ = 0.228 (SD = 0.0192) and the last instar larval measured $\bar{x}$ = 1.339 (SD = 0.0436). The developmental rate, determined by Dyar-Hutchinson's rule, was 1.29. These data may be useful for studies on phenology and age structure of *A. diaperinus* in the field.

Key words: lesser mealworm, larval instars, cephalic capsule, caged layer manure.

RESUMO

Caracterização dos estádios larvais de *Alphitobius diaperinus* (Panzer) (Coleoptera: Tenebrionidae) usando a largura da cápsula cefálica

O valor médio da largura da cápsula cefálica de *Alphitobius diaperinus* foi verificado de acordo com seus estádios larvais, sendo medidos cinco indivíduos para cada estádio. O experimento foi conduzido em temperatura constante de 27ºC (± 0,1ºC). Os resultados obtidos mostraram que as larvas atingem oito estádios, com média de 0,228 mm (SD = 0,0192) para a larva recém-eclodida, até 1,339 mm (SD = 0,0436) no 8º estádio. Também foi observado que o fator de crescimento das larvas corresponde à regra de Dyar-Hutchinson, apresentando média de 1,29 para razões de crescimento ao longo do desenvolvimento. Esses dados poderão ser utilizados em estudos de fenologia e estruturação etária de populações de *A. diaperinus* no campo.

Palavras-chave: cascudinho, ínstares larvais, cápsula cefálica, esterco de aves poedeiras.

INTRODUCTION

The synantropic beetle *Alphitobius diaperinus* (Panzer) (Coleoptera: Tenebrionidae), also vulgarly known in Brazil as "Cascudinho" (Lesser Mealworm), is a cosmopolitan plague commonly found in stored grains and mealy products. Both adults and larvae are also abundant in manure from henneries and poultry farms (MacCreary & Catts, 1954; Legner & Olton, 1970; Pfeiffer & Axtell, 1980; Avancini & Ueta, 1990; Bruno *et al.*, 1993; Lomônaco & Prado, 1994). This beetle is known as an important vector and transmitter of fowl diseases, such as the virus of leukosis or Marek's disease (Eidson *et al.*, 1965) and other viruses (Snedeker *et al.*, 1967; De las Casas *et al.*, 1976; Despins *et al.*, 1994; McAllister *et al.*, 1995), bacteries such as *Salmonella typhimurium* (Loeffler) and *Escherichia coli* (Migula) (De las Casas *et al.*, 1968, 1972; McAllister *et al.*, 1994, 1996), protozoans, like *Eimeria* sp. (Reyns *et al.*, 1983), fungi (Eugenio *et al.*, 1970; De las Casas *et al.*, 1972), helminths as the nematode *Subulura brumpti* Lopes-Neira (Karunamoorthy *et al.*, 1994) and cestodes (Case & Ackert, 1940; Elowni & Elbihari, 1979). Besides, both adults and larvae of *A. diaperinus* can cause intestinal obstruction in poultry for slaughter, since these birds lack **chitinasis** (Despins & Axtell, 1994, 1995). This fact may eventually cause microscopic lesions along the bird's intestinal wall, thus damaging this economic activity.

In countries of temperate climate *A. diaperinus* is considered a structural plague due to damage caused by its habit of, prior to **pupating**, perforating the plates of polyurethane and polyestyrene, materials utilized in the walls of sheds for thermal insulation (Spilman, 1968; Ichinose *et al.*, 1980; Le Torc'h & Letenneur, 1983; Vaughan *et al.*, 1984; Turner Jr., 1986; Despins *et al*., 1987, 1989; Arends, 1987; Geden & Axtell, 1987). During the populational peak of these beetles, in summer, it is a common to find, in the USA (North Carolina), infestations in poultry farms of between 10,000 and 20,000 individuals per m^2 (Arends, 1984). Estimated losses in egg production have been attributed to damage caused by *A diaperinus*, which may be more than 1.35/dozen eggs per year (Vaughan *et al.*, 1984). Thus, the presence of *A. diaperinus* may determine: a) loss in feeding efficiency (mainly during the cold months) due to gradual spoilage of thermal insulation; b) sharp loss while the shed in non-productive due to repairs; c) expenses with insulation maintenance; d) loss of energy; and e) depreciation of the building.

The development, growth and survival of the lesser mealworm according to humidity and temperature are reported in the papers of Wilson & Miner (1969), Preiss & Davidson (1971) and recently by Rueda & Axtell (1996).

Therefore this study has the objective of verifying the average size of each larval instar of *A. diaperinus* and thus contribute toward future population surveys of this plague beetle.

MATERIAL AND METHODS

To verify the average size each larval of *A. diaperinus*, the width of the cephalic capsules was measured on five specimens for each instar, obtained by means of daily individual observations as from the ova. The eggs were obtained from a mass breeding in a modified Arends' trap, as per Steinkraus & Cross (1993). The larva were bred individually in an environment of ground ration for mice contained in plastic flasks (2.5 cm diameter x 4.0 cm in height). The environmental humidity was maintained at a level of 40% (± 5%). The experiment was conducted at 27°C (± 0.1°C) and relative humidity of 70% (± 5%), in germination chamber. Each exuvia observed was considered an instar. The larvae obtained were killed in alcohol 70%, mounted between slide and minor slide in Canadian balsam, width "wedges" (small rectangles cut from glass slides) in order not to alter the dimension of cephalic capsule, which was then measured by means of micrometric ocular in stereoscopical microscope.

For each instar was considered the mean value of the width of cephalic capsules of the larvae. The data obtained were analysed by means of linear regression in the Minitab (1994) statistical program.

RESULTS AND DISCUSSION

The freshly-emerged larvae presented a milky colour. After the third instar a shade of brown is observed, which darkens as the larva develops. The pale colour tinge returns to that of first larva when in ecdysis, however it darkens again on the same day. In this experiment the larvae pupated after 8 larval instars, although Wilson & Miner (1969) observed 11 larval instars for *A. diaperinus* at a temperature of 15.5°C; however at temperature of 26.6°C, the same authors observed only a single individual (in 54 initial larvae) reaching the 9th stage. Several factors can influence the insects' growth. Lower temperatures may determine a reduction in width of the capsule of each larval instars, thus obviously increasing the number of instars in order for the insect to complete its development. Guppy (1969) noted a reduction in size of the cephalic capsules in larvae from *Pseudaletia unipuncta* Haworth (Lepidoptera: Noctuidae) when these were bred at lower temperatures. Maltais (1980) observed smaller dimensions in the cephalic capsule of *Pristiphora erichsonii* Hartig (Hymenoptera: Tenthredinidae) in observations made in New Brunswick, Canada, when compared, as per notes of Drooz (1955) in Minnesota, USA, suggesting that these differences may be determined by climatic conditions. Besides, other factors can influence the growth of the cephalic capsule of insects, such as endoparasitism (McGugan, 1954; Muldrew, 1967; Nealis, 1987).

Nutrition can also be determining factor in larval growth of insects (Scriber & Slansky Jr., 1981). Parra *et al.* (1977) noticed that 20% of *Spodoptera eridania* Cramer (Lepidoptera: Noctuidae) caterpillars bred in soybean leaves attained seven instars while those bred in cotton leaves reached a maximum of six instars. According to Slansky Jr. & Rodriguez (1987), the increase in number of larval instars can be caused by a nutritional inadequacy.

TABLE 1

Average width of cephalic capsule of *Alphitobius diaperinus* larvae and growth rate during larval development.

Larval instar	Width of cephalic capsule (mm) x (± SD)	Variation coefficient (VC)	Rate of growth
I	0.228 (± 0.0192)	0.0842	1.2631
II	0.288 (± 0.0225)	0.0781	1.2083
III	0.348 (± 0.0433)	0.1244	1.3735
IV	0.478 (± 0.0433)	0.1244	1.5083
V	0.721 (± 0.0216)	0.0299	1.4715
VI	1.061 (± 0.0536)	0.0505	1.1385
VII	1.208 (± 0.0769)	0.0603	1.1084
VIII	1.339 (± 0.0436)	0.0325	
Medium rate of growth			1.2904

The equation of a straight line for linear regression, done between the average of cephalic capsule measurements of five individuals for each instar, and the larval instars, was $y = -0.0818 + 0.176x$, with F equal to 118.52 ($p < 0.001$). The r^2 verified was 0.952. Pearson's correlation verified between the size average of each instar and the larval instars was $r^2 = 0.976$.

These results demonstrated that *A. diaperinus* larvae have a development following the model of linear regression (Fig. 1), the width of cephalic capsules evolved according to the constant of Dyar (1.4) has been used to determine the number of instars in various species, however there are many exceptions to it, since the progression factor may change in successive instars (Gaines & Campbell, 1935; Ludwig & Abercrombie, 1940; Richards & Davies, 1977; Wigglesworth, 1965; Parra & Haddad, 1989; Ambrosano *et al.*, 1997).

Caltagirone *et al.* (1983) observed that in *Amyelois transitella* (Walker) (Lepidoptera: Pyralidae) the width of cephalic capsules cannot be used directly to determine the instar of individuals because the measurements of two consecutive instars may superpose. In our experiment, observations were made only with exuviae. Our results showed, as per Fig. 1, that the inclination of the regression line was significant ($p < 0.05$), the progression of the line occurred within Dyar's constant. The diferential growth from one instar to the other suggests to us that this occurs due to the superposition of niches, for, the fewer the larval instars, the greater will be the competition for food items of a given dimension studies in bird populations (MacArthur, 1958; Orians & Horn, 1969; MacArthur, 1971; Cody, 1974; Diamond, 1975; Hespenheide, 1975), in rodent populations (Brown, 1975; Rosenzweig *et al.*, 1975; Mares & Williams, 1977), in lizard populations (Schoener & Gorman, 1968; Pianka, 1973; Schoener, 1975) and in fish populations (Zaret & Rand, 1971; Roughgarden, 1974; Werner, 1977), have suggested that competition exerts a major part regarding structure and function within the communities. These studies have shown that that the differential utilization of micro-habitat and food (size and/or taxons) were the factors that most influenced the minimization of competition and yet contributing to establish coexistence.

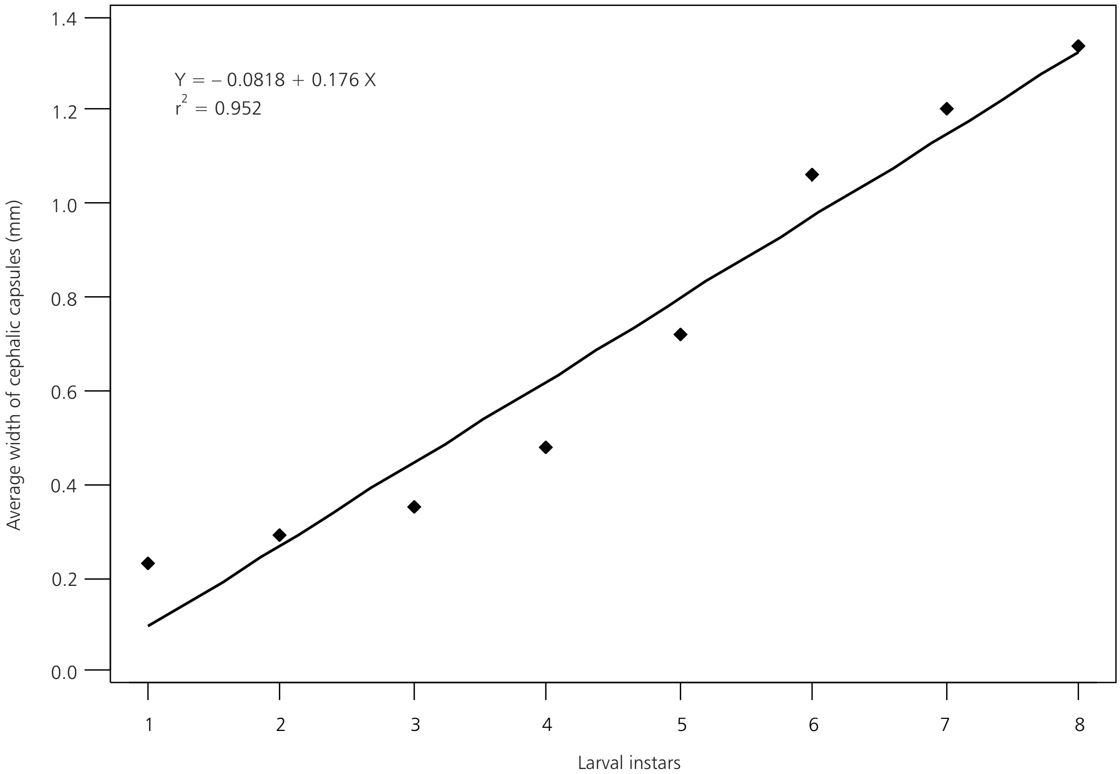

Fig. 1 — Regression between the average width of cephalic capsules and larval instars of *Alphitobius diaperinus*.

The sizes of prey or food items are related to the size of the predator's body and/or size of buccal apparatus. Hutchinson (1959) states that this way the size of the food resource (prey) in a community of predators could influence the number of niches, if members possessed morphological differences. The same author observed furthermore that sympatric species of a given genera tend to differ in the size of their feeding structures by a factor around 1.28, close to Dyar's constant. For Hutchinson (1959) this average represents this the lower limit of similatity between competing species. Horn & May (1977) proposed that Dyar's constant be denominated Dyar-Hutchinson's rule.

Maiorana (1978) postulated that this displacement between sizes of species or age classes diverges according to a relatively constant percentage, irrespective of absolute body size, wich is because they tend to show a relative constant originating from their morphological variability. If ecological separation according to size requires a certain minimum limit as to superposition of frequencies of two species or age classes, and if these tend to show the same degree of morphological variability, then their proportional divergence in average size will likewise be relatively constant.

Simpson *et al.* (1960) observed that the variation coefficient tends to remain between four and ten, more frequently between five and six. For two species in which the size of feeding structure of the larger one is 1.28 times the size of smaller one, VC of 5.5 produces a superposition of 1% or 2% in its distribution of frequency.

The results obtained in this study may be of great use in future surveys of etarian structuring in natural populations of *Alphitobius diaperinus*.

Acknowledgments – This study is part of the MSc. Thesis of the first author, and was supported by the Universidade Estadual de Campinas. We wish to thanks Fundação de Amparo à Pesquisa do Estado de São Paulo (Fapesp), whose assistence we gratefully acknowledge.

REFERENCES

AMBROSANO, G. M. B., IGUE, T. & LOURENÇÃO, A. L., 1997, Determinação do número de ínstares de insetos utilizando modelo de regressão segmentado. *An. Soc. Entom. Brasil., 26*: 371-374.

ARENDS, J. J., 1987, Control, management of the litter beetle. *Poult. Dig.* (April), 172-176.

AVANCINI, R. M. P. & UETA, M. T., 1990, Manure breeding insects (Diptera and Coleoptera) responsible for cestoidosis in caged layer hens. *J. Appl. Ent., 110*: 307-312.

BROWN, J. H., 1975, Geographical ecology of desert rodents. pp. 315-341. *In*: M. Cody & J. Diamond (eds.), *Ecology and evolution of communities*. Harvard University Press, Cambridge.

BRUNO, T. V., GUIMARÃES, J. H., SANTOS, A. M. M. & TUCCI, E. C., 1993, Moscas sinantrópicas (Diptera) e seus predadores que se criam em esterco de aves poedeiras confinadas, no Estado de São Paulo, Brasil. *Rev. Brasil. Ent., 37*: 577-590.

CASE, A. A. & ACKERT, J. E., 1940, New intermediate hosts of fowl cestodes. *Trans. Kans. Acad. Sci., 43*: 393-394.

CODY, M. L., 1974, Competition and the structure of bird communities. Monographs in population Biology. Princeton University Press, New Jersey.

DE LAS CASAS, E., POMEROY, B. S. & HAREIN, P. K., 1968, Infection and quantitative recovery of *Salmonella typhimurium* and *Escherichia coli* from within the lesser mealworm (*Alphitobius diaperinus*). *Poult. Sci., 47*: 1871-1875.

DE LAS CASAS, E., HAREIN, P. K. & POMEROY, B. S., 1972, Bacteria and fungi within the mealworm collected from poultry brooder houses. *Environ. Ent., 1*: 27-30.

DE LAS CASAS, E., HAREIN, P. K., DESHMUKH, D. R. & POMEROY, B. S., 1976, Relationship between the lesser mealworm, foul pox, and Newcastle disease virus in poultry. *J. Econ. Ent., 69*: 775-779.

DESPINS, J. L., TURNER JR., E. C. & RUSZLER, P. R., 1987, Construction profiles of high rise caged layer houses in association with insulation damage caused by the lesser mealworm, *Alphitobius diaperinus* in Virginia. *Poult. Sci., 66*: 243-250.

DESPINS, J. L., TURNER JR., E. C. & RUSZLER, P. R., 1989, Effects of poultry manure moisture and poultry house construction materials on movements of the lesser mealworm, *Alphitobius diaperinus* (Panzer) (Coleoptera: Tenebrionidae), a structural insect pest in high rise layer houses. *Poult. Sci., 68*: 1326-1331.

DESPINS, J. L., AXTELL, R. C., RIVES, D. V., GUY, J. S. & FICKEN, M. D., 1994, Transmission of enteric pathogens of turkey by darkling beetle larvae (*Alphitobius diaperinus). J. Appl. Poult. Res., 3*: 61-65.

DESPINS, J. L. & AXTELL, R. C., 1994, Feeding behavior and growth of turkey poults fed larvae of the darkling beetle, *Alphitobius diaperinus. Poult. Sci., 73*: 1526-1533.

DESPINS, J. L. & AXTELL, R. C., 1995, Feeding behavior and growth of broiler chicks fed larvae of the darkling beetle, *Alphitobius diaperinus. Poult. Sci., 74*: 331-336.

DIAMOND, J. M., 1975, Assembly of species communities. 342-444. *In*: M. Cody & J. Diamond (eds.), *Ecology and evolution of communities*. Harv. Univ. Press, Massachusetts.

DROOZ, A. T., 1955, Head capsule measurements of Minnesota larch sawflies. *U. S. For. Serv. Lake States Forest Exp. Stn. Tech.* Note 428.

DYAR, H. G., 1890, The number of moults of Lepidopterous larvae. *Psyche., 5*: 420-422.

EIDSON, C. S., SCHMITTLE, S. C., GOODE, R. B. & LAL, J. B., 1965, The role of darkling beetle, *Alphitobius diaperinus* in transmission of acute leucosis in chickens. *Poult. Sci., 44*: 1366-1367.

ELOWNI, E. E. & ELBIHARI, S., 1979, Natural and experimental infection on the beetle, *Alphitobius diaperinus* (Coleoptera: Tenebrionidae) with *Choanotaenia infundibulum* and others chickens tapeworms. *Vet. Sci. Commun., 3*: 171-173.

EUGENIO, C., DE LAS CASAS, E., HAREIN, P. K. & MIROCHIA, C. J., 1970, Detection of the mycotoxin F-2 in the confused flour beetle and lesser mealworm. *J. Econ. Ent., 63*: 412-415.

GAINES, J. C. & CAMPBELL, F. L., 1935, Dyar's rule as related to the number of instars of the corn ear worm, *Heliothis obsoleta* (Fab.), collected in the field. *Ann. Entom. Soc. Am., 28*: 445-461.

GEDEN, C. & AXTELL, R. C., 1987, Factors affecting climbing and tunneling behavior of the lesser mealworm (Coleoptera: Tenebrionidae). *J. Econ. Ent*., *80*: 1197-1203.

GUPPY, J. C., 1969, Some effects of temperature on immature stages of armyworm, *Pseudaletia unipuncta* (Lepidoptera: Noctuidae), under controlled conditions. *Can. Ent.*, *101*: 1320-1327.

HESPENHEIDE, H. A., 1975, Prey characteristics and predator niche width. pp. 158-180. *In*: M. Cody & J. Diamond (eds.), *Ecology and evolution of communities*. Harvard Univ. Press, Cambridge.

HORN, H. S. & MAY, R. M., 1977, Limits to similarity among coexisting competitors. *Nature, 270*: 660-661.

HUTCHINSON, G. E., 1959, Homage to Santa Rosalia, or why are there so many kinds of animals? *Am. Nat., 93*: 145-159.

ICHINOSE, T., SHIBAZAKI, S. O. & OHTA, R., 1980, Studies on the biology and mode of the infestation of the tenebrionidae beetles, *Alphitobius diaperinus* Panzer, harmful to broiler – chicken houses. *Jour. Jap. Appl. Ent., 24*: 167-174.

KARUNAMOORTHY, G., CHELLAPPA, D. J. & ANANDARI, R., 1994, The life history of *Subulura brumpti* in the beetle *Alphitobius diaperinus*. *Indian Vet. Jour., 71*(1): 12-15.

LEGNER, E. F. & OLTON, G. S., 1970, The biological method and integrated control of the house and stable flies in California. *Calif. Agric., 22*: 2-4.

LE TORC'H, J. M. & LETENNEUR, R., 1983, Essais en laboratorie de resistence de differents isolants thermiques aux perforations du tenebrion, *Alphitobius diaperinus* Panzer (Coleoptera: Tenebrionidae). *C. R. Sci. Acad. Agric. Fran*., *6*: 188-200.

LOMÔNACO, C. & PRADO, A. P., 1994, Estrutura comunitária e dinâmica populacional da fauna de dípteros e seus inimigos naturais em granjas avícolas. *An. Soc. Ent. Brasil*., *23*(1): 71-80.

LUDWIG, D. & ABERCROMBIE, W. F., 1940, The growth of the head capsule of the Japanese beetle larva. *Ann. Entom. Soc. Am., 33*: 385-390.

MACARTHUR, R. H., 1958, Population ecology of some warblers of northeastern coniferous forests. *Ecology, 39*: 599-619.

MACARTHUR, R. H., 1971, Patterns of terrestrial bird communities. Vol. 1, pp. 189-221. *In*: D. S. Farner & J. R. King (eds.), *Avian Biology*. Academic Press, New York.

MACCREARY, D. & CATTS, E. P., 1954, Ectoparasites of Delaware poultry including a study of litter fauna. *Delaware Agric. Exp. Stn. Bull*., *307*: 1-22.

MAIORANA, V. C., 1978, An explanation of ecological and developmental constants. *Nature, 273*: 375-377.

MALTAIS, P., 1980, Head capsule measurements of the larch sawfly, *Pristiphora erichsonii* (Hymenoptera: Tenthredinidae) in Kouchibouguac National Park, New Brunswick. *Can. Ent., 112*: 111-112.

MARES, M. A. & WILLIAMS, D., 1977, Experimental support for food particle size resource allocation in heteromyid rodents. *Ecology*, *58*: 1186-1190.

MCALLISTER, J. C., STEELMAN, C. D. & SKEELES, J. K., 1994, Reservoir competence of Lesser Mealworm (Coleoptera: Tenebrionidae) for *Salmonella typhimurium* (Eubacteriales: Enterobacteriaceae). *J. Med. Ent*., *31*: 369-372.

MCALLISTER, J. C., STEELMAN, C. D., NEWBERRY, L. A. & SKEELES, J. K., 1995, Isolation of infectious bursal disease virus from the Lesser Mealworm, *Alphitobius diaperinus* (Panzer). *Poult. Sci*., *74*: 45-49.

MCALLISTER, J. C., STEELMAN, C. D., SKEELES, J. K., NEWBERRY, L. A. & GBUR, E. E., 1996, Reservoir competence of *Alphitobius diaperinus* (Coleoptera: Tenebrionidae) for *Escherichia coli* (Eubacteriales: Enterobacteriaceae). *J. Med. Ent*., *33*: 983-987.

MCGUGAN, B. M., 1954, Needle-mining and larval instars of the spruce budworm. *Can. Ent*., *86*: 439-454.

MINITAB, 1994, Minitab user's guide. Windows microcomputer version, release 10.1. Enterprise Drive, State College, PA.

MULDREW, J. A., 1967, Biology and initial dispersal of *Olesicampe (Holocremmus)* sp. near *nemoratum* (Hymenoptera: Ichneumonidae), a parasite of larch sawfly recently established in Manitoba. *Can. Ent*., *99*: 312-321.

NEALIS, V., 1987, The number of instars in jack pine budworm, *Choristoneura pinus pinus* Free (Lepdoptera: Tortricidae), and the effect of parasitism on head capsule width and development time. *Can. Ent., 119*: 773-777.

ORIANS, G. H. & HORN, H. S., 1969, Overlap in foods of four species of blackbirds in the patholes of central Washington. *Ecology, 50*: 1012-1030.

PARRA, J. R. P., PRECETTI, A. A. C. M. & KASTEN JR., P., 1977, Aspectos biológicos de *Spodoptera eridania* (Cramer, 1782) (Lepdoptera: Noctuidae) em soja e algodoeiro. *An. Soc. Entomol. Brasil., 6*: 147-155.

PARRA, J. R. P. & HADDAD, M. L., 1989, *Determinação do número de ínstares de insetos*. Fundação de Estudos Agrários Luiz de Queiroz, Piracicaba, 49p.

PFEIFFER, D. G. & AXTELL, R. C., 1980, Coleoptera of poultry manure in caged-layer houses in North Carolina. *Environ. Entomol*., *9*: 21-28.

PIANKA, E. R., 1973, The structure of lizard communities. *Ann. Rev. Ecol. Syst., 4*: 53-74.

PREISS, F. J. & DAVIDSON, J. A., 1971, Adult longevity, pre-oviposition period and fecundity of *Alphitobius diaperinus* in the laboratory (Coleoptera: Tenebrionidae). *J. Georg. Entomol. Soc., 6*: 105-109.

REYNS, P. S., MACDOUGALD, L. R. & MATHIS, G. F., 1983, Survival of coccidia in poultry litter and reservoirs of infections. *Avian dis*., *27*: 464-473.

RICHARDS, O. W. & DAVIES, R. G., 1977, *Imm's General Textbook of Entomology*. Vol. 1, 10th ed. Chapman & Hall, London, 118p.

ROSENZWEIG, M. L., SMIGEL, B. & KRAFT, A., 1975, Patterns of food, space and diversity. pp. 241-268. *In*: P. R. Prakash and P. K. Ghosh (eds.), *Rodents in desert environments*. Junk, The Hague, Netherlands.

ROUGHGARDEN, J., 1974, Species packing and the competition function with illustrations from coral reef fish. *Theor. Pop. Biol*., *5*: 163-186.

RUEDA, L. M. & AXTELL, R. C., 1996, Temperature-dependent development and survival of the lesser mealworm, *Alphitobius diaperinus*. *Med. Vet. Entomol*., *10*: 80-86.

SCHOENER, T. W., 1975, Presence and absence of habitat shift in some widespread lizard species. *Ecol. Monog., 20*: 233-258.

SCHOENER, T. W. & GORMAN, G. C., 1968, Some niche differences among three species of lesser Antillean anoles. *Ecology*, *49*: 819-830.

SCRIBER, J. M. & SLANSKY JR., F., 1981, The nutritional ecology of immature insects. *Ann. Rev. Entomol*., *26*: 183-211.

SIMPSON, G. G., ROE, A. & LEWONTIN, R. C., 1960, Quantitative Zoology. 2nd ed. Harcourt, Brace & Word (eds.), New York.

SLANSKY JR., F. & RODRIGUEZ, J. G., 1987, Nutritional ecology of insects, mites and invertebrates: an overview. pp. 1-69. *In*: F. Slansky Jr. & J. G. Rodriguez (eds.), *Nutritional ecology of insects, mites, spiders and related invertebrates*. John Wiley & Sons, New York.

SNEDEKER, C., WILLS, F. K. & MOULTHROP, I. M., 1967, Some studies on the infectious bursal agent. *Avian Dis., 11*: 519-528.

SPILMAN, T. J., 1968, (*in* Minutes of meeting: the lesser mealworm, *Alphitobius diaperinus*). *Proc. Ento. Soc. Wash*., *70*: 294-295.

STEINKRAUS, D. C. & CROSS, A., 1993, Description and life history of *Acarophenax mahunkai*, new specie (Acari, Tarsonemina: Acarophenacidae) an egg parasite of the lesser mealworm (Coleoptera: Tenebrionidae). *Ann. Entomol. Soc. Amer., 86*: 239-249.

TURNER JR., E. C., 1986, Structural and litter pests. *Poultry Sci., 65*: 644-648.

VAUGHAN, J. A., TURNER JR., E. C. & RUSZLER, P. L., 1984, Infestation and damage of poultry house insulation by the lesser mealworm, *Alphitobius diaperinus. Poult. Sci., 63*: 1094-1100.

WERNER, E. E., 1977, Species packing and niche complementarity in three sunfishes. *Amer. Nat., 111*: 553-578.

WIGGLESWORTH, V. B., 1965, The Principles of Insect Physiology. 6th ed. Methuen & Co. Ltd., London, 741p.

WILSON, T. H. & MINER, F. D., 1969, Influence of temperature on development of the Lesser Mealworm, *Alphitobius diaperinus* (Coleoptera: Tenebrionidae). *J. Kansas Entomol. Soc., 42*: 294-303.

ZARET, T. M. & RAND, A. S., 1971, Competition in tropical stream fishes: support for the competitive exclusion principle. *Ecology, 52*: 336-342.