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EFFECT OF PARASITOID DENSITY ON THE FUNCTIONAL RESPONSE AND SEX RATIO OF A CYNIPOID HYPERPARASITOID *ALLOXYSTA PLEURALIS* [*HYM. : ALLOXYSTIDAE*]

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Experiment where variable densities (1, 2, 5, 10, 25, 50, 100 and 150) of the parasitoid (5-7 d postparasitised aphids (*Aphis craccivora* Koch) — parasitised by aphidiid parasitoid *Trioxys indicus* Subba Rao & Sharma) were exposed to individual hyperparasitoid *Alloxysta pleuralis* (Cameron) indicated following: (1) with increase of initial host (primary parasitoid) densities the number of hosts hyperparasitised increases sigmoidally reaching to a plateau at 50 host similar to the *type 3* functional response of Holling; the curve was described by a logistic equation [$N_{hyp} = 44.0/(1 + \exp(4.0\text{-}0.16\,N_p))$], (2) greater host mortality was recorded at lower initial host densities ($\leqslant 50$); (3) the area of discovery of the hyperparasitoid is inversely density-dependent at higher host densities ($\geqslant 25$); and (4) the variation in host number has no significant influence on the sex ratio of F_1 offspring of the hyperparasitoid which ranges between 0.56-0.67. The implications of these responses of the hyperparasitoid *A. pleuralis* are discussed.

KEY-WORDS: *Alloxysta pleuralis, Trioxys indicus, Aphis craccivora,* functional response, area of discovery, sex ratio.

Alloxysta pleuralis (Cameron) (= *A. gautieri* Kieffer) is reported to be an obligatory monophagous hyperparasitoid of an aphidiid parasitoid *Trioxys angelicae* Haliday (*Hym.: Aphidiidae*) through the aphids *Aphis craccivora* Koch and *A. pomi* de Geer (*Hem.: Aphididae*) in Europe (**Evenhuis**, 1972). It was first reported from India as a hyperparasitoid of *T. indicus* Subba Rao & Sharma (**Singh & Sinha**, 1979) and very recently its biology (**Singh & Srivastava**, 1987a) and host selection behaviour (**Singh & Srivastava**, 1987b, c) have been studied. Very few attempts have been made to assess the ecological impact of obligate hyperparasitoids and to analyse this numerically (**Hassell & Waage**, 1984). The mathematical models indicate that although an obligate hyperparasitoid contributes to the complexity of the food web and may add stability it also raises the host's equilibrium and increases pest abundance (**Sullivan**, 1987a). Therefore, obligate hyperparasitoids are considered to be detrimental in biological control programme (**Bennett**, 1981; **Sullivan**, 1987a, b). In the pressent contribution we have discussed the density responsiveness behaviour of *A. pleuralis* and therefore, its functional response, and the efficacy (measured as Nicholsonian area of discovery) have been observed.

In the past, **Fisher** (1958) and **Hartl & Brown** (1970) have postulated 0.5 sex ratio (proportion of female) of the offspring of sexually reproducing organisms and arrhenotokous insects respectively which was based on the assumption that natural selection acts to ensure equal parental investment in the production of either sex. However, alteration of this ratio had been observed as a function of environmental changes particularly host size (**Charnov** *et al.*, 1981) and host density (**Legner,** 1967 ; **Sinha & Singh,** 1979) in case of some parasitic wasps. No information is available with cynipoid hyperparasitoids of aphidiid wasps regarding the sex ratio and factors influencing it. In this article we have attempted to test whether host density can alter the sex ratio of *A. pleuralis* or not.

MATERIALS AND METHODS

The procurement and the culture of all the 3 insects involved, *viz.*, the aphid (*A. craccivora*), the parasitoid (*T. indicus*), and the hyperparasitoid (*A. pleuralis*) have already been described by the authors (**Singh & Srivastava,** 1987a). The aphid was reared on the host plant *Cajanus cajan* Millsp. (a legume cultivated in India for pulse). Five to 7 days postparasitised aphids (5-7 d PPA) were utilised as hosts for *A. pleuralis* as these stages were found more vulnerable to hyperparasitoid's attack (**Singh & Srivastava,** 1987a). One day aged, experienced, fully fed with honey and mated female hyperparasitoids were used for the experiments.

For the study of functional response varying densities of host, *viz.*, 1, 2, 5, 10, 25, 50, 100 and 150 were put separately on fresh twigs of the host plant containing 1-5 leaves. The cut end of each twig was placed dipped in water-filled 60 ml vial. Such twigs were kept in jars (10 × 30 cm). Individual hyperparasitoid was introduced in each jar. The openings were closed with muslin cloths tightened with rubber bands. After 6 h, the twigs were withdrawn from the jars and were put separately in small wooden insectaries (20 × 20 × 20 cm). Water in the vials was changed once after 3 days. After the mummification (4-5 d after hyperparasitisation), the mummies along with some part of the host plant leaf were put in market mummy holding tubes (3 × 10 cm). One end of the tube was closed with cork having a tube (0.5 × 3 cm) with synthetic sponge moistened with distilled water and the other end with fine nylon mesh. The emerging parasitoids and hyperparasitoids were sexed and recorded. Ten series of the experiment with new females were performed at 22-25 °C and 60-75 % R.H.

RESULTS

The number of emerging hyperparasitoids increased sigmoidally with increase of initial number of hosts put in reaching to a plateau at 50 hosts (fig. 1). The relationship may be explained by the logistic curve, $N_{hyp} = 44.0/[1 + \exp(4.0\text{-}0.16\, N_p)]$. Greater host mortality was recorded at lower host densities ($\leqslant$ 50).

The area of discovery is the numerical value of the host searching efficiency of the individual hyperparasitoid (parasitoid or predator) (**Nicholson & Bailey,** 1935). Figure 2 illustrates the relationship between the area of discovery of the hyperparasitoid *A. pleuralis* and host density (5-7 d PPA). At lower host densities ($\leqslant$ 5), no surviving host was recorded and therefore, the numerical value of area of discovery approach infinity (the area of discovery (a) is usually calculated by the formula (**Hassell,** 1971) :

$$a = \frac{1}{P} \log_e [N_i/N_f]$$

where P is the density of entomophage (hyperparasitoid or parasitoid or predator) searching for hosts (or prey) ; N_i and N_f are initial and the final surviving host densities. The area of discovery of the hyperparasitoid showed a convex curve within the range of host density between 1-50 taking a maximum value at the density of 25 (fig. 2). However, at a higher host density, *i.e.*, 100-150, the area of discovery expected to stablise at a certain value.

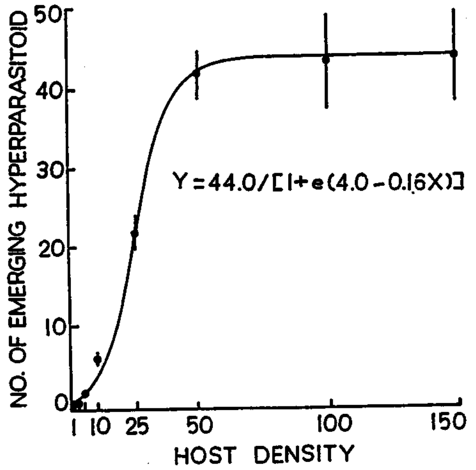

Fig. 1. Relationship between number of the hyperparasitoid's F_1 offspring at different initial densities of the host *Trioxys indicus* hyperparasitised by a single female *Alloxysta pleuralis.*

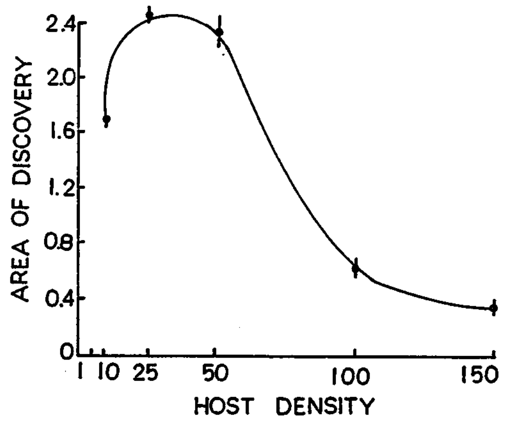

Fig. 2. Relationship between Nicholsonian area of discovery of the hyperparasitoid *Alloxysta pleuralis* at different initial densities of host *Trioxys indicus.*

The indirect mortality of the hosts (from which none of the emergents egressed out) decreased steeply up to 25 hosts and gradually thereafter (fig. 3).

The variation in host number has no significant influence on the sex ratio ($\bar{p}$ = proportion of female) of F_1 offspring of the hyperparasitoid. It ranges between 0.56-0.67 (fig. 4).

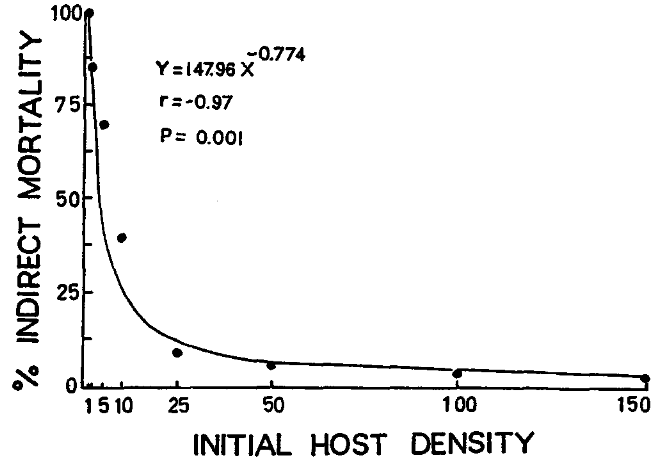

Fig. 3. Relationship between indirect mortality of the host *Trioxys indicus* after exposure to the hyperparasitoid *Alloxysta pleuralis* at its varying initial densities.

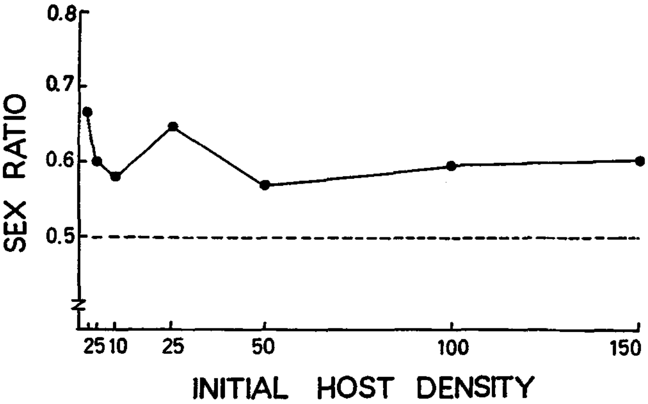

Fig. 4. Relationship between sex ratio of the hyperparasitoid's F_1 offspring emerging from different initial densities of host *Trioxys indicus* hyperparasitised by a single female *Alloxysta pleuralis*.

DISCUSSION

It is often stated that the models for the functional response of predators can be extended to parasitoids (or hyperparasitoids). Several models since **Holling** (1959) have been proposed by workers in the past (**Rogers,** 1972 ; **Lenteren & Bakker,** 1976 ; **Hassel** *et al.*, 1977 ; **Hassell,** 1979 ; **Dransfield,** 1979 ; **Collins** *et al.*, 1981 ; **Arditi,** 1983) to describe the density responsiveness behaviour of the entomophagous insects assuming different factors as constant. For instance, Rogers' "random model" assumes random search and equal handling time for healthy and parasitised hosts, whereas different handling times were assumed for each king of host by **Arditi** (1983). However, none of the models unifies the functional response of the entomophages. For simplicity, we have just explained the functional response of *A. pleuralis* utilising a logistic curve (fig. 1) which corresponds to the *type 3* of **Holling** (1959), an uncommon response shown by the parasitic wasps (**Murdoch & Oaten,** 1975 ; **Lenteren & Bakker,** 1976 ; **Hassell** *et al.*, 1977 ; **Collins** *et al.*, 1981 ; **Pandey** *et al.*, 1982). Similar information is only available for a single cynipoid hyperparasitoid *A. brassicae* (Ashmead) which follow the *type 2* functional response of **Holling** (**Chua,** 1979). The value of constant *K* (upper asymptote) is 44.0 (fig. 1) implying the upper limit of egg laying capacity of the female within 6 h in spite of the availability of large number of host. However, in the fields, the hyperparasitoid might not be able to hyperparasitise even 44.0 hosts within 6 h because the time consumed by healthy aphids (available simultaneously) during host exploration will certainly tend to lessen the frequency of real hosts attacked. The egg laying capacity of its host *T. indicus* is 51.4 within 15 min (**Pandey** *et al.*, 1982), therefore, *A. pleuralis* does not seem to be effective in preventing the population growth pattern of *T. indicus* which in turn regulates the aphid population. It also confirms the field records reported earlier (**Singh & Sinha,** 1980). Hence, as far as, functional response alone is concerned, *A. pleuralis* does not impose any threat for the establishment of *T. indicus* against *A. craccivora.*

Figure 2 illustrates that the area of discovery of *A. pleuralis* is host inverse density-dependent at higher host densities ($\geqslant 25$). Actually the criteria for direct density dependence are that the regression of $\log_{10}$ initial host density on $\log_{10}$ survivors from hyperparasitism (= parasitism) and vice versa should produce slopes significantly different from $b = 1$ and both regression lines should lie on the same side of slope $b = 1$ (**Varley & Gradwell,** 1968). As indicated in figure 5, the regression of $\log_{10}$ initial hosts on $\log_{10}$ survivors from attack ($b = 0.53$; $r^2 = 0.83$) and $\log_{10}$ survivors on $\log_{10}$ initial hosts ($b = 1.55$; $r^2 = 0.83$) clearly met these criteria, thus establishing a direct density dependent mode of action for hyperparasitism.

In general higher host densities have an inverse effect on searching efficiency of the entomophages (**Fernando & Hassell,** 1980). Possibly the time available for searching the host is limiting (**Hassell & Rogers,** 1972). Since the hyperparasitoids had plenty of time (6 h) to oviposit, this factor seems not to be a limiting one. Actually the rate of oviposition by the hyperparasitoid *A. pleuralis* is lower, 0.12 egg/min (44.0 eggs in 6 h), than the parasitoid *T. indicus,* 3.4 egg/min (51.4 eggs in 15 min, **Pandey** *et al.*, 1982) because of greater handling time of hyperparasitoid than the parasitoid.

Higher proportion of indirect mortality of the host at lower host densities (fig. 3) may be explained as follows : At lower host densities ($\leqslant 10$), the hosts are repeatedly explored by the ovipositor of the hyperparasitoid, consequently several eggs are laid inside a parasitoid larva within the aphid. In general hyperparasitoids are less host discriminatory than the parasitoids in host acceptance (**Sullivan,** 1972 ; **Singh & Srivastava,** 1988). All the eggs hatch into 1st stage larvae. Since the host can support the development of only one hyperparasitoid's larva, the supernumerary larvae compel to die before the 2nd moult. However, during the period of their survival they consume considerable amount of food (host content) which ultimately might be leading to death of surviving larva due to nutritional deficiency. Also, by repeatedly jabbing the host's body by the ovipositor, the female hyperparasitoid seriously injures the hosts which may cause the mortality of the hosts before the initial development of the hyperparasitoid. Similar results are known among parasitoids (**Bakker** *et al.*, 1985).

The insignificant variations in the sex ratio of F_1 offspring of *A. pleuralis* with increase of initial host densities exposed for attack (fig. 4) indicates that the hyperparasitoid's ability of differential placement of haplo-diploid eggs (**Flanders,** 1967) is not affected by variation in host number. However, more than predicted value ($\geqslant 0.5$) was maintained throughout.

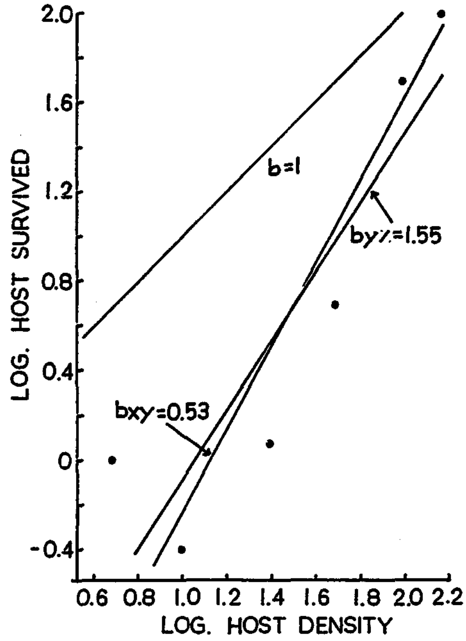

Fig. 5. Relationship between $\log_{10}$ survivor hosts *Trioxys indicus* from attack by the hyperparasitoid *Alloxysta pleuralis* at its different $\log_{10}$ initial densities.

The sex ratio is also influenced by the mechanism by which the sex is determined. In hyperparasitic cynipoids the sex determination is yet to be investigated.

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RÉSUMÉ

Effet de la densité du parasitoïde sur la réponse fonctionnelle et le sex-ratio d'un hyperparasite cynipoïde *Alloxysta pleuralis* [*Hym. : Alloxystidae*]

L'expérience où des densités variables (1, 2, 5, 10, 25, 50, 100 et 150) du parasitoïde (des *Aphis craccivora* KOCH parasités depuis 5 à 7 jours par *Trioxys indicus* SUBBA RAO & SHARMA) furent exposées à l'hyperparasitoïde *Alloxysta pleuralis* (CAMERON) donnait les résultats suivants (1) avec un accroissement des densités de l'hôte initial (parasitoïde primaire) le nombre d'hôtes hyperparasités augmente selon une sigmoïde atteignant son plafond pour une densité de 50 hôtes, ce qui correspond à la réponse fonctionnelle du type 3 de HOLLING ; la courbe avait pour expression l'équation $N_{hyp} = 44{,}0/[1 + e\ (4{,}0\text{-}0{,}16\ N_p)]$; (2) une mortalité hôte plus forte était enregistrée aux densités de l'hôte initial plus faibles ($\leqslant 50$) ; (3) l'aire de découverte de l'hyperparasitoïde est inversément dépendant de la densité aux densités hôte plus fortes ($\geqslant 25$) ; et (4) la variation dans le nombre d'hôtes n'a pas d'influence significative sur le sex-ratio de la descendance F_1 de l'hyperparasitoïde qui s'établit entre 0,56-0,67. Les implications de ces réponses sur l'hyperparasitoïde *A. pleuralis* sont discutées.

MOTS CLÉS : *Alloxysta pleuralis, Trioxys indicus, Aphis craccivora,* réponse fonctionnelle, aire de découverte, sex-ratio.

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REFERENCES

Arditi, R. — 1983. A unifield model of the functional response of predators and parasitoids. — *J. Anim. Ecol.,* 52, 293-303.

Bakker, K., Alphen, J. J. M. van, Batenburg, F. H. W. van, Hoeven, N. vander, Nell, H. W., Strien-van Liempt, W. T. F. H. van & Turlings, T. C. J. — 1985. The function of host discrimination and superparasitisation in parasitoids. — *Oecologia,* 67, 572-576.

Bennett, F. D. — 1981. Hyperparasitism in the practice of biological control, pp. 43-49. In : The Role of Hyperparasitism in Biological Control : A Symposium (**D. Rosen,** ed.). — *Div. Agric. Sci. Univ. Calif.,* Berkeley, California.

Charnov, E. L., Hartogh, R. L., Los-den, Jones, W. T. & Assem, J. vanden. — 1981. Sex ratio evolution in a variable environment. — *Nature,* 289, 27-33.

Chua, T. H. — 1979. A comparison of searching efficiencies of a parasite and a hyperparasite. — *Res. Popul. Ecol.,* 20, 179-187.

Collins, M. D., Wart, S. A. & Dixon, A. F. G. — 1981. Handling time and the functional response of *Aphelinus thompsoni,* a predator and parasite of the aphid *Drepanosiphum plantanoidis.* — *J. Anim. Ecol.,* 50, 479-487.

Dransfield, R. D. — 1979. Aspects of host-parasitoid introductions of two aphid parasitoids *Aphidius urticae* Haliday and *Aphidius uzbekistanicus* Luzhetzki [*Hym. : Aphidiidae*]. — *Ecol. Entomol.,* 4, 307-316.

Evenhuis, H. H. — 1972. Studies on cynipoid *Alloxystinae.* 2. The identity of some species associated with aphids of economic importance. — *Entomol. Ber.,* 32, 210-217.

Fernando, M. H. J. P. & Hassell, M. P. — 1980. Predator-prey response in an acarina system. — *Res. Popul. Ecol.,* 22, 301-322.

Fisher, R. A. — 1958. The Genetical Theory of Natural Selection. — *Dover Publ.,* New York.

Flanders, S. E. — 1967. Deviate-ontogenies in the aphelinid male [*Hymenoptera*] associated with the ovipositional behaviour of the parental female. — *Entomophaga,* 12, 415-427.

Hartl, D. L. & Brown, S. W. — 1970. The origin of male haploid genetic systems and their expected sex ratio. — *Theor. Popul. Biol.,* 1, 165-190.

Hassell, M. P. — 1971. Mutual interference between searching insect parasites. — *J. Anim. Ecol.,* 40, 473-486.

Hassell, M. P. — 1979. The dynamics of predator-prey interactions, polyphagous predators, competing predators and hyperparasitoids. — *Br. Ecol. Soc. Symp.,* 20, 283-306.

Hassell, M. P. & Rogers, D. J. — 1972. Insect parasite response in the development of population models. — *J. Anim. Ecol.,* 41, 661-676.

Hassell, M. P. & Waage, J. K. — 1984. Host-parasitoid population interactions. — *Annu. Rev. Entomol.,* 29, 89-114.

Hassell, M. P., Lawton, J. H. & Beddington, J. R. — 1977. Sigmoid functional response by invertebrate predators and parasitoids. — *J. Anim. Ecol.,* 46, 249-262.

Holling, C. S. — 1959. Some characteristics of simple types of predation and parasitism. — *Can. Entomol.*, 91, 385-398.

Legner, E. F. — 1967. Behaviour changes the reproduction of *Spalangia cameroni, E. endius, Muscidifurax raptor* and *Nasonia vitripennis* [*Hym.: Pteromalidae*] at increasing fly host density. — *Ann. Entomol. Soc. Amer.*, 60, 819-826.

Lenteren, J. C. van & Bakker, K. — 1976. Functional response in invertebrates. — *Neth. J. Zool.*, 26, 567-572.

Nicholson, A. J. & Bailey, V. A. — 1935. The balance of animal population. Part I. — *Proc. Zool. Soc. London*, 1935, 551-598.

Murdoch, W. W. & Oaten, A. — 1975. Predation and population stability. — *Adv. Ecol. Res.*, 9, 2-131.

Pandey, R. K., Singh, R., Kumar, A., Tripathi, C. P. M. & Sinha, T. B. — 1982. Bionomics of *Trioxys indicus*, an aphidiid parasitoid of *Aphis craccivora*. 14. Behavioural activities of the parasitoid associated with its functional response. — *Z. Angew. Entomol.*, 93, 164-175.

Rogers, D. J. — 1972. Random search and insect population models. — *J. Anim. Ecol.*, 41, 369-383.

Singh, R. & Sinha, T. B. — 1979. First record of *Alloxysta* sp., a hyperparasitoid of *Trioxys* (*Binodoxys*) *indicus* Subba Rao & Sharma [*Hym.: Aphidiidae*]. — *Curr. Sci.*, 48, 1008-1009.

Singh, R. & Sinha, T. B. — 1980. Bionomics of *Trioxys* (*Binodoxys*) *indicus* Subba Rao & Sharma, an aphidiid parasitoid of *Aphis craccivora* Koch. 5. The extent of hyperparasitism. — *Z. Angew. Entomol.*, 90, 141-146;

Singh, R. & Srivastava, P. N. — 1987a. Bionomics of *Alloxysta pleuralis*, a cynipoid hyperparasitoid of an aphidiid parasitoid *Trioxys indicus*. — *Entomol. Exp. Appl.*, 43, 11-15.

Singh, R. & Srivastava, P. N. — 1987b. Factors associated with host location by *Alloxysta pleuralis* (Cameron), a hyperparasitoid of *Trioxys indicus* Subba Rao & Sharma [*Alloxystidae: Hymenoptera/Aphidiidae: Hymenoptera*]. — *Entomon*, 12, 325-328.

Singh, R. & Srivastava, P. N. — 1987c. Potential host-habitat location by *Alloxysta pleuralis* (Cameron) [*Alloxystidae: Hymenoptera*]. — *Z. Angew. Zool.*, 74, 337-341.

Singh, R. & Srivastava, P. N. — 1988. Host-acceptance behaviour of *Alloxysta pleuralis*, a cynipoid hyperparasitoid of an aphidiid parasitoid *Trioxys indicus* on aphids. — *Entomol. Exp. Appl.*, 47, 89-94.

Sinha, T. B. & Singh, R. — 1979. Studies on the bionomics of *Trioxys* (*Binodoxys*) *indicus* [*Hym.: Aphidiidae*]: Effect of population densities on sex ratio. — *Entomophaga*, 24, 289-294.

Sullivan, D. J. — 1972. Comparative behaviour and competition between two aphid hyperparasites: *Alloxysta victrix* and *Asaphes califnornicus* [*Hym.: Cynipidae; Pteromalidae*]. — *Env. Entomol.*, 1, 234-244.

Sullivan, D. J. — 1987a. Insect hyperparasitism. — *Annu. Rev. Entomol.*, 32, 49-70.

Sullivan, D. J. — 1987b. Aphid hyperparasites. In: Aphids, Their Biology, Natural Enemies and Control (**P. Harrewigh & A. K. Minks**, eds). — *Elsevier Press*, Amsterdam.

Varley, G. C. & Gradwell, G. R. — 1968. Population models for the winter moth, pp. 132-142. In: Insect Abundance (**T.R.E. Southwood**, ed.). — *Blackwell Scientific Publ.*, Oxford, England.