

## Reproductive strategies and behavioural attributes in some sporophagous Idolothripinae (Tubulifera: Thysanoptera)

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**Abstract.** An analysis of the behavioural aspects of some sporophagous Idolothripinae in terms of the diversity of reproduction is presented, involving aspects such as oviparity, grades of ovoviviparity and viviparity in *Tiarothrips subramanii*, *Elaphrothrips denticollis*, and *Elaphrothrips procer*. Reproductive diapause in *Loyolaia indica* is also reported.

**Keywords.** Sporophagous thrips; oviparity; ovoviviparity; viviparity; oocyte; ovariole index; behaviour.

### 1. Introduction

Contributions to the taxonomy of mycophagous tubuliferous Thysanoptera appear extensive (Ananthakrishnan 1973, 1979; Mound 1971, 1974a,b; Palmer and Mound 1978), but information relating to their biological aspects involving reproductive strategies and behavioural trends appear very restricted, being confined to those of *Bactridothrips brevitubus* (Takahashi) (Haga 1974, 1975, 1980), *Caudothrips buffai* Hood and *Megathrips* sp. (Bournier 1957, 1961), *Diceratothrips* sp. and *Elaphrothrips* sp. (Hood 1940). Ananthakrishnan *et al* (1983) discussed the feeding preferences of some sporophagous Tubulifera in relation to their gut spore composition, mortality rate and post-embryonic development. Although oviparity and ovoviviparity appear common among the Phlaeothripinae (John 1923; Bagnall 1921; Hood 1934, 1938; Hathaway 1938; Haga 1974; Bournier 1957, 1966), facultative viviparity was first reported in *Megathrips lativentris* by John (1923). With ovoviviparity, viviparity and oviparity being evident among the sporophagous idolothripines, an attempt has been made to assess aspects of behavioural and reproductive strategies concerning the following species of sporophagous idolothripines: (i) *Tiarothrips subramanii* (Ramk.) (ii) *Elaphrothrips denticollis* (Bagnall) (iii) *Elaphrothrips procer* (Schmutz) (iv) *Priesneriana kabandha* (Ramk.) (v) *Loyolaia indica* (Anan.).

### 2. Material and methods

Adults, larvae, pupae and unhatched eggs of the above mentioned species of thrips were obtained from their natural habitat and reared in plastic vials (3.4 × 4.5 cm) and polyethylene bags containing fungus infested host material. Both the fungal spores obtained from the thrips gut as well as from the scraping of the host material were cultured in (i) Potato-dextrose-agar medium (ii) Oat meal-agar medium and (iii) Czepek's medium. The cultured fungi were mounted in lactophenol and stained with cotton

blue (Ananthakrishnan *et al* 1983; Ananthakrishnan and William James 1983). Ovaries from apterous, brachypterous and macropterous individuals, as well as from oviparous, ovoviviparous and viviparous individuals were dissected and oocyte-ovariole indices calculated, using ovariole length/oocyte length. To study the stage of the egg development, longitudinal sections of 8  $\mu$  of the lateral oviduct were cut using a rotary microtome.

### 3. Observations

*T. subramanii*, *E. denticollis*, *E. procer* and *P. kabandha* tend to be gregarious, the aggregations often comprising oedymorous, normal and gynaecoid males as well as major and minor females in addition to immature stages. The number of individuals in a colony varying considerably depending upon the available fungal food, environmental conditions as well as the incidental type of reproduction. In species such as *T. subramanii*, *E. denticollis* and *E. procer* which do not exhibit alary polymorphism, oviparity, partial ovoviviparity, complete ovoviviparity and viviparity occur, while oviparity alone is evident in such species as *P. kabandha* and *L. indica* which exhibit alary polymorphism.

Both partial and complete ovoviviparity are evident in *T. subramanii*: (i) oocytes developing in the lateral oviduct upto blastoderm formation and subsequent egg laying and hatching occurring within 1 to 2 days (*partial ovoviviparity*). (ii) oocytes developing within the lateral oviduct upto a fairly advanced stage of development as evident by the eyespots and maxillary stylet formation, the eggs hatching within a few hours after laying (*complete ovoviviparity*). When the eggs develop within the lateral oviduct till the fully developed stage as evident by the formation of maxillary stylets, eyespot, legs, etc. the thin chorion surrounding the fully developed larvae ruptures while within the common oviduct and the fully developed larvae are laid— (*viviparity*).

#### 3.1 Oviparity, ovoviviparity and viviparity

Each oviparous ovariole of *T. subramanii* has 4-8 oocytes as compared with 2-9 oocytes in each ovoviviparous and viviparous ovariole. However, only 2-4 oocytes mature at a time on each side in the oviparous ovary, so that an oviparous female tends to lay 4-8 eggs during oviposition. In the ovoviviparous and viviparous ovaries, the lateral oviducts are 1.5 to 12 times longer and 3 to 4 times wider than that of the oviparous forms. The length of the ovariole and that of the basal oocyte within the ovariole are 2 to 2.5 times and 5 times longer respectively in oviparous forms as compared to those of the ovoviviparous and viviparous forms. All the four oocytes on each side of the ovary develop simultaneously in the ovoviviparous ovary, the dimensions of the basal oocytes in the ovariole being 5 times greater in oviparous ovaries.

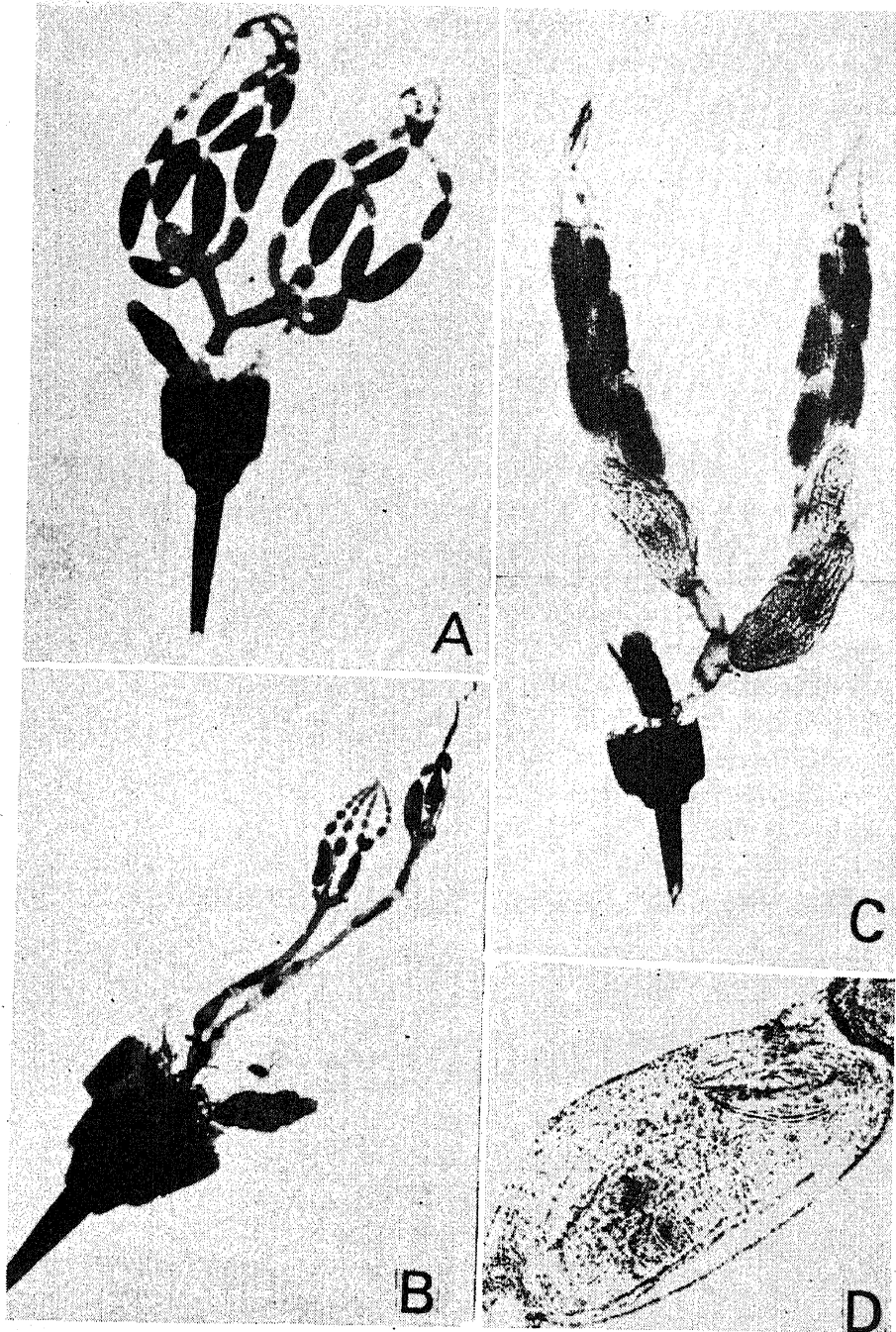
Gregariousness as well as unfavourable conditions of environment induce ovoviviparity and viviparity in *T. subramanii*, but during favourable conditions or when reared in isolation oviparity occurs. The very short oviduct never retains the eggs in the oviparous ovary. The number of eggs laid by the oviparous individuals is comparatively higher (25-33/female) the incubation period of oviparous eggs lasting 6-7 days. The viviparous individuals produce 7-11 larvae/female.

In *Elaphrothrips denticollis* and *E. procer* as in *T. subramanii* mating occurs soon after emergence. All the grades of ovoviviparity and viviparity are evident in addition to normal oviparity. In viviparous and ovoviviparous individuals of *E. denticollis* and *E. procer* the lateral oviduct is very long nearly 2-5 times longer than that of the ovariole. Fully developed embryos are evident, at the distal end of the lateral oviduct of *E. procer* and in the viviparous forms of this species, the eggs hatched within the common oviduct, the first instar larvae emerging as such while the oviparous females laid 3-10 eggs. The first larvae emerging from the viviparous females appear larger than those from the partial ovoviviparous forms. Fecundity is higher in oviparous *E. procer* with 5-37 eggs/female (1-7 eggs/day) laying in 2-3 days than in the viviparous forms with 5-6 larvae/female (1-3 larvae/day) laying in 2-7 days).

In *Priesneriana kabandha*, where only oviparity occurs, both the lateral oviduct as well as the ovarioles appear very much shorter, but with a very long terminal filament (1253-1485  $\mu$ ) attached to the salivary glands. The oocyte-ovariole index of the macropterous and brachypterous individuals was 2.4 to 2.6 and 1.5 to 1.6 respectively, and a maximum of eight oocytes are evident at a time in the mature condition. *Loyolaia indica* is a non-aggregating form, occurring singly, with ovaries showing retarded growth in summer months of April-June with no maturing oocytes, indicating its reproductive diapause, while those examined during January-February and September to December revealed their oviparous nature with 4-9 fully developed oocytes. The oocyte-ovariole indices for the oviparous ovary of this thrips species generally ranges between 1-3.7, in most cases being around 3-3.5, whereas the oocyte-ovariole index for the ovoviviparous types of ovaries is highly variable ranging from 5-12 depending upon the degree of ovoviviparity.

### 3.2 Egg laying sequence and fecundity

The egg laying pattern and the number of eggs laid vary considerably, depending upon the aggregation patterns and sub-social behaviour of the thrips concerned. In *T. subramanii* (30-400 individuals/colony) and *P. kabandha* (40-120 individuals/colony) which form colonies on *Borassus flabellifer* L. and *Eucalyptus globosus* var. *mysoriensis* respectively, lay their eggs in a specific pattern. In oviparous *T. subramanii*, eggs are laid in a linear fashion in the leaf folds or in the laminar regions just near the petioles in order to facilitate the emerging young ones to feed on fungal species such as *Anthostomella consanguinea*, *A. sepelibilis*, *A. phoenicicola*, *Pestalotia algeriensis*, *Alternaria* species and *Melanographium citri* (Ananthakrishnan and William James 1983). The number of eggs laid in each mass varies from 16-42, and the oviposition period ranges from 3 to 5 days, with a fecundity rate of 25-33 eggs/female, the maximum eggs laid per day being 9 and the minimum 3. In *P. kabandha* the eggs are laid in groups of 10-115 in a specific pattern along the underside of the dead barks of *Eucalyptus globosus* (figure 2). The eggs of *E. denticollis* collected from *Areca catechu* and *Tectona grandis* were glued to the surface of the host in a vertical fashion, with the eggs being closer to each other on *T. grandis* than on *A. catechu*, the number of eggs laid being 25-28 and 16-20 respectively. Increased fecundity occurs in the oviparous forms of *E. procer* with 5-37 eggs/female (1-7 eggs/day) than viviparous forms with 5-8 larvae/female (1-3 larvae/day). The oviposition period is higher in ovoviviparous forms (2-7 days) than in the oviparous forms (2-3 days). In *Loyolaia indica* the eggs are laid on the leaf sheaths of *Cynodon dactylon* (Pers) in a



**Figure 1.** Ovarian types of *Tiarothrips subramanii*. **A.** Oviparous ovary of *T. subramanii*. **B.** Parital ovoviviparous ovary of *T. subramanii*. **C.** Viviparous ovary of *T. subramanii*. **D.** Fully developed larvae in the distal end of the lateral oviduct, showing maxillary stylets, eye spots, etc. (enlarged).

scattered manner, the number of eggs laid by a single female ranging from 4-6 with an oviposition period of 3-4 days.

### 3.3 Post-embryonic development

*T. subramanii*, *E. procer*, *E. denticollis* and *L. indica* generally lay their eggs in the leaf folds or in more protected places and rarely on the leaf surface, thus protecting

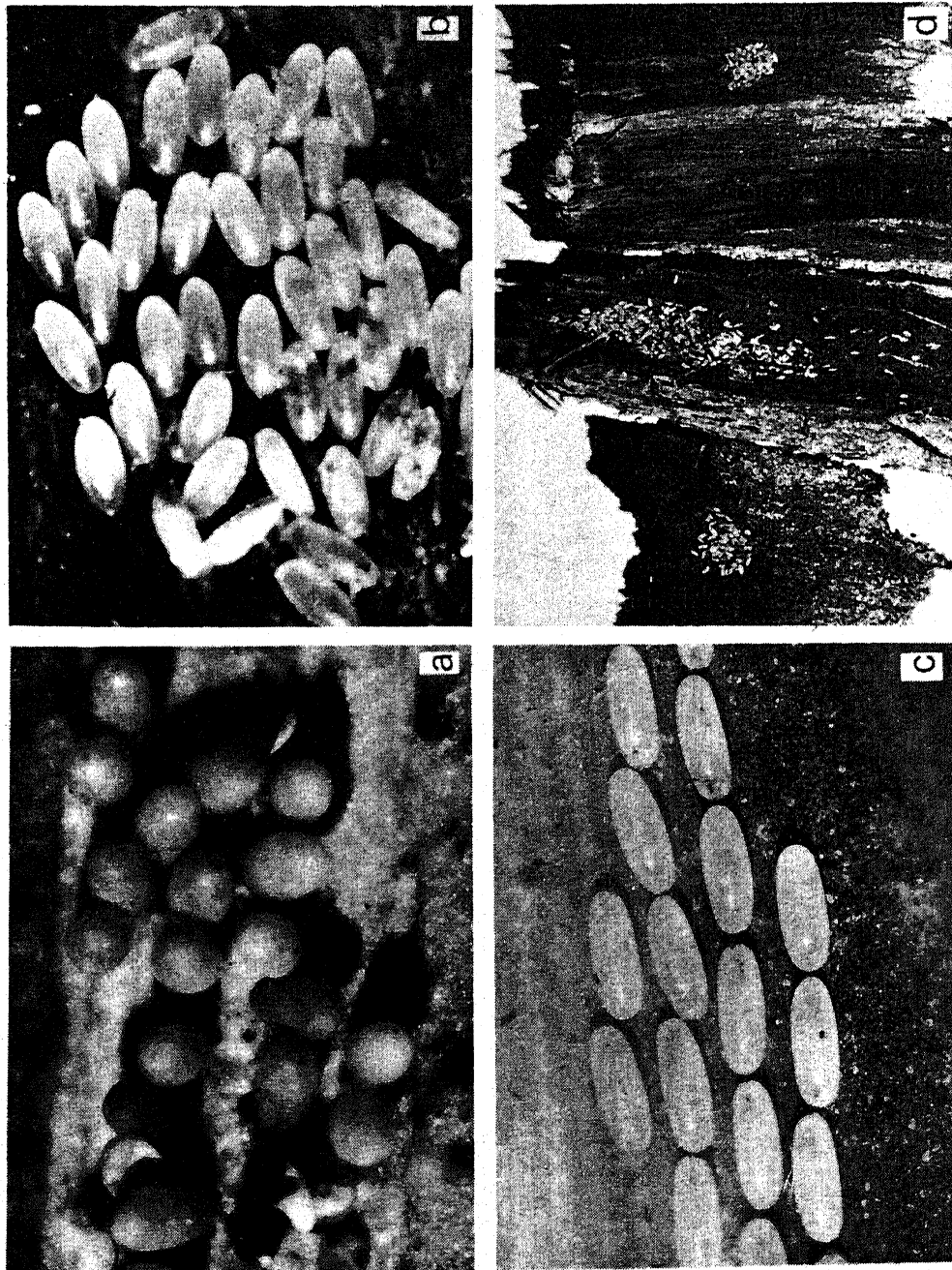


Figure 2. Egg laying pattern of some sporophagous idolothripines. a. Egg mass of *Elaphrothrips idolothripines*. b. Egg mass of *Priesteriana kalandha* (enlarged). c. Egg mass of *Tiarothrips subramanii*. d. Egg mass of *Priesteriana kalandha*.



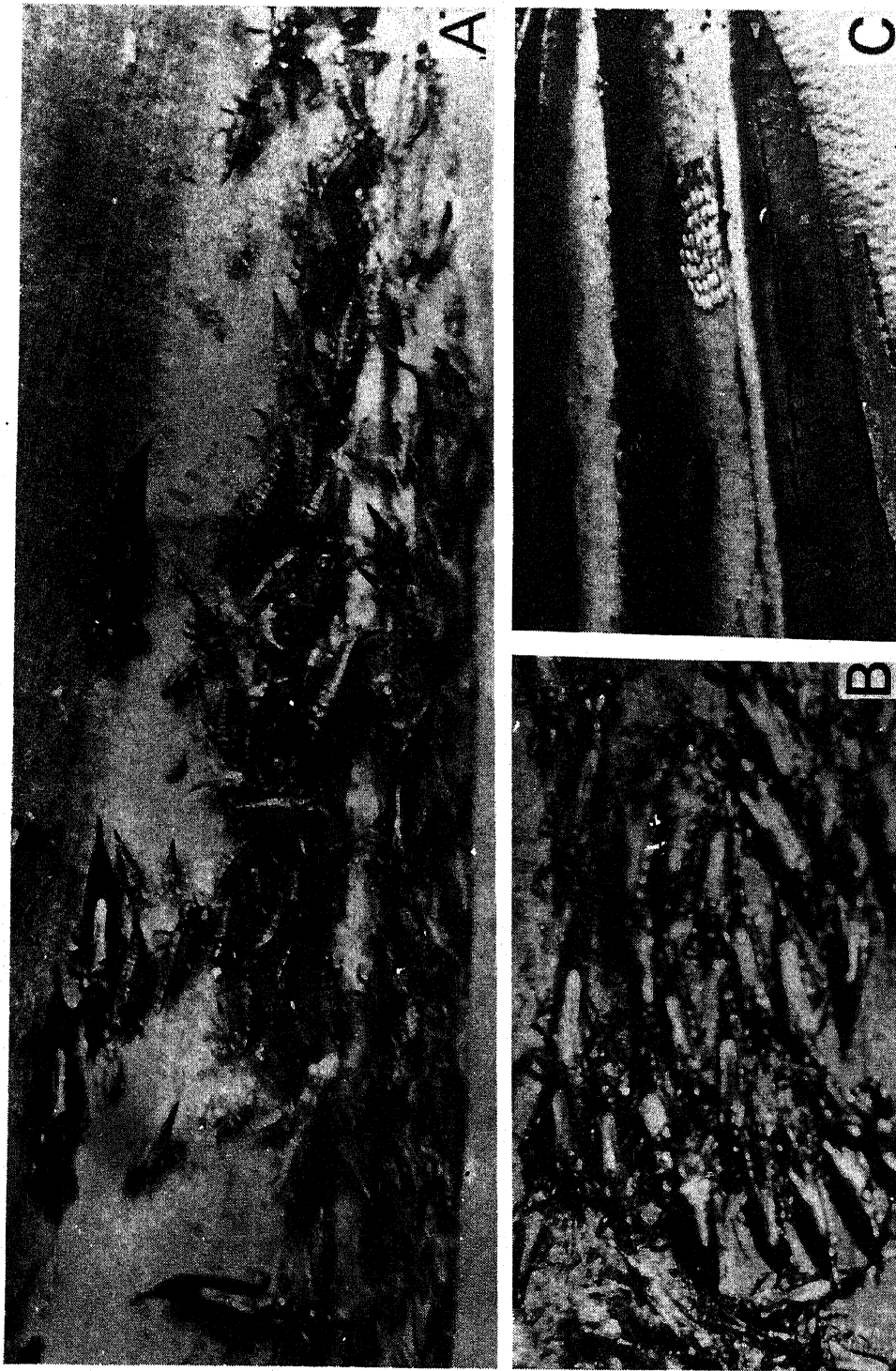


Figure 3. Aggregation and egg protection of some sporophagous idolothripines. A. A colony of *T. subramanii* in dry leaves of *Borassus flabellifer* L. B. Colony of *T. subramanii* (enlarged). C. Oedymereous male of *T. subramanii* guarding the egg mass.

the eggs from direct exposure to sunlight, rain and also from their natural enemies. In these thrips oedymorous males guard the colony as well as the egg mass (figure 3). In *T. subramanii* 4-5 egg masses each with 20-30 eggs occur sometimes within tunnels made by a caterpillar in leaves of *B. flabellifer*. In *P. kabandha* eggs are laid on the underside of dead bark. In colonies of *T. subramanii* and *P. kabandha*, adults, pupae and larvae completely surround the egg mass or stay at the vicinity of the eggs.

The incubation period is determined by the nature of the ovary and the type of reproduction, which in turn are governed by the environmental factors like availability of food, temperature and photoperiod. In partial ovoviviparous *E. procer* incubation period is just one day, whereas in oviparous forms like *L. indica* and *P. kabandha* it is 3-4 days, 6-7 days in *T. subramanii* and 10-12 days in *E. denticollis*, with an average duration of development of 27 and 15.5 days respectively in *E. denticollis* and *L. indica*. The rate of mortality is greater in the first and second larval stages (40-60%) of *E. denticollis* and lesser in first larval stages of *T. subramanii* (4%) (table 1).

### 3.4 Aggregation behaviour

With the exception of *Loyolaia indica*, other species like *T. subramanii*, *P. kabandha*, *E. denticollis* and *E. procer* exhibit a tendency for aggregation. *T. subramanii* shows linear aggregation within folds of dry leaves of *Borassus flabellifer*, while in other thrips species the aggregation pattern is irregular. The number of individuals in a colony is variable with about 30-165 first larvae, 8-275 second larvae, 9-33 pupae, 20-93 adults and 15-46 eggs in *T. subramanii* and 3-27 first larvae, 27-55 second larvae, 7-19 pupae, 16-27 adults and 10-110 eggs in *P. kabandha*, whereas *E. denticollis* and *E. procer* form comparatively smaller aggregations in *Areca catechu* and dense aggregations on *Tectona grandis*. Aggregations occur throughout the year in *T. subramanii*, *E. procer* and *E. denticollis* which occur only as macropterous forms, whereas *P. kabandha* exhibit close aggregation only while feeding on the fungal species *Cytospora* infesting *Eucalyptus globosus* var. *mysoriensis* and they do not aggregate while feeding on the fungal species *Rhytidhysterium rufula* infesting dry twigs. Aggregation among these thrips is favoured by reduced light and in the fields they aggregate in the dark regions covered by the closed leaflets as in *T. subramanii* and *E. denticollis* and the underside of the dry bark as in *P. kabandha*, with the aggregated condition remaining undisturbed even after continuous rainfall. Both the immature and adults aggregate without any specific orientation and form tiers one above the other with the adults occurring in the topmost layer and the oedymorous males occurring in the margins of a colony. Evidence of territorial behaviour was lacking and the antennectomized males were unable to recognise the colony, did not aggregate and moved away from it.

### 3.5 Mating behaviour

In a colony, sexually mature males orient towards mature females, the males making a point of contact, initiating a specific response. The point of contact is either from posterior end or at right angles to the thorax of the female or a head to head contact. In a majority of cases the two latter postures result in antennal palpation, whereas in the former condition antennal palpation rarely occurs. Antennal palpation acting as stimulus, enables acceptance by the female and results in the initiation of mating.

Table 1. Post-embryonic development of some sporophagous Idolothripinae

Thrips species	Mean fecundity rate	Mean incubation (in days)	I Larvae			II Larvae			Pre pupa			I Pupa			II Pupa			Mean duration of development
			Mean duration	Mean % mortality	Mean % mortality	Mean duration	Mean % mortality	Mean % mortality	Mean duration	Mean % mortality	Mean % mortality	Mean duration	Mean % mortality	Mean % mortality	Mean duration	Mean % mortality	Mean % mortality	
<i>Elaphrothrips denticollis</i>	26.5 (25-28)	11 (10-12)	4.5 (4-5)	50 (40-60)	4 (4)	60 (60)	1 (1)	0 (0)	3 (3)	—	—	3.5 (3-4)	—	—	—	—	27 (25-29)	
<i>Tiarothrips subramanii</i>	29 (25-33)	5.5 (6-7)	2.5 (2-3)	4 (4)	4.5 (4-5)	17 (17)	1 (1)	—	4.5 (4-5)	—	—	3.5 (3-4)	—	—	—	—	16.5 (14-19)	
<i>Priesneriana kabandha</i>	—	3.5 (3-4)	3 (2-4)	22 (22)	3 (3)	35 (35)	1 (1)	—	3 (3)	—	—	2.5 (2-3)	—	—	—	—	16 (14-18)	
<i>Loyolaia indica</i>	5.5 (5-6)	3.5 (3-4)	2.5 (2-3)	—	4.5 (4-5)	18 (18)	1 (1)	—	1.5 (1-2)	—	—	2.5 (2-3)	—	—	—	—	15.5 (13-18)	
<i>Elaphrothrips procer</i>	6.5 (3-10)	1 (1)	2.5 (2-3)	—	10 (8-12)	—	1 (1)	—	1 (1)	—	—	3.5 (2-5)	—	—	—	—	19 (15-23)	

Figures in parentheses indicate range.



Mating success greatly depends to a large extent upon the angle of abdominal flexion serving to engage the genitalia. The oedymorous males which are considerably longer than the females, effectively persuade and mate even after several unsuccessful attempts. The longer abdomen of oedymorous males serves to effectively engage the genitalia in mating, there being more frequent mating among them and the major females. Normal females also effectively bend their abdomen upto 90° along the long axis. Frequent matings were also observed among normal males and normal females, unless disturbed by the oedymorous males. Gynaecoid males were less successful in mating, not being favoured by the females. Whenever disturbed by other thrips the females move away from the males resulting in mating failure. With the initiation of mating it is continued either in an end-to-end posture or side-to-side posture (figure 4)

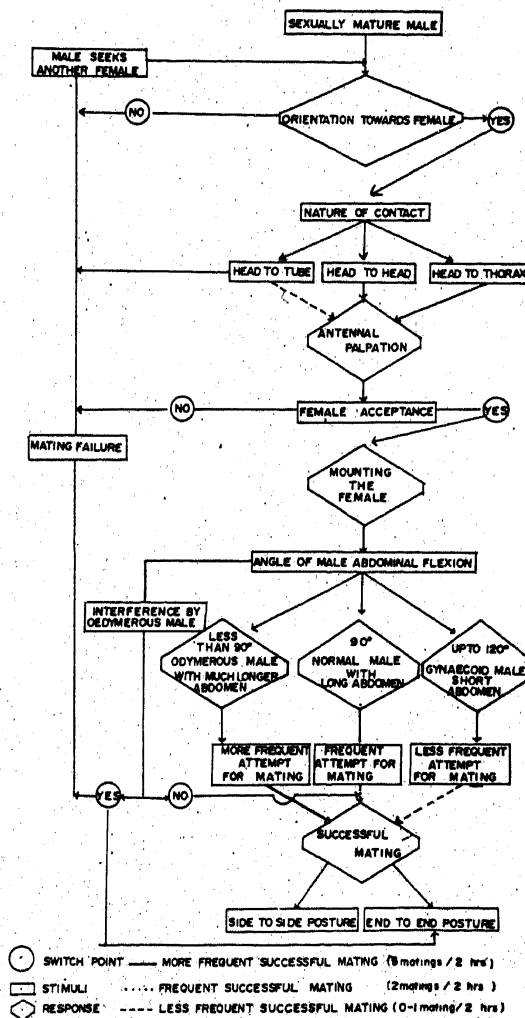


Figure 4. Mating behaviour of *Tiarothrips subramanii*.

#### 4. Discussion

The type of reproduction, whether oviparous or ovoviparous, is determined by factors such as environment, fungal food availability and aggregation behaviour. Oviparity occurs during the more-moist months, when sufficient fungal food is available and a longer incubation period does not result in desiccation. In the drier summer months, reproduction involves the graded types of ovoviviparity and viviparity thus enabling protection of the eggs from desiccation and overcoming the fungal food scarcity. *Caudothrips buffai* (Bournier 1957, 1966), which also feed on fungi, exhibit ovoviviparity as an adaptation to shorten the life-cycle, enabling the young ones to complete development before the food disappears. The emergence of live larvae in *T. subramanii*, *E. procer* and *E. denticollis* supports the observations of John (1923) on *Megathrips lariventris* where the eggs usually hatch after 14 days, but occasionally fully formed larvae emerge within few hours of laying and caged females produced larvae without empty shells. Since the ovoviviparous and viviparous eggs are retained in the lateral oviducts for a longer time, the fecundity and oviposition period are considerably short; on the other hand, in oviparous forms the eggs are never retained in the lateral oviduct, so that the oviposition period and fecundity rates are high and as an adaptation the lateral oviducts are long in the different types of ovoviviparous and viviparous forms. As the eggs pass through the lateral oviduct, most of the development occurs as in the partial and complete ovoviviparous forms and with the larvae fully developed as in the viviparous forms. The larger size of the oviparous basal oocyte is attributed to its high yolk content meant for the further egg development subsequent to laying. Hood (1950) and Priesner (1960) showed that in a number of tropical mycophagous species such as *Diceratothrips armatus* Bagnall, *D. princiceps* Hood, *Spodothrips amplus* Hood, *Anactinothrips vigilans* Hood, young ones are brought forth from adults, instead of eggs. Bournier (1957, 1966) observed that ovoviviparity is much more common in *Caudothrips buffai*, and noticed fully developed and chitinised larvae from the full-sized eggs dissected out from the gravid females. Viswanathan and Ananthkrishnan (1973b) also refer to the prolonged time spent by the oocyte within the oviduct, the presence of large receptaculum seminis with numerous sperm bundles to avoid the necessity of frequent mating, unusual longevity of females and the ability of eggs to survive desiccation for long time in *T. subramanii* as an adaptation for survival in the extreme conditions.

*Loyolaia indica* exhibits oviparity throughout the year except during summer (March-August), when they do not reproduce and maturation of oocytes does not occur. Except adults, eggs and immature stages were not noticed in the field, indicating an ovarian diapause condition. Photoperiod, temperature and food availability appear to be the main factors for ovarian diapause in thrips, wherein gut spore analysis of *L. indica* during this diapause stage revealed the gut to be completely filled with spores of *Lojkania cynodontifolii* (Ascomycete). The occurrence of oviparity during the rest of the year could be attributed to its non-aggregation behaviour, as well as their ability to migrate to alternative hosts. *L. indica* which occurs only in dry fungus infested clumps of *Cynodon dactylon* during the favourable periods, also occurs on other similar dry fungal-infested alternative hosts such as *Chloris barbata*, *Panicum repens* as well as dry twigs during late summer and early wet seasons (July-October) where they feed on the microconidia of *Fusarium oxysporum* and spores of *Penicillium* sp. This change of host during unfavourable conditions is perhaps due to the scarcity

for fungal spores of *Lojkania cynodontifolii* in their original hosts. On the whole non-aggregation behaviour, migration to alternative hosts and availability of fungal food throughout the year appear responsible for its oviparous type of reproduction throughout the year.

Oviparity occurs throughout the year in *Priesneriana kabandha* which forms close aggregations and exhibits a sub-social life on the undersurface of the dead barks of *Eucalyptus globosus* var. *mysoriensis* throughout the year except in summer where they migrate to nearby thorny dry twigs, where they do not form colonies. Thus change in aggregation behaviour, habitats and food fungi appear to be responsible for the density of the colony and surplus of fungi for feeding and rendering oviparity possible even in summer. All polymorphs occur in a colony throughout the year except during the end of the summer and early rainy season when only macropterous forms are evident. Here the production of macropterous forms appear to be due to the lack of sufficient fungal spores of *Cytospora* sp. (Coelomycete), resulting in migration of this thrips to other dry twigs infested with *Rhytidhysterium rufula* (Coelomycetes). Hood (1940) observed that *Hoplothrips flumenelles* exhibiting intraspecific ecological succession, the macropterous forms succeed the apterous forms. He also showed that in a colony nearly every individual is brachypterous and observed that "the immature organism carries within itself an environmentally-activated mechanism which assures a means of escape from the parental home, should inevitable changes make it no longer suitable to the life of the organism or itself". Earlier studies in bark dwelling phlaeothripids such as *Hoplothrips* sp., *Hoplothrips flumenellus* by Hood (1940) and *Megathrips* sp., and *Cephalothrips* sp. by Bournier (1961) also showed that brachypterae are produced when the fungi are fresh and vigorously growing, while macropterae are produced as they age and deteriorate.

In sub-social species such as *T. subramanii*, *E. procer*, *E. denticollis* and *P. kabandha*, females in a colony lay their eggs in a sequence. Each female of *T. subramanii* lays its eggs in a separate linear sequence of three, where as in *P. kabandha* colony all the females lay in a single mass. Both *T. subramanii* and *P. kabandha* when they form aggregations, the oedymorous males guard and protect the colony and egg mass, thus tend to exhibit division of labour. Bagnall (1915) also observed that *Elaphrothrips brevicornis*, a West Indian species, sits over her eggs after laying them on the leaves and protects the eggs from the predators.

The duration of the post-embryonic development varies with the thrips concerned as well as with the fungi they feed on. The highest mortality rate during the second larval stage may be due to longer duration and higher food requirements for further development. Earlier observations (Ananthakrishnan *et al* 1982) showed that the duration of the post-embryonic development and mortality rate vary with the host fungi.

An extreme degree of aggregation and sexual selection was noticed among the colony forming sporophagous idolothropines. Though the variation in numbers among the different polymorphs varies with season, there seems to be a balanced proportion of the extreme morphs (Ananthakrishnan 1964). Ananthakrishnan (1973) also showed the possibility of a genetic factor being involved in the production of these morphs. The nature of aggregation and the population in a colony greatly depend on the fungal food availability which in turn depend upon the environment. In all these species the antennae are found to play an important role in recognition of thrips and its colony. The females tend to exhibit a preference towards the oedymorous males

with enlarged forefemora, very long third antennal segment and long cephalic process, thus exhibiting sexual selection. Hence the success of reproduction to a very large extent appears to be due to sexual selection operating in the colony. This supports the observations by Mayr (1972) and Johnson (1982) where secondary sexual characteristics such as exaggerated size of the individuals or the parts of the body or colouration tend to occur in males presumably as a result of sexual selection, reflecting the competition of males among the female choices. Ananthkrishnan (1972) reported that the mycophagous thrips provide very good instances for studies of sexual selection in view of its large size and occurrence of sex-limited polymorphism. The large size in males appears to confer a greater probability of success in thrips reproductive investments and the behaviour of the female to choose a large mate will be favoured and maintained (Johnson 1982).

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