RESEARCH ARTICLE

Coexistence of three different *Drosophila* species by rescheduling their life history traits in a natural population

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Abstract

We present evidence for coexistence of three different *Drosophila* species by rescheduling their life history traits in a natural population using the same resource, at the same time and same place. *D. ananassae* has faster larval development time (DT) and faster DT(egg-fly) than other two species thus utilizing the resources at maximum at both larval and adult stages respectively. Therefore, *D. ananassae* skips the interspecific competition at preadult stage but suffers more from intraspecific competition. However, *D. melanogaster* and *D. biarmipes* have rescheduled their various life history traits to avoid interspecific competition. Differences of ranks tests for various life history traits suggest that except for DT(egg-pupa), the difference of ranks is highest for the combination of *D. melanogaster* and *D. ananassae* for all other life history traits. This difference is maintained by tradeoffs between larval development time and pupal period and between pupal period and DT(egg-pupa) in *D. ananassae*.

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Introduction

Interspecific competition is often thought to be most intense between closely related species. Often, the species that are studied in the laboratory do not compete in nature because they have widely separated geographic distributions or are widely separated either taxonomically or ecologically. Understanding how interspecific interactions drive changes in the abundance and genetic composition of species has been a major goal of ecology and evolutionary biology for over century. Environmental variability and adaptive foraging behaviour have been shown to favour coexistence on an ecological time scale. Egas *et al.* (2004) have provided evidence that coexistence is evolutionarily stable whenever it is ecologically stable but in most cases, such coexistence cannot be reached through gradual evolution. Their results suggest that tradeoffs in fitness determining traits can have counterintuitive effects on the evolution of specialisation. In another approach, Palmer *et al.* (2003) have discussed the mechanisms that restrict and maintain diversity within mutualistic guilds. Mutualistic interactions are diverse and widespread and often involve multispecies guilds of mutualists competing for access to one or more partner species.

The coexistence of competing species may be mediated by various mechanisms including resource partitioning and various kinds of environmental heterogeneity. According to the principle of competitive exclusion (Hardin 1960), species using the same resources cannot coexist unless interspecific competition is weak compared to intraspecific competition. The interspecific competition is weakened, if resources or physical spaces are different or competing species are using the same resources, in the same place at the same time, thus resulting in coexistence by competitive exclusion. The results of interspecific competition are of great interest because it either results in equilibrium adjustment by two species or replacing the other interacting species. Interspecific competition can be broadly categorized into two types, exploitation and in-

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terference (Park 1954). Exploitation competition (scramble type competition) occurs when there is limitation of resource. Interference competition (contest type competition) occurs when organisms impede the access of others to a resource, even if the resource is not limiting and it usually involves chemical or behavioural interactions between organisms before the utilisation of a resource (Neal 2004). The competitive exclusion principle has been tested in various organisms some of which are (discussed in Neal 2004) yeasts (by Gause in 1930s), *Paramecium*, flour beetles (*Tribolium*, *Oryzaephilus* and *Rhizopertha*), duck weeds (*Lemna* and *Wolffia*) and *Drosophila* (Merrell 1951; Miller 1954; Barker and Podger 1970; Budnik and Brncic 1972, 1974; Sevenster and Van Alphen 1993; Joshi and Thompson 1995).

Two species exhibit strong interspecific competition because they overlap considerably in their use of a common resource such as food. Natural selection may promote a divergence in their resource requirements resulting in the reduction of interspecific competition and allowing for the coexistence of the two species. Where there is interspecific competition, each species reduces the growth potential of the other(s) and there is a mutual reduction of fitness. The Lotka–Volterra model of interspecific competition predicts that species can coexist if the effect of interspecific competition is much lower than intraspecific competition, but if the reverse is true, only one species will survive the interaction.

The Indian subcontinent, with its subtropical climate and varied physiographic conditions, including variable altitudes and luxuriant flora offers an abode for the rich and wide distribution of *Drosophila* fauna. A survey of literatures shows that various species of *Drosophila* were collected from the same natural population at a given time (see Reddy and Krishnamurthy 1973–74; J. P. Gupta, personal communication). Therefore, it is a well-established fact that various species of *Drosophila* coexist in nature and collection of various species at a time, from the same place, is not a chance factor. Thus, coexistence is an important issue in ecology. *Drosophila* species enjoy reproductive isolation to save their genetic identity in the natural populations. However, it is not enough for their existence in the nature. There are several other factors (like resource limitation, predation, etc.), which compel different drosophilid species to share the same niche and thus coexistence cannot be ruled out. Since complete competitors cannot coexist (Gause's principle, see Odum 1996) therefore, they are forced again in nature probably to reschedule their life cycles through different life history traits to avoid competition, particularly at preadult stages, with each other. We have tested the competitive exclusion principle and present evidence to show that these *Drosophila* species, by rescheduling their life history traits provide a mechanism enhancing coexistence of these species, which are using exactly the same resources, in the same place and at the same time, at two different temperatures. We performed the experiments at 20°C and 25°C temperatures because during the time of collection (during the month of September) the temperature of Bangalore (12.96 N, 77.58 E and 3021 feet above sea level) climate fluctuates between 19°C to 28°C (see www.climate-zone.com/climate/india/celcius/bangalore.htm). Also, for ectothermic organisms like *Drosophila*, temperature is a most important factor of the environment and adaptation to temperature appears to be involved in the geographic distribution of species (Davis and Tsacas 1981). We used the pure culture method unlike others, who used the mixed culture methods (Barker and Podger 1970; Budnik and Brncic 1974; Sevenster and Van Alphen 1993; Joshi and Thompson 1995) because metabolic waste products of the first species probably interferes with the development of other coexisting species. (Budnik and Brncic 1974). All three *Drosophila* species used in the present study belong to different subgroups of the *melanogaster* species group. *D. melanogaster* belongs to the *melanogaster* subgroup and is cosmopolitan in distribution. *D. ananassae* belongs to the *ananassae* subgroup and is one of the most common species in tropical and subtropical regions of the world, especially in and around places of human habitations (domestic habitat) and appears to be cosmopolitan (Tobari 1993; Singh 1996). *D. biarmipes* belongs to the *suzukii* subgroup (Hsu 1949) and was originally described by Malloch (1924) from Coimbatore, India and is less frequent in nature than the other two species described above. In the review of the *melanogaster* species group (Bock and Wheeler 1972) and in the catalogue of world fauna prepared by Wheeler (1981), both *D. rajasekari* (described as a new species by Reddy and Krishnamurthy 1968) and *D. raychaudhurii* (described as a new species by Gupta 1969) are listed as synonymous with *D. biarmipes*. *D. biarmipes* males possess an apical dark black patch on their wings. A variation in male wing patch has been observed and males without the patch have also been found. Males possessing a wing patch have greater mating success than those without a patch, thus suggest the role of black wing patch as a visual stimulus in mating behaviour of the species (Singh and Chatterjee 1987). *D. biarmipes* males in our collection have a dark black patch on their wings.

Coexistence of closely related species, using exactly the same resource, in the same place and at the same time, may be mediated by various mechanisms. In *Drosophila* species, as in many other taxa, the faster development rate enhances the competitive ability of the species. In this study, we present evidence for coexistence of three *Drosophila* species by rescheduling their life history traits at two different temperatures. The rescheduling in various life history traits are maintained either by tradeoffs or by increasing the growth rate during the preadult stage.

Materials and methods

Drosophila melanogaster, *D. ananassae* and *D. biarmipes* flies were sampled in September 2002 from Yashavantpur fruit market, Bangalore (hereafter referred as Bangalore) on the same day (morning and evening), at the same place, using the same resource (from a shop selling only bananas). All these flies were brought to the laboratory and each female was put in a single vial for identification as well as F_1 progeny. We found nine *D. melanogaster*, 28 *D. ananassae* and 21 *D. biarmipes* flies by looking at sex comb patterns of a male from each vial. F_1 virgin flies were collected from each vial and sexed and kept in different vials with a density of 25 flies per vial. These virgin flies were aged for 5–7 days and five isofemale lines of each species were selected randomly (for having uniformity in data/data analyses) for this study. From each line of each of three species, 10 males and 10 females (in duplicate) were selected randomly (after mixing all flies from several vials of a concerned line) for the initiation of F_2 generation. These flies were allowed to lay eggs using Delcour's process (Delcour 1969) for 7–8 h to get sufficient eggs in petri dish at 25°C and then parents were transferred for the study of larval feeding rate. Two hundred eggs were taken randomly from each plate and eggs were kept in vials (in duplicate; 50 eggs in each vial) at two different temperatures, 25°C and 20°C, of each line of each species at constant light condition in BOD incubators. The time of egg keeping is recorded. All these vials were monitored regularly (after 12 h) at the interval of two hours for the emergence of first instar larvae. The larval development time (LDT) is recorded as the time from emergence of first instar larvae to the start of their pupation. The time from the start of pupation to the eclosion of fly is recorded as the pupal period. The pupal period is also monitored at the interval of 2 h for eclosed flies at both temperatures from 8 A.M. to 8 P.M. Flies that emerged between 8 P.M. to 8 A.M., were not used in this study. The total development time, DT(egg-fly), is recorded as the time from egg laying (median of egg laying) to the eclosion of fly. Similarly, the development time from egg to pupa, DT(egg-pupa), is recorded as the time from median of egg laying to the start of pupation. However, the DT(egg-pupa), is included in the DT(egg-fly), but we have taken the former as a new development time to understand the development rate at this level, if any. Virgin F_2 flies were scored and sexed immediately after the eclosion and kept in separate food vial (maximum 10 flies per vial at a given time) for ageing. After 5–7 days of ageing, body sizes (thorax and wing length) of males and females were measured. The left wing of each etherized fly was kept horizontally and length was measured between anterior cross vein to the tip of the third longitudinal vein. The thorax length was measured from anterior margin of the thorax to the posterior tip of the scutellum (laterodorsal position). Data for body measurements were recorded in units (one unit = 16.67 μm).

For each line of each species 20–25 third instar larvae were collected randomly and allowed to feed on a generous smear of live yeast paste. Larvae were placed one at a time in a small petri dish (4.00 cm in diameter) containing agar coated with a thin layer of 10% yeast solution. After a one minute of acclimination period, the feeding rate was observed for one minute with the use of a stopwatch. The feeding rate was recorded as the number of cephalo pharyngeal sclerite retraction per minute (Joshi and Mueller 1996) in 10 larvae of each duplicate of each line (total five lines) in each species. The feeding rate of larvae at 25°C was considered only for this study. The feeding rate of larvae, grown at 20°C, could not be performed as most of larvae remain sitting and even after an acclimination of 30 min at 25°C did not show any significant deviation with feeding rate of larvae grown at 25°C. During the study, we raised all species simultaneously and provided the same food. Throughout the study, a simple culture medium, containing agar-agar, crude sugar, dried yeast and active yeast (50 : 50), maize powder, nipagin, propionic acid and water, was used.

Statistical analyses

Since, there are no statistically significant differences between both the duplicates' data on body size as well as on different life history traits, we pooled data in different analyses of body size and of different life history traits respectively. In order to know the rank order and pairwise differences between means of different species for body size as well as in their different life history traits, we performed Student–Newman–Keuls test or SNK test (Zar 2003).

Results

The mean body size of all three species at two different temperatures are presented in figure 1. It is evident from figure 1 that these three species differ significantly in their body size at both temperatures (25°C and 20°C). Mean of all ten lines (data of duplicate line of each species is pooled because there is no significant differences between duplicate lines) is considered for comparative study. Amongst all males, the wing length is highest in *D. melanogaster* (77.14 and 83.09 at 25°C and 20°C respectively), followed by *D. ananassae* (74.44 and 80.94 at 25°C and 20°C respectively) and *D. biarmipes* (71.65 and 79.75 at 25°C and 20°C respectively). On an average, the male thorax length is highest in *D. biarmipes* (53.82 and 56.10 at 25°C and 20°C respectively) followed by *D. ananassae* (52.94 and 57.28 at 25°C and 20°C respectively; it is highest at 20°C) and the lowest thorax length is of *D. melanogaster* (51.02 and 53.01 at 25°C

and 20°C respectively). Amongst all females, the wing length is more or less similar in *D. melanogaster* (85.48 and 93.21 at 25°C and 20°C respectively) and *D. ananassae* (85.73 and 92.25 at 25°C and 20°C respectively) and lowest in *D biarmipes* (82.16 and 90.51 at 25°C and 20°C respectively). The female thorax length in *D. biarmipes* is (62.12 and 62.94 at 25°C and 20°C respectively), followed by *D. ananassae* (60.49 and 63.25 at 25°C and 20°C respectively) and the lowest female thorax length is in *D. melanogaster* (56.24 and 59.67 at 25°C and 20°C respectively). Our results on body size for *D. melanogaster* and *D. ananassae* are partly consistent with that of Morin *et al*. (1997), which suggests that *D. ananassae* has a bigger thorax but shorter wing than *D. melanogaster* at all temperatures. Figure 2 shows the mean wing/thorax ratio (W/T ratio) of males and females of all three species at both 25°C and 20°C. It is obvious from figure 2 that the mean W/T ratio is highest in *D. melanogaster* in both sexes at both temperatures, followed by *D. ananassae* and *D. biarmipes*. J. R. David group (see Morin *et al*. 1997 and references therein) has suggested the W/T ratio as a specific trait inversely proportional to wing loading. In order to understand the exact nature of interactions based on body size and W/T ratio, we performed SNK test (Zar 2003), presented in table 1. Based on thorax size at 25°C, the difference of rank is highest between *D. biarmipes* and *D. melanogaster* in both sexes ($q = 5.819$, $P < 0.05$) and the lowest for males of *D. ananassae* and *D. melanogaster* ($q = 2.886$, $P < 0.05$) and lowest for females of *D. biarmipes* and *D. ananassae* ($q = 3.661$, $P < 0.05$). However, at 20°C both *D. biarmipes* and *D. ananassae* show nonsignificant difference in rank order in both sexes and the highest difference of ranks are shown by *D. ananassae* and *D. melanogaster* in both sexes. Similarly, for wing lengths in both sexes at both temperatures, the difference of ranks is highest for *D. melanogaster* and *D. biarmipes* ($P < 0.05$ in all cases except for female wing at 20°C). For W/T ratio, *D. melanogaster* and *D. biarmipes* combination shows the highest difference in rank in both sexes at both temperatures ($P < 0.05$) except for male W/T ratio at 20°C (see table 1). The one-tailed *t*-test suggests statistically significant differences

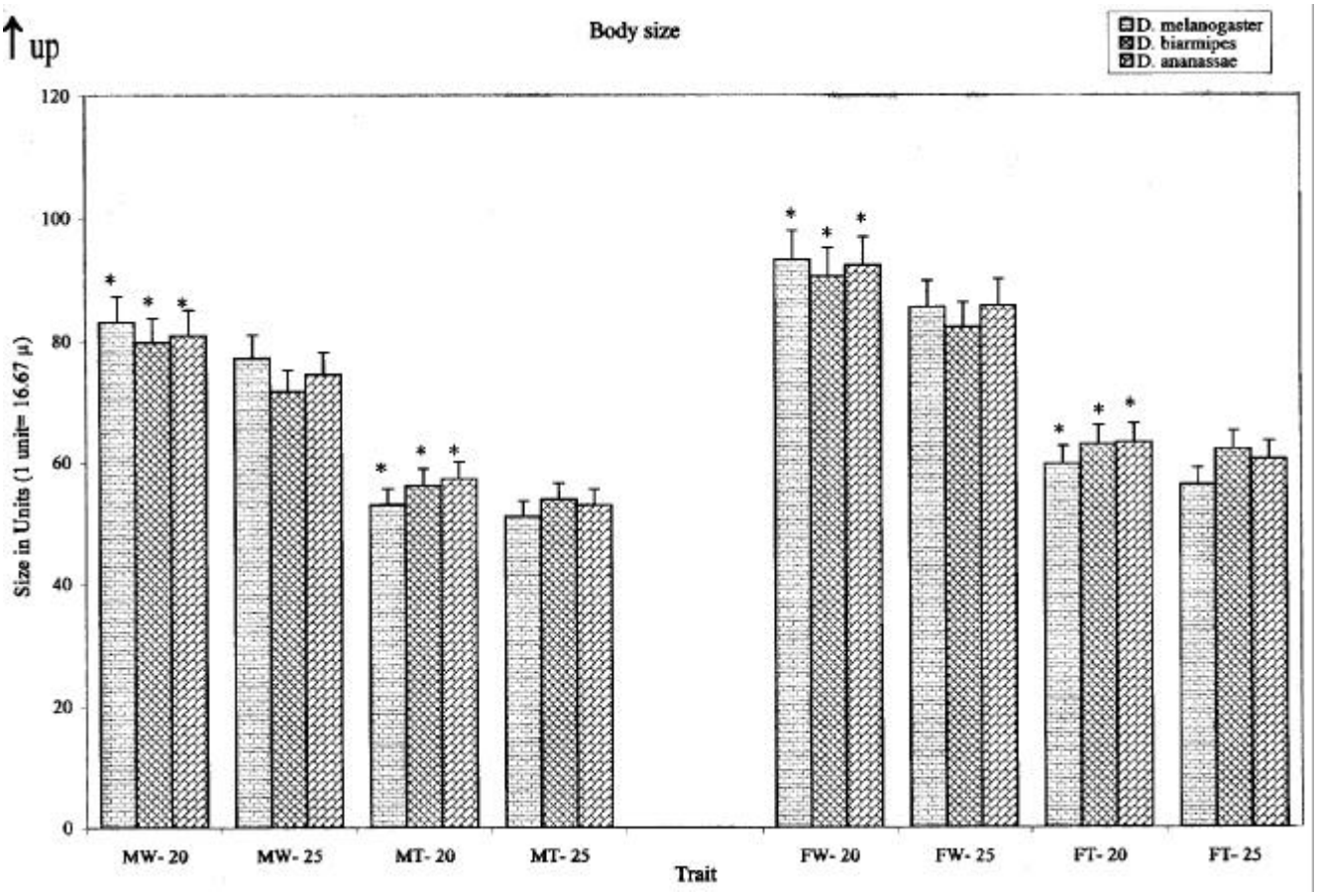

Figure 1. Mean (± SE) body size of males and females of *D. ananassae*, *D. biarmipes* and *D. melanogaster* at 20°C and 25°C. The values 20 and 25 indicate the temperatures at 20°C and 25°C respectively. The size is in units (1 unit = 16.67 µm). The standard error is fixed at 5% level.

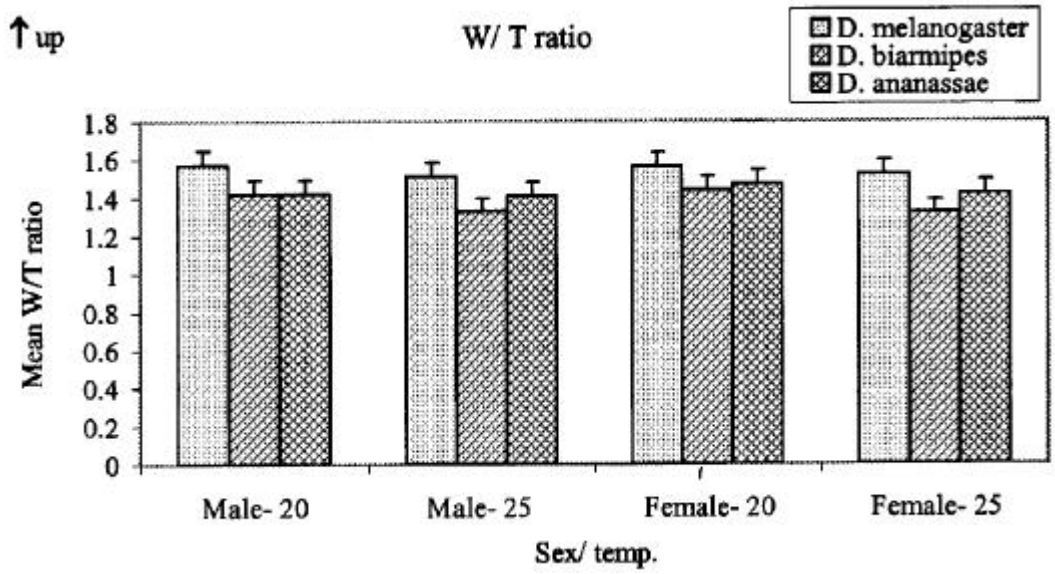

Figure 2. Mean (± SE) W/T ratio of males and females of *D. ananassae*, *D. biarmipes* and *D. melanogaster* at 20°C and 25°C. The values 20 and 25 indicate the temperatures at 20°C and 25°C respectively. The standard error is fixed at 5% level.

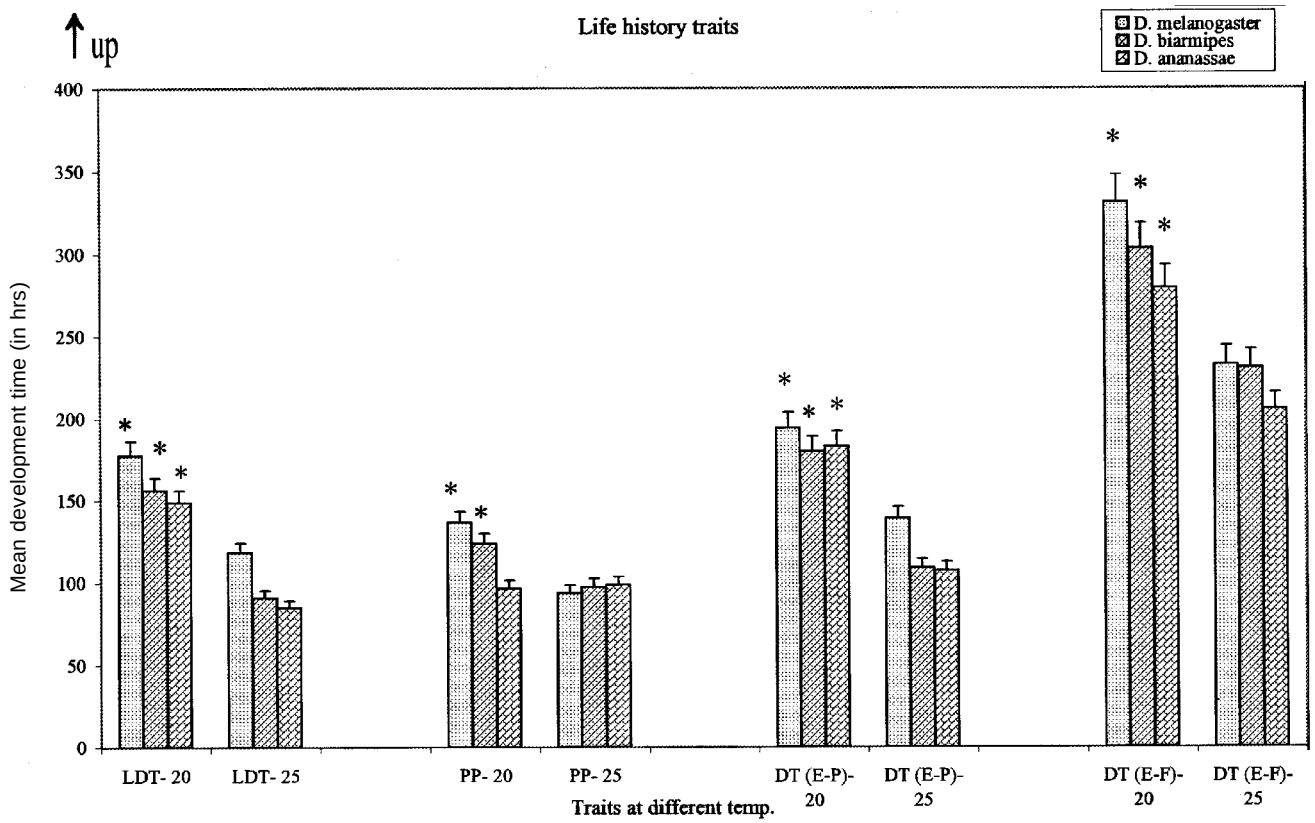

Figure 3. Mean (± SE) life history traits of males and females of *D. ananassae*, *D. biarmipes* and *D. melanogaster* at 20°C and 25°C. The values 20 and 25 indicate the temperatures at 20°C and 25°C respectively. The standard error is fixed at 5% level.

from zero between body size at 25°C and 20°C (figure 1) and between W/T ratio at 25°C and 20°C (data not shown) in all three species of *Drosophila* except for male W/T ratio of *D. ananassae*. Mean of LDT, pupal period, DT(egg-pupa) and DT(egg-fly) at both 25°C and 20°C and one-tailed *t*-test between traits at both 25°C and 20°C are presented in figure 3. The LDT and DT(egg-pupa) are highest (in hours) in *D. melanogaster* at both temperatures and the LDT is lowest in *D. ananassae* but pupal period and DT(egg-pupa) are more or less similar in *D. ananassae and D. biarmipes* (figure 3). The *t*-tests for temperature difference in each species show highly significant differences from zero except for pupal period of *D. ananassae* (figure 3). Tables 2, 3 show the phenotypic correlations among different life history traits, mean body size and mean W/T ratio at 25°C and 20°C respectively. As expected, both *D. melanogaster* and *D. biarmipes*, do not show any significant correlations between body size and any life history traits at 25°C (table 2), thus indicating that their coexistence at the same place is

Table 1. Pairwise multiple comparison rank test (SNK test) for analysing differences in mean body size and mean W/T ratio at 25°C and 20°C among three different species of *Drosophila*.

Trait	Comparison	Difference of ranks	*p*	*q*	$P < 0.05$
Male thorax – 25°C	*D. biarmipes* vs *D. melanogaster*	162.00	3	5.819	Yes
	D. biarmipes vs *D. ananassae*	108.00	2	5.773	Yes
	D. ananassae vs *D. melanogaster*	54.00	2	2.886	Yes
Male thorax – 20°C	*D. ananassae* vs *D. melanogaster*	160.00	3	5.747	Yes
	D. ananassae vs *D. biarmipes*	32.00	2	1.710	No
	D. biarmipes vs *D. melanogaster*	128.00	2	6.842	Yes
Female thorax – 25°C	*D. biarmipes* vs *D. melanogaster*	173.00	3	6.214	Yes
	D. biarmipes vs *D. ananassae*	68.50	2	3.661	Yes
	D. ananassae vs *D. melanogaster*	104.50	2	5.586	Yes
Female thorax – 20°C	*D. ananassae* vs *D. melanogaster*	133.00	3	4.778	Yes
	D. ananassae vs *D. biarmipes*	12.50	2	0.669	No
	D. biarmipes vs *D. melanogaster*	120.50	2	6.441	Yes
Male wing – 25°C	*D. melanogaster* vs *D. biarmipes*	185.00	3	6.645	Yes
	D. melanogaster vs *D. ananassae*	74.50	2	3.982	Yes
	D. ananassae vs *D. biarmipes*	110.50	2	5.906	Yes
Male wing – 20°C	*D. melanogaster* vs *D. biarmipes*	105.00	3	3.790	Yes
	D. melanogaster vs *D. ananassae*	64.00	2	3.421	Yes
	D. ananassae vs *D. biarmipes*	41.50	2	2.218	No
Female wing – 25°C	*D. melanogaster* vs *D. biarmipes*	117.00	3	4.203	Yes
	D. melanogaster vs *D. ananassae*	6.00	2	0.321	No
	D. ananassae vs *D. biarmipes*	111.00	2	5.933	Yes
Male W/T ratio – 25°C	*D. melanogaster* vs *D. biarmipes*	0.1810	3	26.733	Yes
	D. melanogaster vs *D. ananassae*	0.1070	2	15.770	Yes
	D. ananassae vs *D. biarmipes*	0.0742	2	10.963	Yes
Male W/T ratio – 20°C	*D. melanogaster* vs *D. ananassae*	0.150	3	15.342	Yes
	D. melanogaster vs *D. biarmipes*	0.146	2	14.911	Yes
	D. biarmipes vs *D. ananassae*	0.004	2	0.431	No
Female W/T ratio – 25°C	*D. melanogaster* vs *D. biarmipes*	0.199	3	22.756	Yes
	D. melanogaster vs *D. ananassae*	0.103	2	11.836	Yes
	D. ananassae vs *D. biarmipes*	0.095	2	10.920	Yes
Female W/T ratio – 20°C	*D. melanogaster* vs *D. biarmipes*	0.124	3	18.601	Yes
	D. melanogaster vs *D. ananassae*	0.093	2	13.858	Yes
	D. ananassae vs *D. biarmipes*	0.032	2	4.744	Yes

Difference of ranks of female wing –20°C is not given in the table because difference in median values among the treatment groups for female wing –20°C is nonsignificant ($H = 4.645$, df = 2, $P = 0.098$).

not affected by the body size and they coexist by rescheduling their different life history traits (see figure 3). Both, *D. melanogaster* and *D. biarmipes* differ in LDT and DT(egg-pupa) only at 25°C (figure 3). However, *D. ananassae* flies at 25°C show significant negative correlations between body size and various life history traits (table 2). Thus, it is speculated from the results that *D. ananassae* flies adjust their preadult life cycle by increasing growth rate, thus have shorter development time (DT(egg-fly)), to reach the adult stage faster than other coexisting species. We also found the novel tradeoffs in *D. ananassae* between LDT and pupal period at 25°C and between pupal period and DT(egg-pupa) at both 25°C and 20°C (see tables 2, 3); which have been reported earlier for the first time in our previous study (J. P. Yadav and B. N. Singh 2005 Evolutionary genetics of *Drosophila* ananassae: evidence for tradeoffs among several fitness traits; submitted). At 20°C, *D. melanogaster* flies also show significant negative correlations between DT(egg-pupa) and male W/T ratio, female wing and thorax lengths (table 3) while *D. ananassae* flies at 20°C show significant negative correlation between male W/T ratio and pupal period also. *D. biarmipes* flies do not show significant negative correlations with any life history traits at either temperature. We further investigated the difference of ranks based on various life history traits among these three species of *Drosophila* by SNK test (Zar 2003) and results are presented in the table 4. The differences of ranks are highest between *D. melanogaster* and *D. ananassae* for LDT and DT(egg-fly) at both tem-

Table 2. Test of correlations among different life history traits and mean body size (wing and thorax lengths) and mean W/T ratio at 25°C in three different species of *Drosophila*.

D. melanogaster	LDT	Pupal period	DT (egg-pupa)	DT (egg-fly)	Male wing	Male thorax	Male W/T ratio	Female wing	Female thorax
LDT	–								
Pupal period	0.72361**	–							
DT(egg-pupa)	0.94192****	0.63833*	–						
DT(egg-fly)	0.95461****	0.78077***	0.97935****	–					
Male wing	– 0.00427	0.13771	– 0.13991	– 0.07739	–				
Male thorax	– 0.00510	0.06417	– 0.10696	– 0.06997	0.85508***	–			
Male W/T ratio	– 0.02444	0.12527	– 0.11427	– 0.05986	0.57761	0.07163	–		
Female wing	– 0.30582	– 0.00532	– 0.48249	– 0.39304	0.86781***	0.72162**	0.52468	–	
Female thorax	– 0.22978	– 0.14458	– 0.43462	– 0.39076	0.84703***	0.66749*	0.57456	0.92857****	–
Female W/T ratio	0.05418	0.33278	0.24162	0.28352	– 0.53674	– 0.35517	– 0.47896	– 0.51981	– 0.79906***
D. biarmipes									
LDT	–								
Pupal period	0.79901***	–							
DT(egg-pupa)	0.84704***	0.58606	–						
DT(egg-fly)	0.73724**	0.30982	0.82649***	–					
Male wing	– 0.25900	– 0.35499	0.02730	– 0.15095	–				
Male thorax	– 0.26445	– 0.07934	– 0.11174	– 0.06712	– 0.00367	–			
Male W/T ratio	– 0.03987	– 0.21944	0.07767	– 0.09658	0.76908***	– 0.640438*	–		
Female wing	0.34178	– 0.07449	0.56985	0.42591	0.67609*	– 0.26489	0.67404*	–	
Female thorax	– 0.18074	– 0.59839	– 0.11332	0.12153	0.53106	– 0.42646	0.66697*	0.58849	–
Female W/T ratio	0.58886	0.43777	0.80582***	0.42861	0.35893	0.03774	0.24494	0.70863*	– 0.15266
D. ananassae									
LDT	–								
Pupal period	**– 0.97502****	–							
DT(egg-pupa)	0.92181****	**– 0.81677*****	–						
DT(egg-fly)	0.35971	– 0.17223	0.66576*	–					
Male wing	0.01123	0.11709	0.20101	0.26513	–				
Male thorax	0.38269	– 0.27315	0.49306	0.45918	0.65505*	–			
Male W/T ratio	– 0.47347	0.43975	– 0.45719	– 0.36851	– 0.00958	– 0.76115**	–		
Female wing	**– 0.95616****	0.92094****	**– 0.91663****	– 0.37198	– 0.03969	– 0.25956	0.28855	–	
Female thorax	– 0.59059	0.55022	– 0.59123	– 0.08421	– 0.16341	0.06552	– 0.25008	0.70833*	–
Female W/T ratio	**– 0.69224***	0.68911*	**– 0.63338***	– 0.42192	0.12150	– 0.43929	0.68211*	0.62603	– 0.10684

*$P < 0.05$; **$P < 0.02$; ***$P < 0.01$; ****$P < 0.001$; df = 8. Bold values indicate tradeoffs.

peratures and for pupal period at 20°C only. However, the differences of ranks are highest between *D. melanogaster* and *D. biarmipes* for DT(egg-pupa) at both temperatures (table 4). Thus, it is now clear from the results presented in table 4 that different *Drosophila* species have rescheduled their various preadult stages in a mutualistic environment to avoid competition among them for food and space. Figure 4 presents the mean larval feeding rate (grand mean of different lines of a species), in all three species at 25°C. It is evident from the figure 4 that *D. ananassae* shows the highest feeding rate (80.82), followed by *D. melanogaster* (71.80) and *D. biarmipes* (64.51). In addition, the range of feeding rate is also highest in *D. ananassae* (32.3) but more or less similar in other two species (20 and 20.1 in *D. melanogaster* and *D. biarmipes* respectively, data not shown). The same results are found for minimum and maximum feeding rates, being highest in *D. ananassae* and lowest in *D. biarmipes* (data not shown). One-way ANOVA suggests the significant difference ($P < 0.001$) between feeding rates of these species (data not shown). The correlation analyses between larval feeding rate and LDT, pupal period, DT(egg-pupa) and DT(egg-fly) do not show any significant correlation with any trait (data not shown).

Discussion

Over 2000 *Drosophila* species are known and many of them coexist in the nature thus, interspecific competition

Table 3. Test of correlations among different life history traits and mean body size (wing and thorax lengths) and mean W/T ratio at 20°C in three different species of *Drosophila*.

D. melanogaster	LDT	Pupal period	DT (egg-pupa)	DT (egg-fly)	Male wing	Male thorax	Male W/T ratio	Female wing	Female thorax
LDT	–								
Pupal period	0.92981****	–							
DT(egg-pupa)	0.57993	0.44366	–						
DT(egg-fly)	0.90561****	0.89874****	0.72548**	–					
Male wing	0.22736	0.42705	– 0.54781	0.05438	–				
Male thorax	0.50188	0.68705*	– 0.10664	0.48961	0.77470***	–			
Male W/T ratio	– 0.29876	– 0.24472	– 0.69324*	– 0.56260	0.51653	– 0.14028	–		
Female wing	– 0.34784	– 0.10165	**– 0.75882****	– 0.40386	0.60893	0.22381	0.61856	–	
Female thorax	– 0.43631	– 0.18451	**– 0.75207****	– 0.37719	0.50381	0.22399	0.44455	0.91788****	–
Female W/T ratio	0.29590	0.25075	0.08878	0.01249	0.19773	– 0.00941	0.34920	0.08134	– 0.32051
D. biarmipes									
LDT	–								
Pupal period	0.52804	–							
DT(egg-pupa)	0.90025****	0.28141	–						
DT(egg-fly)	0.89418****	0.79653***	0.80431***	–					
Male wing	0.71760**	0.08278	0.80367***	0.55761	–				
Male thorax	0.13579	– 0.13649	0.24992	0.07294	0.68167*	–			
Male W/T ratio	0.40988	0.25469	0.32492	0.36243	– 0.10477	– 0.79879***	–		
Female wing	0.53567	– 0.19997	0.73205**	0.33740	0.86685***	0.73809**	– 0.28467	–	
Female thorax	0.11648	– 0.37574	0.36099	– 0.00522	0.65616*	0.77185***	– 0.51501	0.75379**	–
Female W/T ratio	0.61535	0.24128	0.55723	0.50049	0.34228	– 0.00964	0.31059	0.39495	– 0.30588
D. ananassae									
LDT	–								
Pupal period	– 0.54363	–							
DT(egg-pupa)	0.69197*	**– 0.90145******	–						
DT(egg-fly)	0.65215*	– 0.42158	0.77257***	–					
Male wing	0.02334	– 0.23601	0.25037	0.17829	–				
Male thorax	– 0.16476	0.09296	– 0.08569	– 0.04316	0.91984****	–			
Male W/T ratio	0.50551	**– 0.72497****	0.84089***	0.69813*	0.47106	0.10069	–		
Female wing	– 0.06682	– 0.16944	0.17931	0.12709	0.94573****	0.94382****	0.28562	–	
Female thorax	– 0.11572	0.30171	– 0.22837	– 0.03585	0.68675*	0.77579***	0.03011	0.63841*	–
Female W/T ratio	0.14947	– 0.61507	0.40681	– 0.04998	0.59391	0.37624	0.51419	0.47238	0.22559

*$P < 0.05$; **$P < 0.02$; ***$P < 0.01$; ****$P < 0.001$; df = 8. Bold values indicate tradeoffs.

is obvious among them (Powell 1997). Studies of interspecific competition are difficult to perform in natural populations, therefore initially considerable attention was given to laboratory studies of mixed species populations (Barker and Podger 1970; Budnic and Brncic 1974; Joshi and Thompson 1995). Sevenster and Van Alphen (1993) have carried out a combination of theoretical modeling, laboratory studies and field observations on the coexistence of neotropical *Drosophila* in Panama. Their major premise is that different *Drosophila* species adopt two different life history strategies – the fast developers die young when there is plentiful of food and breeding sites while the slow developers live longer to find a suitable breeding site when there is scarcity of food and breeding site.

The differences in body size among these three species are obvious. *D. melanogaster* and *D. ananassae* are domestic and have human commensals (Powell 1997) while *D. biarmipes* is a wild species and thus the later requires more migration than other two species. Figure 2 presents the evidence that *D. biarmipes* has the lowest mean W/T ratio and the study of Morin *et al*. (1997, and references therein) suggest that the W/T ratio is inversely proportional to the wing loading, i.e. the smaller the W/T ratio the more flight capacity. Also, the SNK test presented for difference of ranks on body size (table 1) clearly show that at 25°C, *D. melanogaster* and *D. biarmipes* combinations show largest differences which are significant from zero in all the cases, i.e. a distance is maintained by these two species to avoid interspecific competition between them.

A simplistic view of natural selection is that all organisms have adapted an ideal life history, which results in a high rate of survival, but this is not the case in nature. Interspecific competition between pairs of species results in one species eliminating the other, or both species coexisting at reduced densities. Egas *et al*. (2004) have demonstrated that coexistence is evolutionarily stable depending upon the stability of ecology of the environment and have suggested that tradeoffs in fitness determining traits can have counterintuitive effects on the evolution of specialisation. Krijger *et al*. (2001) have argued that LDT is a major determinant of competitive rank order among drosophilid species. In addition, it provides a basis for studying the role of life history tradeoffs in community level process. Our results (figure 3) also suggest that these three species have developed a kind of adjustment by rescheduling their

Table 4. Pairwise multiple comparison rank test (SNK test) for analysing differences in different mean life history traits at 25°C and 20°C among three different species of *Drosophila*.

Trait	Comparison	Difference of ranks	*p*	*q*	$P < 0.05$
LDT– 25°C	*D. melanogaster* vs *D. ananassae*	172.00	3	6.178	Yes
	D. melanogaster vs *D. biarmipes*	128.00	2	6.842	Yes
	D. biarmipes vs *D. ananassae*	44.00	2	2.352	No
LDT– 20°C	*D. melanogaster* vs *D. ananassae*	28.00	3	13.347	Yes
	D. melanogaster vs *D. biarmipes*	21.00	2	9.952	Yes
	D. biarmipes vs *D. ananassae*	7.300	2	3.395	Yes
Pupal period – 20°C	*D. melanogaster* vs *D. ananassae*	40.00	3	19.271	Yes
	D. melanogaster vs *D. biarmipes*	12.80	2	6.167	Yes
	D. biarmipes vs *D. ananassae*	27.20	2	13.105	Yes
DT – (egg-pupa) – 25°C	*D. melanogaster* vs *D. biarmipes*	160.00	3	5.747	Yes
	D. melanogaster vs *D. ananassae*	140.00	2	7.483	Yes
	D. ananassae vs *D. biarmipes*	20.00	2	1.069	No
DT – (egg-pupa) – 20°C	*D. melanogaster* vs *D. biarmipes*	14.20	3	5.670	Yes
	D. melanogaster vs *D. ananassae*	11.00	2	4.392	Yes
	D. ananassae vs *D. biarmipes*	3.20	2	1.278	No
DT – (egg-fly) – 25°C	*D. melanogaster* vs *D. ananassae*	95.00	3	3.413	Yes
	D. melanogaster vs *D. biarmipes*	1.00	2	0.054	No
	D. biarmipes vs *D. ananassae*	94.00	2	5.025	Yes
DT – (egg-fly) – 20°C	*D. melanogaster* vs *D. ananassae*	51.80	3	19.253	Yes
	D. melanogaster vs *D. biarmipes*	27.80	2	10.333	Yes
	D. biarmipes vs *D. ananassae*	24.00	2	8.920	Yes

Difference of ranks of pupal period –25°C is not given in the table because difference in median values among the treatment groups for pupal period –25°C is nonsignificant ($H = 1.827$, df = 2, $P = 0.401$).

LDT and DT(egg-fly). Table 2 shows positive correlations among different life history traits in *D. melanogaster* and *D. biarmipes* at 25°C, i.e. these two species are better adapted than *D. ananassae* which shows tradeoffs for LDT and pupal period and for pupal period and DT (egg-pupa). Therefore, it is suggested that the major adjustment is made by *D. ananassae* flies at the time of pupal period (longest pupal period at 25°C and the shortest pupal period at 20°C). These variations in pupal period and tradeoff between pupal period and DT(egg-pupa) in *D. ananassae* suggest that inclusion of pupal period as a new life history trait is a right decision. Unlike SNK test for differences of ranks on body size (*D. melanogaster* and *D. biarmipes* combinations show largest differences which are significant from zero in all the cases), the differences of ranks for various life history traits show largest differences which are significant from zero in all the cases at both temperatures except for DT (egg-pupa) for *D. melanogaster* and *D. ananassae* combination (table 4). This suggests that the LDT and pupal period are two crucial stages for making decision for the coexistence of *D. melanogaster* and *D. biarmipes*, while *D. ananassae* flies coexist with them by establishing a tradeoff between the pupal period and DT(egg-pupa) in its life cycle and by increasing its larval feeding rate, thus resulting the faster growth. The higher larval feeding rate in *D. ananassae* (80.82) could be attributed to the intraspecific competitive ability of larvae (Joshi and Mueller 1996). In interspecific competition, species with a short development time (fast species) are expected to suffer less than species with a long development time (slow species), while their rapid consumption enables 'fast' species to consume a disproportionally large share of the resource patch (Sevenster and Van Alphen 1993). Therefore, *D. ananassae* qualifies as a fast species and the slow species in this case is *D. melanogaster*. The longer DT(egg-fly) in *D. melanogaster* could be to avoid the direct effects of exploitation competition. Thus, as shown by various studies (Hardin 1960; Sevenster and Van Alphen 1993; Odum 1996), two or more species can coexist if the interspecific competition is weak and the intraspecific competition is strong. Further, the interspecific competition is weakening, if species are using the same resource, in the same place and at the same time. Overall, it is concluded that

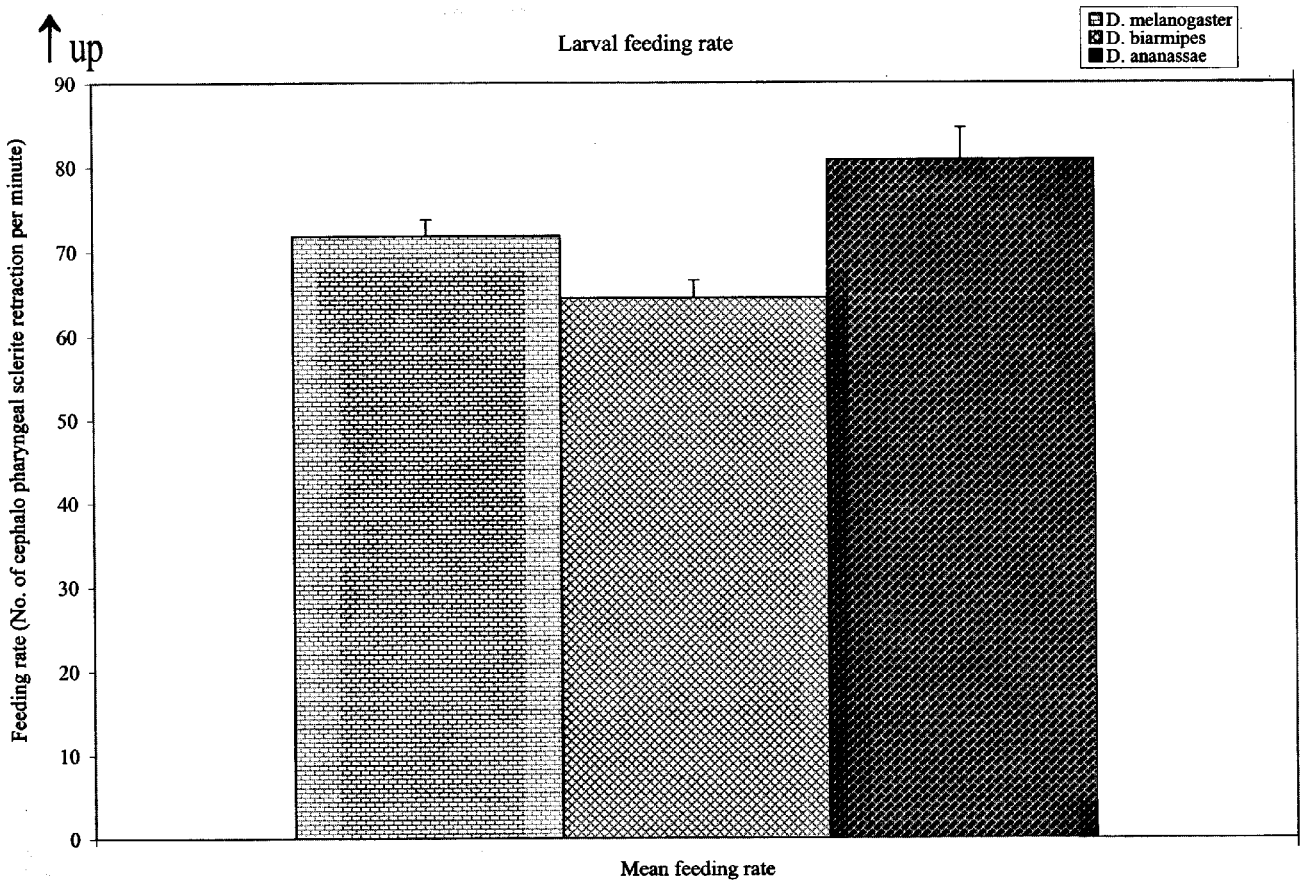

Figure 4. Mean (± SE) larval feeding rate of *D. ananassae*, *D. biarmipes* and *D. melanogaster* at 25°C. The feeding rate is recorded as the number of cephalo pharyngeal sclerite retraction per minute.

different species can coexist using the same resource, in the same place and at the same time by either rescheduling their life history traits or by increasing intraspecific competition by increasing growth rate or by using both phenomena. Our results may help partly in understanding the ecological character displacement maintained truly based on phenotypic evolution or by resource competition between species coexisting in the same place, at the same time.

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