UDC 595.7:502.2

TEMPERATURE DEPENDENT LARVAL PUPATION SITE PREFERENCE IN *DROSOPHILA*

N.B. Vandal, N. Shivanna

Department of Studies in Zoology, *Karnatak University*
Dharwad-580003, *Karnataka state*, *India*
Email: *drnshivanna@rediffmail.com*

Поступила в редакцию 10.04.06 г.

Temperature dependent larval pupation site preference in *Drosophila*. – **Vandal N.B., Shivanna N. –** The pupation site preferences (PSP) in sibling, sympatric and closely related species of *Drosophila* belonging to different groups were studied at different temperatures. The study has revealed that the pupation site choice varies significantly at extreme temperatures compared to the control one. Different species of *Drosophila* differ in PSP at different temperatures. The deviations from the control among the sibling species, sympatric and closely related species indicate that temperature affects the PSP.

Key words: *Drosophila*, adaptation, temperature, larva, habitat choice.

Влияние температуры на выбор мест окукливания личинками дрозофилы. – Вандал Н.Б., Шиванна Н.– Изучен выбор мест окукливания сёстринскими, симпатрическими и тесно связанными друг с другом видами дрозофилы, принадлежащими к различным группам, при различных температурах. Показано, что этот выбор существенно меняется при экстремальных температурах по сравнению с контрольной. Различные виды дрозофилы различаются в выборе мест окукливания при различных температурах. Отличия от контрольной группы, встречающиеся между сёстринскими, симпатрическими и тесно связанными друг с другом видами, указывают на влияние температуры на выбор мест окукливания.

Ключевые слова: *Drosophila*, адаптация, температура, личинка, биотопические предпочтения.

INTRODUCTION

The environmental conditions at which a species can carry out its vital life-history stages will directly influence its geographical and habitat distribution. Conditions that influence pre-adult stages can be just as important as those affecting the adults. Since insect pupae are immobile, they can remain exposed to potentially harmful biotic and abiotic factors for varied periods of time (desiccation, predation, infection etc...). Pupation site choice can be critical for survival. Differences in pupation site choice can reflect larval differences in the methods of finding food, as well as differences in niche breadth and competitive ability in general.

The effect of temperature has been studied in different species of *Drosophila* on both adult and preadult characters. Interspecific competitions of larvae have shown to be influenced by temperature in *Drosophila* (Fogleman, Wallace, 1980; Budnik, Brncic, 1984; Ricci, Budnik, 1984). *Drosophila* species usually show less specificity in their adaptations for larval sites than for oviposition sites and adaptive differentiation in response to temperature stress among populations of *D. pseudoobscura* is more pronounced

for puparia than adults (Kaneshiro et al., 1973; Coyene et al., 1983). Adaptation to high and low temperatures produced different adult body sizes in two temperate populations of *D. pseudoobscura* and two tropical populations of *D. melanogaster* (Anderson, 1973; Noach et al., 1996; Crill et al., 1996; Moed et al., 1997, 1999; Eanes, 1999; Blankenhorn, 1999; Robinson, Partridge, 2001; Bochdanovits, Jong, 2003; Bochdanovits et al., 2003). *Drosophila* reared under stressful conditions has been shown to increase phenotypic variations in its developmental time, dry weight eclosion, thorax length, wing length, ovariole numbers and sterno pleural chaeta (Gebhardt, Stearns, 1988, 1992; David et al., 1994; Delpuech et al., 1995; Lazebry et al., 1996; Imasheva et al., 1997, 1998).

R.R. Sokal et al. (1960) observed the maximum pupation height at 22 – 25°C. J.L. Mensua (1967) found that the pupation height increased from 13 – 25°C and then decreased at 29°C. J.C. Fogleman and T.A. Markow (1982) detected small but significant differences in PSP of *D. metleri* and *D. nigrospiracula* at 24.4±0.2°C and 23.1±0.2°C. At high temperature extremes, all the species show little or no upward movement. At low temperature extremes, the maximum height is observed in some species within the *repleta* and *willistoni* groups, and the entire *melanogaster* traid. However, the other species within the *repleta* and *willistoni* groups, and the entire *virilis* traid show no upward movement at all under the same low-temperature conditions (Schnebel, Grossfield, 1992). The maximum pupation height occurs at 24°C in *D. ananassae*, *D. bipectinata* and *D. malerkotliana* (except *D. biarmipes*) and there is a considerable decrease in the pupation height at low/high temperatures (Pandey, Singh, 1993).

The PSP has been analysed by two types of phenotypic characters, one is the pupation height and the other is pupation site choice. The pupation height studies have been made by different factors such as moisture, light, temperature, density, sex, larval developmental time, selection for high and low pupation height and its genetic control (Sokal et al., 1960; Mensua, 1967; Sameoto, Miller, 1968; Markow, 1979; Fogleman, Markow, 1982; Ringo, Wood, 1983; Bauer, 1984; Bauer, Sokolowski, 1985; Casares, Carracedo, 1987; Singh, Pandey, 1991, 1993 *a*, *b*; Pandey, Singh, 1993). An environmental variable known to influence pupation in *Drosophila* is temperature. Species differences in the ability to pupate successfully, as well as in pupation height choice have been shown to be temperature-dependent (Grossfield, 1978; McKenzie, McKenzie, 1979; Fogleman, Markow, 1982; Schnebel, Grossfield, 1986 *a*; Kimura, 1988; Schnebel, Grossfield, 1992; Pandey, Singh, 1993).

J.S.F. Barker (1971), P.D. Shirk et al. (1988), N. Shivanna et al. (1996), N. Shivanna and S.R. Ramesh (1997) have studied the pupation site preference (PSP) at constant conditions and classified the species into three categories depending on the quantity of glue protein and percentage of pupation and showed the lack of intraspecific variations in PSP. For the present investigation the species occupying different sites for pupation at constant conditions and belonging to varied ecological backgrounds were used. Intra- and interspecies variations in pupation height and competition studies in *D. ananassae*, *D. bipectinata*, *D. malerkotliana* and *D. rajasekari* have revealed that these are sympatric species (Ranganath et al., 1985; Singh, Pandey, 1991). PSP of larvae belonging to different species occupying different sites in the cultures has not been studied at different temperatures. In view of this the present study was undertaken to know the effect of temperature on PSP in different species of *Drosophila*.

MATERIALS AND METHODS

For the present investigation, closely related sibling species, *D. melanogaster*, *D. simulans*, *D. yakuba* and *D. mauritiana* belong to *melanogaster* subgroup species, *D. ananassae*, *D. bipectinata*, *D. malerkotliana* and *D. rajasekari* are closely related sympatric species belonging to *ananassae* subgroup of the *melanogaster* species group. *D. virilis*, *D. novamexicana* belong to *virilis* group and *D. hydei* belongs to *repleta* species group were taken to study the effect of temperature on the larval PSP (Bock, Wheeler, 1972; Ehrman, 1978; Ranganath et al., 1985; Ashburner, 1989; Singh, Pandey, 1991). *D. virilis* and *D. novamexicana* all are cosmopolitan species. The cosmopolitan *Drosophila* species (*D. melanogaster*, *D. simulans*, *D. virilis*, *D. ananassae* and *D. hydei*) feeds on anything small enough, often man's garbage. *D. melanogaster* and its sibling species *D. simulans, D. yakuba*, and *D. mauritiana* are primarily tropical but have expanded to temperate zones. In contrast, the *D. ananassae* distribution is restricted to the tropics and subtropics where it needs not have tolerance for temperature extremes. *D. ananassae*, *D. bipectinata*, *D. malerkotliana* and *D. rajasekari* are sympatric species. *D. ananassae* is a domestic species while *D. bipectinata*, *D. malerkotliana* and *D. rajasekari* are semiwild species. *D. virilis* and *D. novamexicana* are subtropical/tropical of the southern China / India and arid environment species belonging to *virilis* group and being able to live in warmer lines than the cooler subarctic regions (Grossfield, 1978; Parson, Stanley, 1981; Ranganath et al., 1985; Schnebel, Grossfield, 1986; Singh, Pandey, 1993 *a*). These *Drosophila* species were collected from the *Drosophila* stock centre, University of Mysore, Mysore, India maintained about 20 years (table 1).

Table 1

Origin and Ecological backgrounds of isofemale lines of *Drosophila* species

Species	Stock No	Origin	Ecological backgrounds
*D. melanogaster**	1.001	Mysore	Cosmopolitan
*D. simulans**	2.001	Varanasi	Cosmopolitan
*D. yakuba**	3.001	Germany	Cosmopolitan
*D. mauritiana**	4.001	Germany	Cosmopolitan
*D. ananassae***	11.001	Mysore	Cosmopolitan
*D. bipectinata***	13.001	Mysore	Cosmopolitan
*D. malerkotliana***	12.001	Mysore	Cosmopolitan
*D. rajasekari***	70.001	Mysore	Cosmopolitan
*D. virilis****	309.001	Mysore	Subtropical / tropical of the southern China / India
*D. novamexicana****	308.001	Germany	Arid environment
D. hydei^{+}	306.001	Germany	Cosmopolitan

* – Sibling species, ** – sympatric species, *** – closely related *virilis* group species, $^{+}$ – repleta group species.

In order to maintain uniformity with regard to the density and age of the larvae the eggs were collected every 6 hours using a modified technique of Delcour described by N.B. Ramachandra and H.A. Ranganath (1988) and allowed to hatch. First instar larvae about 50 from the cultures were isolated and transferred to a vial (10×3.8 cm) containing equal quantities of wheat cream agar medium (Shivanna et al., 1996). The cultures were

kept at four different temperatures viz; (22°C control) 15°C, 20°C, 25°C, and 30°C. About 50µl of dilute yeast was added to the culture vials to feed the larvae everyday.

Ten replicates were carried out for each experiment. The mean values as well as the percentage of pupation were calculated based on the number of larvae pupated at different sites viz; cotton, glass, and medium. The primary data (number of pupae on different sites) were subjected to one-way ANOVA followed by DMRT to analyze the effect of temperature on PSP in different species within the species at different sites. Between the species at three different sites viz; cotton, glass and media pupation in ten replicates of each species were compared using two-way ANOVA (species × temperature).

RESULTS

Table 2 reveals that the percentage of glass pupation is maximum at all the temperatures in *D. melanogaster*, *D. ananassae*, *D. virilis*, *D. novamexicana*, and *D. hydei*. Compared to the control the percentage of glass pupation is decreased in *D. melanogaster* 30.0%, *D. ananassae* 45.0% at 30°C, and *D. virilis* 9.0% at 15°C, respectively. Whereas the percentage of pupation increased at 20°C about 7.0% in *D. ananassae*, 15.0% at 15°C in *D. novamexicana*, and 6.0% at 25°C in *D. hydei*. Except *D. hydei* at 15°C it is decreased to 16.0%. The glass pupation is minimum at all the temperatures: in *D. simulans* it ranges from 0.2 to 7.0%, in *D. yakuba* it ranges from 10.2 to 37.2%, in *D. mauritiana* it ranges from 15.4 to 32.6%, in *D. bipectinata* it ranges from 3.0 to 15.4%, in *D. malerkotliana* it ranges from 6.4 to 16.8%, and in *D. rajasekari* it ranges from 6.0 to 13.4% and nil at 30°C compared to control.

Table 2

Mean ± SD and percentage (in parentheses) of glass pupation at different temperatures in different species of *Drosophila*

Species	15°C	20°C	22°C (Control)	25°C	30°C
D. melanogaster	40.5±2.12* (81)	43.8±2.25 (87.6)	47.1±4.35 (94.2)	45.4±1.64 (90.8)	31.9±2.96* (65.8)
D. simulans	0.7±0.82 (1.4)	3.5±1.43 (7)	2.3±1.15 (4.6)	2.0±0.94 (4)	0.1±0.31* (0.2)
D. yakuba	18.6±5.58* (37.2)	12.0±1.76 (24)	18.6±1.89 (36.8)	9.0±2.0 (18)	5.1±2.99* (10.2)
D. mauritiana	14.1±2.13 (28.2)	14.5±2.46 (29)	16.3±3.32 (32.6)	12.1±2.28 (24.2)	7.7±3.80* (15.4)
D. ananassae	38.1±3.72 (76.2)	42.8±1.98 (85.6)	39 ± 5.03 (78)	35.2±1.75 (70.4)	16.5±3.83* (33)
D. bipectinata	2.0±0.94 (4)	7.7±3.56* (15.4)	1.9±1.66 (3.8)	3.5±1.08 (7)	1.5±1.58 (3)
D. malerkotliana	5.7±2.98 (11.4)	8.0±1.24 (16)	8.4±4.71 (16.8)	7.2±1.75 (14.2)	3.2±4.89* (6.4)
D. rajasekari	3.0±2.16* (6)	8.5±1.08* (17)	5.2±1.2 (10.40)	6.7±1.70 (13.4)	0.0±0.0* (0)
D. virilis	48.1±1.28 (96.2)	42.4±1.26 (84.8)	47.5±1.26 (95)	44.4±1.07 (88.8)	45.9±1.79 (91.8)
D. novamexicana	45.6±1.56 (91.2)	38.8±2.09* (77)	38.3±4.52 (76.6)	40.4±2.91 (80.8)	42.1±2.23 (84.2)
D. hydei	32.8±2.22* (65.6)	39.4±2.36 (78.8)	37.1±2.13 (74.2)	40.3±2.40 (80.6)	40.5±2.36 (81)

* – Significant at 5% level according to DMRT.

Table 3 reveals that the percentage of media pupation is maximum at all the temperatures in *D. simulans*, *D. yakuba*, *D. mauritiana*, *D. bipectinata*, and *D. malerkotliana*. Compared to control the percentage of media pupation is decreased in *D. simulans*, *D. yakuba*, *D. mauritiana* and *D. bipectinata*: 7.0, 13.2, 2.0 and 11.4% at 20°C, 15°C, 20°C and 20°C, respectively. The percentage of media pupation increased by 2.0% in *D. simulans* and by 12.0% in *D. yakuba* at 30°C, respectively, in *D. mauritiana* 14.6,

10.4 and 25.4%, *D. bipectinata* 1.4, 2.6 and 6.0% at 15°C, 25°C and 30°C, respectively. In *D. malerkotliana* the media pupation is increased at all the temperatures. The media pupation is minimum in *D. melanogaster* it ranges from 3.2 to 16.0%, in *D. ananassae* it ranges from 3.4 to 58.8%, and in *D. rajasekari* it ranges from 13.0 to 93%. In *D. virilis* it ranges from 0 to 9.4%, in *D. novamexicana* it ranges from 3.4 to 18.4%, and in *D. hydei* it ranges from 11.6 to 27.2%.

Table 3

Mean ± SD and percentage (in parentheses) of media pupation at different temperatures in different species of *Drosophila*

Species	15°C	20°C	22°C (Control)	25°C	30°C
D. melanogaster	4.3±1.49 (8.6)	3.5±1.58 (7)	1.6±2.83 (3.2)	3.1±0.94 (6.2)	13.0±2.26* (16)
D. simulans	46.2±1.22 (92.4)	43.1±0.87* (86.2)	46.6±1.71 (93.2)	44.6±1.50 (89.2)	47.2±1.61* (94.2)
D. yakuba	29.1±5.22* (58.2)	34.3±2.0 (68.6)	37.2±2.20 (74.4)	35.6±2.59 (71.2)	41.7±2.98* (83.4)
D. mauritiana	33.9±1.91 (67.8)	25.6±2.79* (51.2)	26.6±4.24 (53.2)	31.8±2.14 (63.6)	39.3±3.46* (78.6)
D. ananassae	1.7±1.63 (3.4)	4.2±1.39 (8.4)	4.6±2.59 (9.2)	11.6±1.50 (23.2)	29.4±3.62* (58.8)
D. bipectinata	44±1.41 (88)	37.1±3.17* (74.2)	44.8±3.93 (86.6)	44±1.15 (89.2)	46.3±1.76 (92.6)
D. malerkotliana	41±3.91 (82)	38.5±1.50 (77)	37±5.75 (74)	38.8±2.57 (77.6)	43.2±5.15* (86.4)
D. rajasekari	29.9±7.06* (59.8)	6.5±1.35* (13)	8.9±1.26 (17.8)	24±1.69* (48)	46.5±1.08* (93)
D. virilis	0.0±0.0* (0)	4.7±1.05* (9.4)	1.6 ± 0.96 (3.2)	4.2±0.91 (8.4)	1.8±1.47 (3.6)
D. novamexicana	1.7±1.63* (3.4)	4.6±0.96 (9.2)	9.2±4.13 (18.4)	5.5±1.84 (11)	3.4±1.07 (6.8)
D. hydei	13.8±1.81* (27.2)	6.6±2.31 (13.2)	12.9±1.10 (25.8)	6.1±2.28 (12.2)	5.8±2.04* (11.6)

* – Significant at 5% level according to DMRT.

Table 4 reveals that the percentage of cotton pupation is maximum at all the temperatures in *D. rajasekari*. Compared to the control the cotton pupation is decreased to 32.0% and 0% at 15°C and 30°C, respectively. Whereas the percentage of cotton pupation increased by 3.2% at 20°C. The cotton pupation is minimum in *D. yakuba* it ranges from 1.8 to 3.6%, in *D. mauritiana* it ranges from 4.2 to 14.2%. In *D. ananassae* it ranges from 1.4 to 15.2%. The cotton pupation in *D. bipectinata* and *D. malerkotliana* is 3.6% and 4.0% in control, 1.8% and 3.8% at 15°C, respectively. At other temperatures it is nil. At 30°C the cotton pupation is nil in all the species except *D. melanogaster*. The cotton pupation is nil in *D. yakuba* and *D. mauritiana* at 15°C.

Table 4

Mean ± SD and percentage (in parentheses) of cotton pupation at different temperatures in different species of *Drosophila*

Species	15°C	20°C	22°C (Control)	25°C	30°C
D. melanogaster	2.1±0.99 (4.2)	0.2±0.42 (0.4)	0.0±0.0 (0)	0.0±0.0 (0)	0.1±0.31 (0.2)
D. simulans	0.0±0.0 (0)	0.0 ±0.0 (0)	0.0±0.0 (0)	0.0±0.0 (0)	0.0±0.0 (0)
D. yakuba	0.0±0.0 (0)	0.9±0.87 (1.8)	1.4±0.97 (2.8)	1.8±0.78 (3.6)	0.0±0.0 (0)
D. mauritiana	0.0±0.0 (0)	5.6±1.17 (11.2)	0.7±1.87 (14.2)	2.1±0.99 (4.2)	0.0±0.0 (0)
D. ananassae	7.6±4.16 (15.2)	1.2±1.13 (2.4)	5.1±5.17 (10.2)	0.7±0.08* (1.4)	0.0±0.0 (0)
D. bipectinata	0.9±1.10 (1.8)	0.0±0.0 (0)	1.8±3.01 (3.6)	0.0±0.0 (0)	0.0±0.0 (0)
D. malerkotliana	1.9±1.28 (3.8)	0.0±0.0 (0)	1.8±4.39 (4)	0.0±0.0 (0)	0.0±0.0 (0)
D. rajasekari	16±7.19* (32)	32.5±1.71* (65)	27.8±2.2 (55.6)	16.7±2.49 (33.4)	0.0±0.0 (0)
D. virilis	0.0±0.0 (0)	0.0±0.0 (0)	0.0±0.0 (0)	0.0±0.0 (0)	0.0±0.0 (0)
D. novamexicana	0.0±0.0 (0)	0.0±0.0 (0)	0.0±0.0 (0)	0.0±0.0 (0)	0.0±0.0 (0)
D. hydei	0.0±0.0 (0)	0.0±0.0 (0)	0.0±0.0 (0)	0.0±0.0 (0)	0.0±0.0 (0)

* – Significant at 5% level according to DMRT.

The percentage of larval mortality varies from species to species (Table 5). The highest percentage of mortality is found in *D. melanogaster* (18.0%) at 30°C, *D. novamexicana* (13.2%) and (9.0%) at 20°C and at 30°C, respectively. In *D. hydei* the mortality is 8.0% at 20°C. The lowest mortality is 4.4% in *D.bipectinata* at 30°C, 2.8% in *D. virilis* at 25°C, 3.6% in *D. ananassae* at 20°C, and 2.2% in *D. rajasekari* at 15°C.

Table 5

Percentage of larval mortality at different temperatures in different species of *Drosophila*

Species	15°C	20°C	22°C (Control)	25°C	30°C
D. melanogaster	6.2	5.0	2.6	3.0	18.0
D. simulans	6.2	6.8	2.2	6.8	5.0
D. yakuba	4.6	5.6	0.0	7.2	6.4
D. mauritiana	4.0	8.6	0.0	8.0	6.0
D. ananassae	5.2	3.6	2.6	5.0	8.2
D. bipectinata	6.2	10.4	3.0	5.0	4.4
D. malerkotliana	2.8	7.0	5.2	8.0	7.2
D. rajasekari	2.2	5.0	0.0	5.2	7.0
D. virilis	3.8	5.8	1.8	2.8	4.6
D. novamexicana	5.4	13.2	5.0	8.2	9.0
D. hydei	7.2	8.0	0.0	7.2	7.4

Statistical analysis reveals a significant decrease in glass pupation in *D. melanogaster*, *D. simulans*, *D. yakuba*, *D. mauritiana*, *D. ananassae*, *D. malerkotliana* and *D. rajasekari* at 30°C, *D. hydei* at 15°C, *D. virilis* at 20°C and *D. melanogaster* at 15°C and 30°C compared to control. Whereas *D. yakuba* and *D. novamexicana* show a significant increase in glass pupation at 15°C, *D. rajasekari* at 20°C and 25°C. *D. yakuba* and *D. novamexicana* show a significant decrease in media pupation at 15°C, *D. bipectinata* at 20°C and *D. hydei* at 30°C. Whereas *D. melanogaster*, *D. simulans*, *D. yakuba*, *D. bipectinata* and *D. malerkotliana* show a significant increase in media pupation at 30°C, *D. virilis* and *D. hydei* at 20°C, *D. ananassae* at 25°C and 30°C, *D. mauritiana* at 20°C and 30°C, *D. rajasekari* at 15°C, 25°C and 30°C. Table 4 reveals that *D. rajasekari* shows a significant increase at 20°C and a decrease at 15°C, *D. ananassae* shows a significant decrease at 25°C in cotton pupation. The remaining comparison between different temperatures on glass, in media and in cotton pupation is insignificant (tables 2 – 4). The comparisons among some species at different temperatures are significant except *D. simulans*, *D. virilis*, *D. novamexicana* and *D. hydei* ($p < 0.001$, $df_1 = 4$, $df_2 = 49$, table 6). The

Table 6

One-way ANOVA of PSP at different sites at all the temperatures in different species of *Drosophila*

Species	Cotton	Glass	Media
D. melanogaster	32.645	46.533	54.204
D. simulans	0.00*	17.882	13.802
D. yakuba	13.152	3.782	21.067
D. mauritiana	3.495	42.859	124.887
D. ananassae	11.675	83.897	187.870
D. bipectinata	11.902	13.159	20.806
D. malerkotliana	2.779	3.905	27.516
D. rajasekari	121.058	62.442	212.087
D. virilis	0.00*	29.258	37.595
D. novamexicana	0.00*	10.084	15.576
D. hydei	0.00*	22.608	37.611

* – Insignificant.

analysis of variance (two-way ANOVA) has revealed that the variation of pupation site preference at three different sites such as glass, media and cotton, between species and temperatures is significant (table 7).

Table 7

Two-way analysis of variance of pupation site preference at three different sites in *Drosophila*

Sites	Source of variation	Degrees of freedom	*F*-value	*p*-value
Glass	Species	10		
	Temperature	3	42.45*	< 0.001
	Temperature × sites	30		
Media	Species	10		
	Temperature	3	57.67*	< 0.001
	Temperature × sites	30		
Cotton	Species	10		
	Temperature	3	18.59*	< 0.001
	Temperature × sites	30		

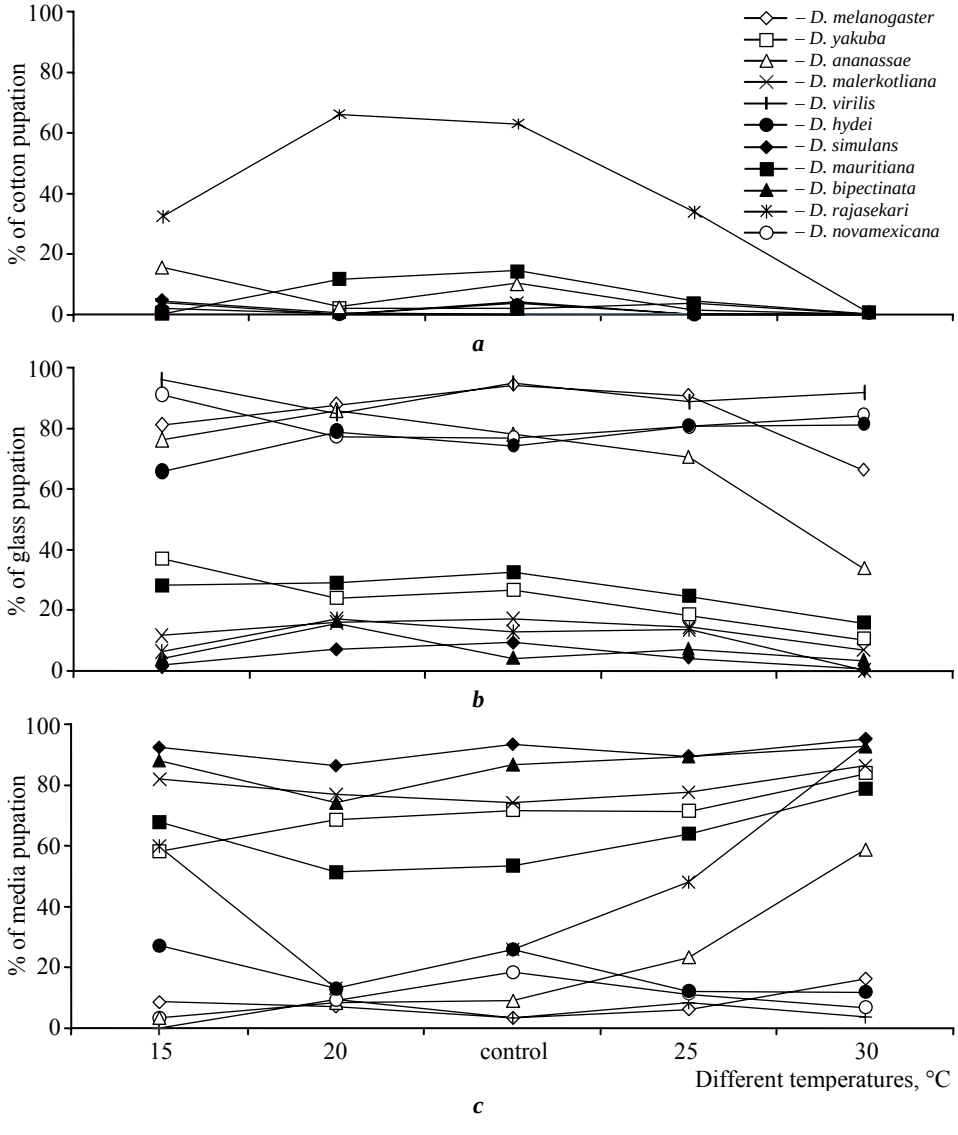
* – Significant.

DISCUSSION

The pupation site preference (PSP) is one of the behaviour of late third instar larva in *Drosophila*. It has been analysed by two types of phenotypic characters, one is the pupation height and the other is pupation site preference. The pupation height is the distance a larva moved upward and pupated above the food media. PSP is the percentage of larvae moved / not moved upward and pupated at different sites. Figure 1*b* and table 2 indicate that the PSP both at control and different temperatures of *D. melanogaster*, *D. ananassae*, *D. virilis*, *D. novamexicana* and *D. hydei* is on glass, *D. simulans*, *D. yakuba*, *D. mauritiana*, *D. bipectinata*, *D. malerkotliana* is in/on media, and *D. rajasekari* is on cotton. The PSP in all the species analysed is affected by temperature. The percentage of pupation increased by 7.0, 15.0 and 6.0% in *D. ananassae*, *D. novamexicana* and *D. hydei* on glass at 20°C and decreased by 16.0% at the lowest temperature 15°C in *D. hydei*. The percentage of pupation increased by 10.2 and 1.2% in *D. novamexicana* and *D. virilis* on glass at 15°C, *D. bipectinata* by 12.4% at 20°C and *D. rajasekari* by 4.2 and 0.6% on glass at 15°C and 25°C. At higher temperatures (25°C and 30°C) *D. hydei* and *D. novamexicana* preferred glass whereas in other species it is decreased compared to control. *D. hydei* is a cosmopolitan and *D. novamexicana* is an arid environment species.

Effects of different external factors on oviposition patterns have been investigated in various species of *Drosophila* (Gruwez et al., 1971; McKenzie, 1975; Ohnishi, 1977; Rockwell, Grossfield, 1978; Parson, 1978; Seizer, Sanner, 1983; Schnebel, Grossfield, 1986 *b*). Temperature plays a very important role in the oviposition behaviour of *Drosophila* species. It is severely reduced at low temperatures in *D. melanogaster*, *D. simulans*, *D. ananassae*, *D. bipectinata*, *D. malerkotliana* and *D. biarmipes* (McKenzie, 1975; Parson, 1978; Srivastava, Singh, 1998). J.R. David and M.F. Clawel (1968) found less than one half of the maximum daily eggs production in *D. melanogaster*. *D. melanogaster*, *D. simulans* and *D. ananassae* are cosmopolitan species and *D. ananassae* is restricted to the tropics and subtropics where it need not have a high tolerance for temperature ex-

tremes. *D. bipectinata* and *D. malerkotliana* are cosmopolitan and semiwild species. At the lowest temperature, the maximum pupation height occurs within *repleta* and *willistoni* group and at higher temperatures all the species show a little pupation height or no upward movement (Schnebel, Grossfield, 1992).



PSP at different temperatures in different species of *Drosophila*: *a* – Cotton, *b* – Glass, *c* – Media

Figure 1*c* and table 3 reveal that *D. yakuba*, *D. bipectinata*, *D. rajasekari* and *D. virilis* correspondingly increase glass pupation at 15°C and *D. novamexicana* at 15°C, 20°C, 25°C and 30°C. Whereas media pupation in *D. bipectinata* (1.4%), *D. rajasekari* (34.0%) and *D. hydei* (1.2%) increased at 15°C. In *D. virilis* the media pupation decreased to 0.5% and increased to 6.2% and 5.2% at 20°C and 25°C. *D. ananassae* pupated highest on cotton at a lower temperature 15°C. *D. rajasekari* is a cosmopolitan and semiwild species, wherein the cotton pupation decreased to zero and media pupation increased to 58.8% at 30°C. As temperature increases the media pupation in *D. simulans*, *D. yakuba*, *D. mauritiana*, *D. bipectinata* and *D. malerkotliana* increased to 1.0, 12.0, 25.4, 6.0 and 12.4% at 30°C, respectively. Whereas the minimum media pupating domestic species *D. melanogaster* and *D. ananassae* increased to 11.8 and 49.6% on media at 30°C (Figure 1*a* and table 4). The maximum pupation height occurs at 24°C in *D. ananassae*, *D. bipectinata*, and *D. malerkotliana* (except *D. biarmipes*) and there is a considerable decrease in pupation height at high / low temperatures in *D. biarmipes* (Pandey, Singh, 1993).

J.S.F. Barker (1971), P.D. Shirk et al. (1988), N. Shivanna et al. (1996), N.B. Vandal et al. (2003) reported that at a constant temperature most of the species (*D. simulans*, *D. gibberosa*, *D. bipectinata*, *D. malerkotliana*, *D. yakuba*, *D. mauritiana*, *nasuta* subgroup species (*D. nasuta nasuta*, *D. nasuta albomicans*, *D. nasuta kepulauana*, *D. sulfurigaster sulfurigaster*, *D. sulfurigaster neonasuta*), *D. immigrans*, *D. rubida* and *D. pararubida*) preferred to pupate maximum on media, *D. melanogaster*, *D. ananassae*, *D. virilis*, *D. novamexicana* and *D. hydei* larvae preferred to pupate highest on glass and *D. rajasekari* preferred to pupate highest on cotton. They reported that the PSP depends on the quantity of glue protein synthesized by the salivary glands of larvae. The present study revealed a significant decrease in glass pupation in *D. simulans*, *D. yakuba*, *D. mauritiana*, *D. ananassae*, *D. bipectinata*, and *D. malerkotliana* at 30°C, *D. rajasekari* and *D. hydei* at 15°C, *D. virilis* at 20°C and *D. melanogaster* at 15°C and 30°C compared to control. Whereas the glass pupation increased significantly in *D. yakuba* and *D. novamexicana* at 15°C and *D. rajasekari* at 20°C and 25°C. *D. yakuba*, *D. ananassae* and *D. novamexicana* showed a significant decrease in media pupation at 15°C, *D. bipectinata* at 20°C and *D. hydei* at 30°C. Whereas the *D. melanogaster*, *D. simulans*, *D. yakuba*, *D. bipectinata* and *D. malerkotliana* media pupation is significantly increased at 30°C, *D. virilis* and *D. hydei* at 20°C, *D. ananassae* at 25°C and 30°C and *D. mauritiana*, *D. rajasekari* at 15°C, 25°C and 30°C. *D. yakuba* and *D. mauritiana* are primarily tropical but have expanded to the temperate zones. The cotton pupation in *D. rajasekari* significantly increased at 20°C and decreased at 15°C and 30°C. At 15°C and 25°C the cotton pupation is increased and decreased in *D. ananassae*.

In *Drosophila*, temperature is the most important environmental factor which affects all the biological processes at the molecular, cellular and organismic levels (David et al., 1983). Different strains of *D. nasuta nasuta* showed intraspecific variations with respect to preadult fitness at constant and ambient temperatures (Ashadevi, Ramesh, 1998). The temperature involves limitations on *Drosophila* activity while temperature sensitivity involves behavioural alterations, which are expressed only at or above some critical temperature. Different species show different optimum temperatures for growing

and some of them cannot be grown above a certain temperature, which may be 16 – 30°C depending on the species and that the flies were moved to the cooler end of the tube at 22°C when the temperature was higher (above 41°C) (Grossfield, 1978). The present study revealed that the minimum media pupating species *D. melanogaster*, *D. ananassae* pupated 16.0%, 58.0% on media at a higher temperature (30°C) whereas the maximum cotton pupating species *D. rajasekari* pupated 93.0% on media at 30°C. The maximum media pupating species *D. simulans*, *D. yakuba*, *D. mauritiana*, *D. bipectinata* and *D. malerkotliana* showed no change in pupation.

A high temperature and dry periods for several days may act as a strong selective force on developing pupae (Tonzetich, Ward, 1972). S. Spassky (1951) found that a particular homokaryotype of *D. pseudoobscura* showed a higher viability on wet food at high temperatures whereas another one had a higher viability on dry food at a lower temperature. The pupal survivorship decreases at a lower temperature than the higher temperature in *D. melanica* (Tonzetich, Ward, 1972). At a stressful temperature ranging 30°C to 34ºC adults of the sibling species *D. simulans* flies died after 15 hours at 32ºC and *D. melanogaster* being low after 24 hours. At 28ºC, no death occurred for both the species after 15 hours (Parson, 1978). Table 5 reveals that the highest mortality is found in *D. melanogaster* (18.0%), *D. ananassae* (8.2%) and *D. rajasekari* (7.0%) at 30ºC. *D. simulans* (6.8%), *D. yakuba* (7.2%) and *D. malerkotliana* (8%) at 25ºC, *D. simulans* (6.8%), *D. mauritiana* (8.6%), *D. bipectinata* (10.4%), *D. virilis* (5.8%), *D. novamexicana* (13.2%) and *D. hydei* (8.0%) at 20ºC. At 15ºC, the mortality is less than 6% except *D. hydei*, *D. melanogaster* and *D. simulans*. Whereas the mortality is nil in *D. yakuba*, *D. rajasekari*, *D. mauritiana* and *D. hydei* in control.

The acidic resource of pH exerts clear effects on pupation height than the natural resource in *D. melanogaster* and *D. hydei* and the larva pupated closer to the lowest pH of resource than the highest pH resource (Hodge et al., 1996; Hodge, Caslaw, 1997; Hodge, 2001). *Drosophila* is sensitive to a wide variety of odorants and capable of odor discrimination. It is likely that olfactory response plays an important role in the selection of food and identification of hazardous substances (Fuyama, 1978; Shaver et al., 1998). The olfactory response is slow when the larvae keep away from the odour and a larva near the source responds early if the concentration of the odourant is high (Bala et al., 1998; Hussain et al., 2003).

Among the species analyzed in the present study, *D. melanogaster*, *D. simulans*, *D. yakuba* and *D. mauritiana* are closely related sibling species belonging to the *melanogaster* subgroup. It is evident that the larvae of *D. melanogaster* pupate maximum (94.2%) on glass in control and it is decreased gradually from control to 90.8, 87.6, 81.0 and 65.8% at 25°C, 20°C, 15°C and 30°C. The lowest percentage of pupation is at 30°C. These results indicate that the maximum pupation is found at 20°C and 25°C whereas its highest activity is within 15 – 32°C (Ashburner, Thompson, 1978). The media pupation is highest (16.0%) at 30°C. The larvae of the sibling species *D. simulans* pupate minimum on glass (0.2 to 7.0%) at different temperatures analyzed. This shows that the maximum (7.0%) glass pupation is at 20°C. Whereas the media pupation is found to be highest at all the temperatures 94.2% at 30°C, 92.4% at 15°C, 89.2% at 25°C and 86.2% at 20°C. The media pupation is comparatively more than the glass one at all

the temperatures. *D. yakuba* and *D. mauritiana* show increased glass pupation compared to *D. simulans* at all the temperatures. Among these two species, *D.yakuba* pupates about 37.2% at 15°C and *D. mauritiana* pupates 29.0% at 20°C whereas both species pupate less on glass at 30°C. The media pupation is comparatively lesser for *D. simulans.* This shows that the maximum media pupation is at 30°C in these two species.

D. ananassae, *D. bipectinata*, *D. malerkotliana* and *D. rajasekari* are sympatric species (Ranganath et al., 1985; Singh, Pandey, 1991). *D. ananassae* pupates maximum on glass (85.6%) at 20°C and it decreases to 33.0% at 30°C. Whereas the media pupation is highest (58.8%) at 30°C and lowest (3.4%) at 15°C. This indicates that the media pupation of this species is highest at the highest temperature (30°C), whereas its highest activity reported is at 25°C (Ashburner, Thompson, 1978). The present study reveals that in *D. ananassae* the glass pupation is more at 20°C and media pupation is highest at 30°C. *D. bipectinata* and *D. malerkotliana* show similarity in their pupation site preference. The glass pupation is very less compared to *D. ananassae*. The glass pupation is highest at 20°C in both the species (15.4% and 16.0%) and very less at 30°C (3.0% and 6.4%). The media pupation is highest compared to *D. ananassae*. Both species show the highest pupation on media at 30°C (92.6% and 86.4%). *D. rajasekari* shows a contrast result compared to all the species analyzed. The glass and cotton pupation is not found at 30°C. 17.0% (highest) of the larvae pupated at 20°C on glass. Whereas the media pupation is 93.0% at 30°C the cotton pupation is highest (65.0%) at 20°C. *D. ananassae*, *D. bipectinata*, *D. malerkotliana* and *D. rajasekari* belong to sympatric species, their pupation varies. *D. ananassae* pupates more on glass. *D. rajasekari* pupates more on cotton. Whereas *D. bipectinata* and *D. malerkotliana* equally pupate on media at the varied temperatures analyzed. This shows that the sympatric species prefer different sites for their pupation.

D. virilis, *D.novamexicana* and *D. hydei* pupate similar to *D. melanogaster* and *D. ananassae*. All these species do not belong to the same group. *D. virilis* and *D. novamexicana* belong to *virilis* group and *D. hydei* belongs to *repleta* species group, they show similarity in their glass pupation site preference to the *melanogaster* species group species (*D. melanogaster* and *D. ananassae*). Whereas the media pupation is also similar in all the three species and it resembles the media pupation of *D. melanogaster* and *D. ananassae* at all the temperatures analyzed. The highest pupation on glass is at 30°C. *D. virilis* does not pupate on media at 15°C whereas the *D. hydei* pupates highest (27.2%) at 15°C. At 15°C both the species show contrast pupation site preference. *D. virilis* and *D. hydei* are active at 24°C (Ashburner, Thompson, 1978). The sibling species show similarity in their pupation site preference except *D. melanogaster*. The sympatric species also shows similarity in their pupation site preference except *D. ananassae.* The closely related species *D. virilis*, *D. novamexicana* and *D. hydei* show similarity in their pupation and also it is related to the pupation site preference of *D. melanogaster* and *D. ananassae* even though they belong to different groups. One-way ANOVA on pupation site preference within species at different sites differs from non-significant to significant in different species (F = 0.000 to 121.658 on cotton, F = = 3.758 to 62.4 on glass and F = 13.802 to 212.087 in media). This shows that closely related species show similarity in their pupation site preference. Statistical analysis (two-

way ANOVA) between species and within sites shows a significant difference (F = = 18.59 on cotton, F = 42.45 on glass and F = 57.67 in media). This indicates that the pupation site preference between species significantly varies.

Comparison between sibling, sympatric and closely related species showed a variation in pupation at different temperatures. The species collected from different geographical distribution and ecological backgrounds were maintained for about 2 decades at a constant temperature in the laboratory. They were not adapted for a constant temperature. When temperature changes their PSP also changes. This indicates that temperature influences the PSP in different species the temperature range is not similar for all the species. Differences in the temperature-dependent pupation responses among closely related species have been implicated as a possible basis for reducing interspecific competition (Fogleman, Markow, 1982; Ricci, Budnik, 1984; Schnebel, Grossfield, 1986 *a*; Kimura, 1988). The present study reveals that the significant variation in larval pupation site choices in different species is due to extreme temperatures. High and low temperatures affect the behavioural activities / response of the larvae, which may cause pupation site / habitat variations. It is an adaptation of larvae to protect pupa from hazardous effects of temperature.

Acknowledgement. Thanks are due to Professor H.A. Ranganath Drosophila Stock Centre Department of Zoology, University of Mysore, 'Manasagangotri' Mysore, for Drosophila stocks and UGC-SAP-II and COSIST for financial assistance.

REFERENCES

Anderson W.W. Genetics divergence in M. Vetukhiv's experimental populations *Drosophila pseudoobscura*. 3. Divergence in body size // Genetics Research. 1973. Vol. 7. P. 255 – 266.

Ashburner M. *Drosophila* // A laboratory handbook / Cold Spring Harbor Laboratory, Cold Spring Harbor, New York, 1989.

Ashadevi J.S., *Ramesh S.R*. Intraspecific variation with respect to certain components of fitness in *Drosophila nasuta nasuta* at different temperature // Indian J. of Experimental Biology. 1998. Vol. 37. P. 37 – 42.

Barker J.S.F. Ecological differences and competitive interaction between *D. melanogaster* and *D. simulans* in small laboratory populations // Oecologia. 1971. Vol. 8. P. 139 – 143.

Bala A.D.S., *Panchal P*., *Siddiqi O*. Osmotropotaxis in larvae of *Drosophila melanogaster* // Current Science. 1998. Vol. 75. P. 48 – 51.

Bauer S.J. Sex differences in pupation site choice in *Drosophila melanogaster* // Drosophila Information Service. 1984. №60. P. 58.

Bauer S.J., *Sokolowski M.B*. A genetic analysis of path length and pupation height in natural population of *Drosophila* // Canadian J. of Genetics Cytology. 1985. Vol. 27. P. 334 – 340.

Blankenhorn M. Different growth responses to temperature and resource limitation in three fly species with similar life histories // Evolutionary Ecology. 1999. Vol. 13. P. 395 – 409.

Bochdanovits Z., *Jong G. de*. Temperature dependent larval resource allocation shaping adult body size in *Drosophila melanogaster* // J. of Evolutionary Biology. 2003. Vol. 16. P. 1159 – 1167.

Bochdanovits Z., *Klis H. van der*, *Jong G. de*. Covariation of gene expression and adult body size in natural populations of *Drosophila melanogaster* // Molecular Biology and Evolution. 2003. Vol. 20. P. 1760 – 1766.

Bock I.R., *Wheelar M.R*. The *Drosophila melanogaster* species Group. Univ Tex. 1972. №7213. P. 1 – 102.

Budnik M., *Brncic D*. Preadult competition between population of *Drosophila subobscura* and established populations of *Drosophila simulans* in Chile // Oecologia. 1983. Vol. 58. P. 137 – 140.

Casares. P., *Carracedo M.C*. Pupation height in *Drosophila*: sex differences and influence of larval developmental time // Behaviour Genetics. 1987. Vol. 17. P. 523 – 535.

Coyen J.A., *Bundgaard J*., *Prout T*. Geographic variation of tolerance to environmental stress in *Drosophila subobscura* // American Naturalist. 1983. Vol. 122. P. 478 – 488.

Crill W.W., *Huey R.B*., *Gilchrist G.W*. Within- and between – generation effects of temperature on the morphology and physiology of *Drosophila melanogaster* // Evolution. 1996. Vol. 50. P. 1205 – 1218.

David J., *Clawel M.F*. Influence de la temperature sur le nombre le pourcentage eclosion et la tail le des oenfs pondus par *D. melanogaster* // Annual Society of Entomology. 1968. Vol. 5. P. 161 – 177.

David J.R., *Allemand R*., *Herrewege J. van*, *Cohet Y*. Ecophysiology: abiotic factors // The Genetics and Biology of Drosophila / Eds. M. Ashburner, H.L. Carson, J.N. Thompson. London: Acad. Press, 1983. Vol. 3B. P. 106 – 109.

David J.R., *Moreteau B*., *Gautier J.R*., *Stockel A*., *Imasheva A.G*. Reactions norms of size characters in relation to growth temperature *Drosophila melanogaster*: an isofemale line analysis // Genetics Selection of Evolution. 1994. Vol. 26. P. 229 – 251.

Delpuech J.M., *Moreteau B*., *Chicke J*., *Pla E*., *Vouidibio J*., *David J.R*. Phenotypic plasticity and reaction norms in temperate and tropical population of *Drosophila melanogaster*: ovarion size and development temperature // Evolution. 1995. Vol. 49. P. 670 – 675.

Eanes W.F. Analysis of selection on enzyme polymorphism // Annual Review of Ecology and Systamatics. 1999. Vol. 30. P. 301 – 326.

Ehrman P. Sexual behaviour // The genetics and biology of Drosophila / Eds. M. Ashburner, T.R.F. Wright. New York: Academic Press, 1978. Vol. 2b. 171 p.

Fogleman J.C., *Markow T. A*. Behavioural differentiation between two species of cactophilic *Drosophila* II Pupation site preference // Southwest Naturalist. 1982. Vol. 27. P. 315 – 319.

Fogleman J.C., *Wallace B*. Temperature-dependent development and competitive ability of three species in the *D. affinis* subgroup // American Middle Naturalist. 1980. Vol. 104. P. 341 – 351.

Fuyama Y. Behaviour genetics of olfactory responses in *Drosophila*. II and odorant specific variant in natural population of *Drosophila melanogaster* // Behaviour Genetics. 1978. Vol. 8. P. 399 – 414.

Gebhardt M.B., *Stearns S.C*. Reaction norms for developmental time and weight at eclosion in *Drosophila mercatorum* // J. of Evolutionary Biology. 1988. Vol. 1. P. 335 – 354.

Gebhardt M.B., *Stearns S.C*. Phenotypic plasticity for life history characters in *Drosophila melanogaster*. III. Effect of the environment on genetic parameters // Genetics Research. 1992. Vol. 60. P. 87 – 101.

Grossfield J. Non-sexual behaviour of *Drosophila* // The genetics & biology of *Drosophila* / Eds. M. Ashburner, T.R.F. Wright. New York: Academic Press, 1978. Vol. 2a. P. 1.

Gruwez G., *Hoste C*., *Lints C.Y*., *Lints F.A*. Oviposition rhythm in *Drosophila melanogaster* and its alteration by change in photoperiodicity // Experientia. 1971. Vol. 27. P. 1414 – 1416.

Hodge S. The effect of pH and water content of natural resources on the development of *Drosophila melanogaster* larvae // Drosophila Information Service. 2001. №84. P. 38 – 43.

Hodge S., *Caslaw P*. The effect of resource pH on pupation height in *Drosophila* (Diptera: Drosophilidae) // J. of Insect Behaviour. 1997. Vol. 11. P. 47 – 59.

Hodge S., *Campbell-Smith R*., *Wilson N*. The effect of resource of acidity on the development of *Drosophila* larvae // Entomologist. 1996. Vol. 115. P. 129 – 139.

Hussain A., *Krishna P*., *Abhishek V*., *Siddiqi O*. A rapid method for measuring olfactory responses of *Drosophila* // Current Science. 2003. Vol. 85. P. 857 – 859.

Imasheva A.G., *Loeschcke V*., *Zhivatovsky L.A*., *Lazebny O.E*. Effects of extreme temperature on phenotypic variation and developmental stability in *Drosophila melanogaster* and *Drosophila buzzatti* // Biological J. of Linnean Society. 1997. Vol. 6. P. 117 – 126.

Imasheva, A.G., *Loeschcke V.*, *Zhivatovsky L.A.*, *Lazebny O.E.* Stress temperature and quantitative variation in *Drosophila melanogaster* // Heredity. 1998. Vol. 31. P. 246 – 253.

Kaneshiro K.Y., *Carson H.*, *Fowler K.*, *Heed W.D.* Niche separation in pair of homosequential *Drosophila* species from the island of Hawaii // American Naturalist. 1973. Vol. 197. P. 766 – 774.

Kimura M.T. Adaptation to temperate climates and evolution of over wintering strategies in the *Drosophila melanogaster* species group // Evolution. 1988. Vol. 42. P. 1288 – 1297.

Lazebny O.E., *Zakharchuk E.B.*, *Imasheva A.G.* Larval density and variation of body size in laboratory lines of *Drosophila melanogaster* // Rus. J. of Genetics. 1996. Vol. 32. P. 1010 – 1012.

Markow T.A. Survey of intra and interspecific variation for pupation height in *Drosophila* // Behaviour Genetics. 1979. Vol. 9. P. 209 – 217.

Mensua J.L. Some factors affecting pupation height of *Drosophila* // Drosophila Information Service. 1967. №76. P. 42.

McKenzie J.A. The influence of low temperature on survival and reproduction in population of *Drosophila melanogaster* // Australian J. of Zoology. 1975. Vol. 23. P. 237 – 247.

McKenzie J.A, *McKenzie S.W.* Comparative study of resource utilization in natural population *Drosophila melanogaster* and *Drosophila simulans* // Oecologia. 1979. Vol. 40. P. 299 – 309.

Moed G.H. de, *Jong G. de*, *Scharloo W.* Environmental effects on body size variation in *Drosophila melanogaster* and its cellular basis // Genetics Researchers. 1997. Vol. 70. P. 35 – 43.

Moed G.H. de, *Kruitwagen C.L.J.J.*, *Jong G. de*. Critical weight for the induction of pupariation in *Drosophila melanogaster*: genetic and environmental variation // J. of Evolutionary Biology. 1999. Vol. 12. P. 852 – 858.

Noach E.J.K., *Jong G. de*, *Scharloo W.* Phenotypic plasticity in morphological traits in drosophila melanogaster // J. of Evolutionary Biology. 1996. Vol. 9. P. 831 – 844.

Ohnishi S. Oviposition pattern of several *Drosophila* species under various light environments // J. of Insect Physiology. 1977. Vol. 23. P. 1157 – 1162.

Parson P.A. Boundary conditions for *Drosophila* resource utilization in temperate regions. Especially at low temperatures // American Naturalist. 1978. Vol. 112. P. 1063 – 1074.

Peter P.A. Resistance of the sibling species *Drosophila melanogaster* and *Drosophila simulans* to high temperature in relation to humidity: evolutionary implications // Evolution. 1978. Vol. 33. P. 131 – 136.

Pandey M.B., *Singh B.N.* Effect of biotic and abiotic factors on pupation height in four species of *Drosophila* // Indian J. Experimental Biology. 1993. Vol. 31. P. 912 – 917.

Ranganath H.A., *Gowda L.S.*, *Rajasekarshetty M.R.* Competition studies between three sympatric species of *Drosophila* // Entomon. 1985. Vol. 10. P. 249 – 253.

Ramachandra N.B., *Ranganath H.A.* Estimation of population fitness of parental races *Drosophila nasuta nasuta* and *Drosophila nasuta albomicana* and of the newly evolved Cytoraces I and II // Genome. 1988. Vol. 30. P. 58.

Ricci M., *Budnik M.* Influence of temperature density and interspecific competition on the preadult development of Chilean populations of *Drosophila subobscura* and *Drosophila immigrans* // Brazilian J. of Genetics. 1984. Vol. 7, №2. P. 255 – 264.

Ringo J., *Wood D.* Pupation site selection in *Drosophila simulans* // Behaviour Genetics. 1983. Vol. 13. P. 17 – 27.

Robinson S.J., *Partridge L.* Temperature and clinal variation in larval growth efficiency in *Drosophila melanogaster* // J. of Evolutionary Biology. 2001. Vol. 14. P. 14 – 21.

Rockwell R.V., *Grossfield J. Drosophila* behavioural cues for oviposition // American Middle Naturalist. 1978. Vol. 99. P. 316 – 368.

Spassky S. Effect of temperature and moisture content of the nutrient medium on the viability of chromosomal types in *Drosophila pseudoobscura* // American Naturalist. 1951. Vol. 85. P. 177 – 180.

Seizer M.B., *Sanner A.B.* Selection for light preference during oviposition in *Drosophila pseudoobscura* // Canadian J. of Genetics Cytology. 1983. Vol. 25. P. 446 – 449.

Shaver S.A., *Varnam C.J.*, *Hilliker A.J.*, *Sokolowski M.B.* The foraging gene affects adult but not larval olfactory related behaviour in *Drosophila melanogaster* // Behavioural Brain Research. 1998. Vol. 95. P. 23 – 29.

Shirk P.D., *Roberts P.A.*, *Harn C.H.* Synthesis and secretion of salivary gland proteins in *Drosophila gibberosa* during larval and prepupal development // Roux's Archives in Developmental Biology. 1988. Vol. 197. P. 66 – 72.

Shivanna N., *Siddalinga Murthy G.S.*, *Ramesh S.R.* Larval pupation site preference and its relationship to the glue proteins in a few species of *Drosophila* // Genome. 1996. Vol. 39. P. 105 – 111.

Shivanna N., *Ramesh S.R.* Intraspecific larval pupation site preference in *D. melanogaster* // Drosophila Information Service. 1997. №80. P. 1 – 2.

Singh B.N., *Pandey M.B.* Intra and interspecies variation in pupation height in *Drosophila* // Indian J. of Experimental Biology. 1991. Vol. 29. P. 926 – 929.

Sokal R.R., *Ehrlich P.*, *Hunter P.*, *Schlager G.* Some factors affecting pupation site in *Drosophila* // Annals of Entomological Society of America. 1960. Vol. 53. P. 174 – 182.

Sameoto D.D., *Miller R.S.* Selection of pupation sites by *Drosophila melanogaster* and *Drosophila simulans* // Ecology. 1968. Vol. 49. P. 177 – 180.

Srivastav T., *Singh B.N.* Effect of temperature on oviposition in four species of the *melanogaster* group of *Drosophila* // Revista Brazilaria Biologica. 1998. Vol. 58. P. 491 – 495.

Schnebel E.M., *Grossfield J.* Oviposition temperature range in four *Drosophila* species traids from different ecological backgrounds // American Middle Naturalist. 1986 *a*. Vol. 16. P. 25 – 35.

Schnebel E.M., *Grossfield J.* Pupation- temperature range in 12 species *Drosophila* species from different ecological backgrounds // Experientia. 1986 *b*. Vol. 42. P. 600 – 604.

Schnebel E.M., *Grossfield J.* Mating-temperature range in *Drosophila* // Evolution. 1986 *c*. Vol. 38. P. 1296 – 1307.

Schnebel E.M., *Grossfield J.* Temperature effects on pupation height response in four *Drosophila* species traids // J. of Insect Physiology. 1992. Vol. 38. P. 727 – 732.

Stanley S.M., *Parson P.A.* The response of the cosmopolitan species, *Drosophila melanogaster* to ecological gradients // Proceedings of Ecological Society of Australia. 1981. Vol. 11. P. 121 – 130.

Tonzetich J., *Ward C.L.* Interaction effects of temperature and humidity on pupal survival in *Drosophila melanica* // Evolution. 1972. Vol. 27. P. 495 – 504.

Vandal N.B., *Modagi S.A.*, *Shivanna N.* Larval pupation site preference in a few species of *Drosophila* // Indian J. of Experimental Biology. 2003. Vol. 41. P. 918 – 920.