126.91 ± 22.60 min in *C. capitata*. The post-extrication behavior of both flies exarate adults was analyzed and compared. Figure 2 A,B show representative examples of the respective pathways followed in a restricted circular arena. During this post-extrication stage *D. melanogaster* shows a walking behavior frequently interrupted by numerous stationary periods of resting (Figure 2 A,C), whereas medflies displayed first a rapid exploratory behavior (on the average 7.86 ± 3.75 min) followed by a single long period of resting (119.04 ± 25.24 min) until the final phenotype of the imago is attained (Figure 2 B,D). The diameters of the circumferences in the diagrams (Figure 2 C,D) are proportional to the duration of the resting time in that position. The length of the path for the examples in Figure 2 was 12.65 cm for *D. melanogaster* and 48.10 cm for *C. capitata*. The average length of the pathways was 11.02 ± 1.91 cm for *D. melanogaster* and 45.40 ± 13.47 cm for *C. capitata*. Total time for *D. melanogaster* periods of walking represented 6.1% of the time of the whole phase and for *C. capitata* the single walking period represented 11.31% of the total BMP (Figure 1). Significantly, when the extrication times were added to the mobility times, total activity time represented 12.12% of the *Drosophila* BMP, whereas the equivalent time for *Ceratitis* represented 8.15% (Figure 1). Comparing these observations with the previously reported equivalent post-ecdysial behavior in other flies like the sarcophagids *Sarcophaga crassipalpis*, *S. bullata*, and *S. argirostoma* (Žďárek and Denlinger, 1986, 1987), all seem to follow a similar pattern to that of *C. capitata*, very different from that of *D. melanogaster* and (probably) other drosophilids. The mobility parameters in our experimental conditions of reduced movement might be proportional to the remainder of the energy resources available for metamorphosis, mainly haemolymph trehalose, muscle glycogen and lipids (Bochicchio, 2012; Nestel *et al.*, 2003) and in this case might be very different in wild conditions. Although behavior heterogeneity among individuals of each species is significant, the post-ecdysial exarate adult behavioral pattern indicates that in both flies around 90% of resting time is required during this period (Figure 1). This seems to indicate that for full completion of exarate adult body features, a similar proportion of resting time is required in both flies. In turn, this suggests that in the wild, a bottleneck for the behavior of cyclorrhaphans during the non-eating BMP might be the availability of energetic reserves to be spent during that phase of the life cycle. This kind of data is also important for the male-sterile programs for pest flies control.

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The effect of pyrogallol on the resistance to starvation in *Drosophila bipectinata.*

Krishna, M.S., and Uchenna U. Waturuocha. Drosophila Stock Centre, Department of Studies in Zoology, University of Mysore, Mysore, India.

Organisms often face stressful environmental conditions in nature, defined as environmental factors that reduce fitness (Koehn and Bayen 1989). Common environmental stressors, desiccation

and starvation, are the most important sources of natural selection. Development of behavioral and physiological mechanisms by organisms to deal with periods of starvation and desiccation allow them to alleviate the consequences of environmental stress (Hoffmann and Parsons, 1993; Randall *et al*., 1997). Studies carried out on insect groups, such as Lepidoptera, Orthoptera, and Coleoptera, showed that females mate with multiple males during periods of starvation and desiccation, perhaps because males transfer nuptial gifts containing large amounts of water and nutrients that may improve female stress resistance (Boucher and Huignard, 1987; Butlin *et al*., 1987; Ivy *et al*., 1999; Edvardsson, 2006). Also, studies in fruit flies of the genus *Drosophila* inhabiting desertic areas have shown that mated females are more resistant to desiccation than unmated females (Knowles *et al*., 2004, 2005). These physiological responses suggests that male-female may affect ecologically relevant traits and indicates that, in a natural scenario, mating may not be harmful as previously thought (Chapman *et al*., 1995; Wolfner, 1997; Lung *et al*., 2002; Chapman and Davies, 2004).

Apart from the physiological and genetic factors that influence the starvation resistance, the quantity and quality of food also plays an important role in the flies' ability to survive starvation. Studies conducted on the quality of nourishment have shown that a protein enriched diet increases the resistance to starvation more than the diet enriched with carbohydrates (Djawdan *et al*., 1998). Antioxidants, which are a constituent of the flies natural diet in the wild, have, however, so far not been tested to check their effect on resistance to starvation in flies. For this reason, here we carry out the experiments in order to determine if any such relationship exists. Most starvation studies have been focused on *D. melanogaster* (Service *et al*., 1985; Rose *et al*., 1992; Rion and Kawecki, 2007) and hence we use the species *D. bipectinata*, which is a member of the *bipectinata* species complex of the *ananassae* subgroup of the *melanogaster* species group (Bock and Wheeler, 1972), and is of common occurrence in India (Gupta and Panigrahy, 1990).

Materials and Methods

Establishment of stock:

The experimental stock of *Drosophila bipectinata*, was established from progenies of 50 iso-female lines collected from Chamundi Hills at Mysore, Karnataka, using mixed fruit bait. These flies were cultured in a standard wheat cream agar medium and maintained at a constant temperature of 22 ± 1ºC with a relative humidity of 70%. In each generation, the emerged flies were mixed together and redistributed to ten new culture bottles each with 20 flies (10 males + 10 females). This procedure was continued for 3 generations to acclimatize the flies to laboratory conditions. At the fourth generation eggs were collected using Delcour's procedure (1969) and 100 eggs were seeded in new culture bottles. When adults started emerging, virgin females and males were isolated within 3 hours of their eclosion. These flies were aged for 5-6 days to be used in the present experiments.

Preparation of antioxidant media at different concentrations:

The antioxidant pyrogallol was dissolved in water at a concentration of 1000 ppm (*i.e*., 1 g in 100 ml of distilled water), which was maintained as stock solution from which different amounts were taken and mixed in 30 ml of the standard wheat cream agar media in concentrations of 1 ppm, 10 ppm, 15 ppm, 20 ppm, and 25 ppm, respectively, to check the LD_{50} concentration of the compound (that is, the concentration at which 50% of the progeny dies). The LD_{50} was found to be 10 ppm. The flies raised in three sublethal doses of 1 ppm, 3 ppm, and 5 ppm were used for the present experiments.

Effect of pyrogallol on SOD enzyme levels:

Enzyme preparation for Superoxide Dismutase analysis: The flies cultured on different sub-lethal concentrations of 1 ppm, 3 ppm, and 5 ppm of pyrogallol were subjected to assay the effect of pyrogallol on the stress enzyme Superoxide Dismutase (SOD). To assay this, five adult (5 males and 5 females) flies from each concentration were taken along with the untreated (control) in different Eppendorff tubes. 200 microlitres of 50 mM Phosphate buffer of pH 7 for Catalase assay, 200 microlitres of 250 mM Phosphate buffer of pH 7.8 for SOD Assay were added and crushed using tissue homogenizer in ice cold conditions and centrifuged at 8000 rpm for 20 min in a cooling Microfuge. After this, the supernatants were poured into other Eppendorff tubes. 0.1 ml/100 µl of this enzyme extract was used for the assay.

Measurement of Superoxide Dismutase enzyme activity: SOD enzyme was assayed using a modified procedure originally described by Beauchamp and Fridovich (1971). The enzyme extract was added to a mixture of solutions containing 250 mM phosphate buffer (0.8 ml), 100 mM Methionine (1 ml), 100 mM Riboflavin (0.5 ml), 5 mM EDTA (0.1 ML), 750 mM NBT (0.1 ML), the volume of which was made up to 3 ml with distilled water. A mixture without the enzyme and NBT was prepared which served as blank and a control with NBT and no enzyme was prepared. These mixtures are exposed to sunlight or a bright light of about 400 watts; during this reaction NBT gets reduced to formazone, and was read at 560 nm. The total protein content of enzyme was estimated by Lowry's method, and the activity was expressed in units /mg of protein.

Effect of pyrogallol on starvation resistance:

To study the effect of pyrogallol on starvation resistance, 5-6 day old adults, mated and unmated males and females obtained from untreated and pyrogallol treated (1 ppm, 3 ppm, 5 ppm) media. Ten mated/unmated, males/ females from each medium (untreated/pyrogallol treated) were transferred into vials containing non-nutritive agar (12.4 g agar and 2.4 g *p*-hydroxybenzoic acid in 23 ml ethanol per litre). The number of days survived by each mated/unmated, male/ female was recorded by observing the vials every 12-24 hours for mortality, and the assay was continued until all the flies died. A total of four replicates (40 males and 40 females) were run separately for both mated and unmated flies. The results obtained were subjected to one way ANOVA followed by the Tukey's *post hoc* test.

Effect of pyrogallol on the accessory gland proteins:

Unmated males from the untreated and pyrogallol treated groups were obtained to study the effect of pyrogallol on the quantity of Accessory gland proteins.

Sample preparation of unmated males:

Accessory glands of unmated (etherized) males (untreated and treated males) were individually and separately dissected out using insect saline with the help of entomological needles. These glands were fixed in 95% ethanol. Fixed glands were taken on a clean slide and membrane was removed with the help of fine needles and a stereomicroscope. The result secretion alone was washed in a mixture of methanol and chloroform (1:1) and dried at 37°C in an incbator for about 15 minutes. About 100 µl of sample buffer of about 100 µl (0.623 M Tris HCl pH 6.8, 1% Sodium Dodecyl Sulphate, 1% β-mercaptoethanol, 10% glycerol) was added to each sample to dissolve the glands and secretions. 10 pairs of accessory glands from each group were separately collected for quantitative estimation of total accessory gland proteins using Lowry's method (1951).

Sample preparation of mated males:

To obtain mated males, a 5-6 day old virgin female (untreated and treated) and an unmated untreated and treated male were individually aspirated into Elens-Wattiaux mating chamber (1964) and observed for 1 hour (untreated male with untreated female and treated male with treated female of the same concentration). Pairs that remain unmated within 1 hour were discarded. If mating occurs, mating latency (time between introduction of male and female into a mating chamber until initiation of copulation) and the Copulation Duration (time between initiations to termination of copulation of each pair) was recorded. Soon after copulation (within 5 minutes), mated males were etherized and sacrificed to obtain Acps and fixed in 95% ethanol. Ten pairs of accessory glands from each group were collected separately for quantitative estimation of Acps using Lowry's method (1951).

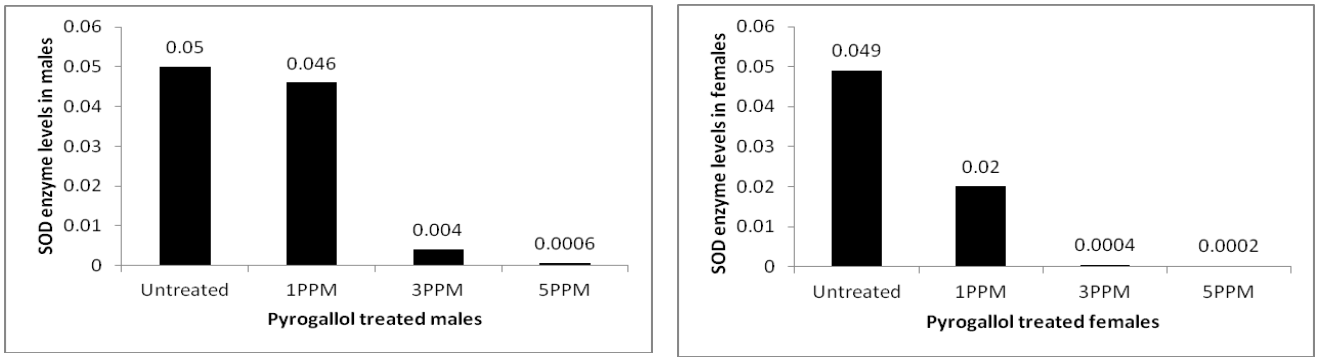

Figure 1a, Left: Effects of pyrogallol on the SOD levels in males of *D. bipectinata.* SOD enzyme levels in µl/fly in untreated and pyrogallol treated flies. Figure 1b, Right: Effects of pyrogallol on the SOD levels in females of *D. bipectinata.*

Results

Effect of pyrogallol on Superoxide Dismutase enzyme activity:

Figure 1a shows the SOD enzyme levels in the pyrogallol treated males of *D. bipectinata.* It was observed that the SOD enzyme levels were found to be higher in the untreated males when compared to the treated males. Among the pyrogallol treated males the levels of SOD were found to have decreased with an increase in the concentration of pyrogallol. The lowest level of the SOD enzyme was found at the 5 ppm concentration and highest was at the 1 ppm concentration. This suggests that in males of *D. bipectinata* SOD activity decreased with increasing pyrogallol concentration.

SOD enzyme levels of untreated and pyrogallol treated females of *D. bipectinata* is depicted in Figure 1b. SOD levels were found to be higher in the untreated when compared to the pyrogallol treated females. Among the pyrogallol treated females SOD activity was the least at 5 ppm and highest at 1 ppm. Futher SOD activity decreased with increase in the concentration of pyrogallol. Between the sexes the SOD enzyme levels in the female flies was lower than that of the males, both in the untreated and the pyrogallol treated groups, suggesting that the females had a lower level of SOD enzyme activity than the males.

Effects of pyrogallol on starvation resistance:

The Kaplan-Meier survival curve of unmated and mated female flies grown in treated and control groups when subjected to starvation are shown in Figures 2a and 2b. The variation in

survival of the flies could be clearly observed between the mated and unmated flies, with the mated flies surviving significantly longer than the mated flies. Also a variation between the control and treated groups could be observed with the treated surviving longer than the control. In the treated groups of 3 ppm and 5 ppm females survived longer than that of the 1 ppm group. Between the sexes, both mated and unmated females survive longer than the males, and the females of 3 ppm and 5 ppm survive longer than that of the control and 1 ppm.

The Kaplan-Meier survival curve of unmated and mated male flies grown in control and treated groups when subjected to starvation are depicted in Figures 2c and 2d. A variation was observed in the survival of the mated and unmated flies where, the survival of the mated flies was higher than that of the unmated flies. Between the control and treated groups, the survival of the flies increased with an increase in the concentration of the antioxidant. Within the treated group, among the unmated males there was an increase in the survival with an increase in the concentration of pyrogallol, whereas, among the mated males the 3 ppm flies survived the longest followed by the 5 ppm and the 1 ppm.

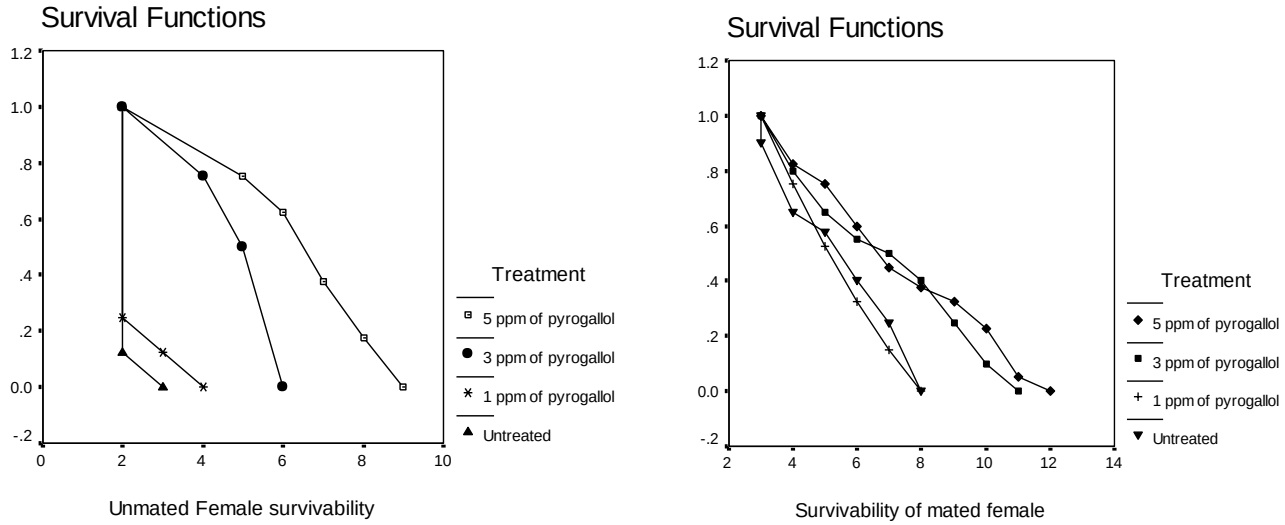

Figure 2. Survival curve of of *D. bipectinata.* (a, Left) unmated females; (b, Right) mated females.

Effect of pyrogallol on the accessory gland proteins:

The mean values of the amount of accessory gland proteins present in unmated and mated males grown in untreated and pyrogallol treated groups, along with the amount transferred, are depicted in Table 3. A slight variation was observed in the concentration of Acps in the untreated and the pyrogallol treated groups, in the unmated males, lower concentrations were observed in the untreated group than the treated. The highest concentration was seen in 5 ppm followed by 1 ppm and the least in 3 ppm concentration, while in the mated males, the least concentration was in the 3 ppm group followed by the 5 ppm and 1 ppm, however the untreated group had a higher concentration of Acps than the 3 ppm group. The amount of Acp transferred between the untreated and the 3 ppm concentration of the pyrogallol treated groups was the same. Among the treated groups there was a difference seen between the three groups, with the highest amount of transfer seen in the 5 ppm concentration and the least seen in 1 ppm concentration of the pyrogallol treated groups.

The one way ANOVA followed by the Tukey's *post hoc* test, when carried out on the data obtained for the unmated and mated males, showed that there was a significant variation between the

untreated and 3 ppm pyrogallol treated group, while within the treated group, significant difference between 1 ppm, 5 ppm, and 3 ppm was seen. However, there was no significant difference seen between the untreated and the 1 ppm and 5 ppm groups. In the case of the amount of Acp transfer, a significant difference was seen between the untreated and the 5 ppm concentration of the pyrogallol treated groups; however, there was no significant difference between the other concentrations with the untreated group. Within the pyrogallol treated group significant difference was seen between the 5 ppm group and the 1 ppm and 3 ppm groups; however, there was no significant difference seen between the 1 ppm and 3 ppm groups by the Tukey's *post hoc* test.

Table 1a. Mean and median of survival time in unmated females of *D. bipectinata.*

Treatment Unmated female)	Mean				Median			
	Estimate	Std. Error	95% Confidence Interval		Estimate	Std. Error	95% Confidence Interval	
			lower bound	upper bound			lower bound	upper bound
Untreated	2.13	0.05	2.02	2.23	2.00			
1 ppm	2.38	0.11	2.16	2.59	2.00			
3 ppm	5.25	0.13	4.99	5.51	5.00	0.21	4.59	5.41
5 ppm	6.93	0.23	6.48	7.37	7.00	0.31	6.40	7.60
Overall	4.16	0.18	3.83	4.51	4.00	0.50	3.02	4.98

- Overall comparisons

	Chi Square	df	Sig.
Log Rank (Mantel-Cox)	192.86	3	0.00*
Breslow (Generalized Wilcoxon)	159.07	3	0.00*
Tarone-Ware	174.80	3	0.00*

* Significant at $p < 0.01$

Table 1b. Mean and median of survival time in mated females of *D. bipectinata*

Treatment (mated females)	Mean				Median			
	Estimate	Std. Error	95% Confidence Interval		Estimate	Std. Error	95% Confidence Interval	
			lower bound	upper bound			lower bound	upper bound
Untreated	5.78	0.28	5.23	6.33	6.00	0.44	5.13	6.87
1 ppm	5.75	0.22	5.31	6.19	6.00	0.35	5.32	6.68
3 ppm	7.25	0.39	6.46	8.02	7.00	1.05	4.93	9.06
5 ppm	7.60	0.42	6.76	8.42	7.00	0.52	5.97	8.03
Overall	6.59	0.18	6.24	6.95	6.00	0.27	5.46	6.54

- Overall comparisons

	Chi Square	df	Sig.
Log Rank (Mantel-Cox)	28.48	3	0.00*
Breslow (Generalized Wilcoxon)	16.46	3	0.001*
Tarone-Ware	21.64	3	0.00*

* Significant at $p < 0.01$

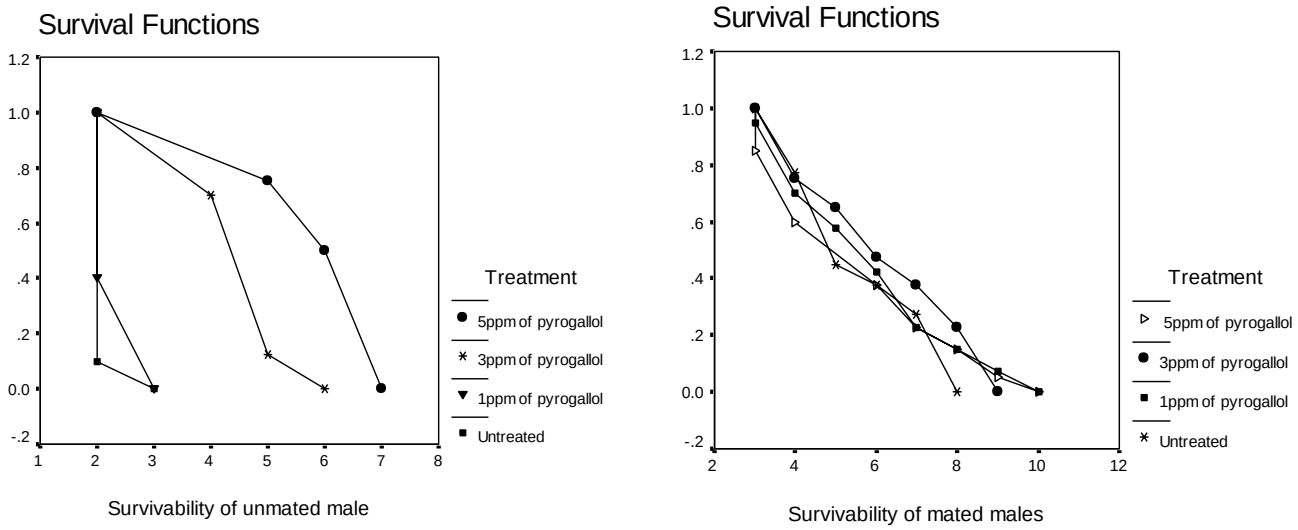

Figure 2. Survival curve of of *D. bipectinata.* (c, Left) unmated males; (d, Right) mated males.

Discussion

The Table 2a and 2b shows that females of *D. bipectinata* had a significantly greater resistance to starvation, when compared to males. This supports the work of Rion and Kawecki (2007), who also found that the females in a species have a greater resistance to starvation than males. This variation can be explained by the energy budget, the major ways of which can be elucidated to increase starvation resistance: (1) sequestering greater energy reserves; (2) reducing the rate at which the reserves are used under starvation conditions; (3) lowering the minimal level of body energy content which allows survival (Rion and Kawecki, 2007). In addition to these, greater resistance to starvation by females could also be due to higher lipid contents than males (Hoffman and Harshman, 1999), because of which females have a higher body weight than males (Chippindale *et al*., 1998). In the present study also, it was observed, that females had a greater body weight than the males of both the untreated and treated groups; therefore, an observed variation in the body weight of males and females flies could be attributed to greater lipid content in females than males of *D. bipectinata*. The SOD levels in the untreated male and female flies (shown in Figures 1a and b) were more or less the same, suggesting that the greater resistance to starvation in females of *D. bipectinata* could be due to the difference in the lipid contents in the body.

Apart from the reserve materials available in the body, other sources of energy comes from the quantity and quality of nutrients available, which are also known to play an important role in overcoming stressful conditions (Djawdan *et al*., 1998). Flies grown on protein rich diet show a significantly greater resistance to starvation in *Drosophila* (Djawdan *et al*., 1998). The tables show that pyrogallol treated males and females had a significantly greater starvation resistance when compared to untreated males and females suggesting the influence of pyrogallol on starvation resistance in *D. bipectinata*. Our study supports the role of antioxidants in resisting environmental stress, thus confirming the results of earlier studies on the role of nutrition in starvation resistance. In the present study the SOD enzyme activity levels were also in the untreated and pyrogallol treated flies, in order to understand the role of the antioxidant pyrogallol on resistance to starvation. It was noticed that the treated flies had lower levels of enzyme activity when compared to the untreated flies, which supports the "free radical theory", as the SOD (Super Oxide Dismutase) enzyme, which is an antioxidant enzyme is used as a defence against free oxygen radicals generated in the cell due to

oxidative stress. Antioxidants are known to reduce the free reactive oxygen species (ROS), which are produced when the cells are subjected to stress or oxidative stress, in turn decreasing the SOD enzyme levels and thus, known to increase the longevity of the flies under starvation resistance. Furthermore this study on *D. bipectinata* showed that an increase in the concentration of pyrogallol there is an increase in the resistance to starvation. Hence, with an increased intake of the antioxidant the flies show higher rates of survival at higher concentrations, which leads us to propose a hypothesis that greater the quantity of antioxidants in the food the higher the resistance to starvation.

Table 2a. Mean and median of survival time in unmated males of *D. bipectinata.*

Treatment (unmated male)	Mean				Median			
	Estimate	Std. Error	95% Confidence Interval		Estimate	Std. Error	95% Confidence Interval	
			lower bound	upper bound			lower bound	upper bound
Untreated	2.1	0.05	2.01	2.19	2.00			
1 ppm	2.4	0.08	2.45	2.55	2.00			
3 ppm	4.83	0.1	4.63	5.02	5.00	0.91	4.82	5.18
5 ppm	6.25	0.13	5.99	6.51	6.00	0.21	5.59	6.41
Overall	3.89	0.15	3.61	4.17	3.00	0.39	2.23	3.76

➢ Overall comparisons

	Chi Square	df	Sig.
Log Rank (Mantel-Cox)	200.39	3	0.00 *
Breslow (Generalized Wilcoxon)	164.48	3	0.00 *
Tarone-Ware	181.49	3	0.00 *

* Significant at $p < 0.01$

Table 2b. Mean and median of survival time in mated males of *D.bipectinata.*

Treatment (mated male)	Mean				Median			
	Estimate	Std. Error	95% Confidence Interval		Estimate	Std. Error	95% Confidence Interval	
			lower bound	upper bound			lower bound	upper bound
Untreated	5.86	0.25	5.39	6.36	5.00	0.24	4.53	5.47
1 ppm	6.1	0.32	5.48	6.72	6.00	0.52	4.98	7.02
3 ppm	6.48	0.3	5.88	7.07	6.00	0.57	4.87	7.13
5 ppm	5.85	0.34	5.19	6.51	6.00	0.68	4.67	7.33
Overall	6.08	0.15	5.78	6.37	6.00	0.25	5.51	6.49

➢ Overall comparisons

	Chi Square	df	Sig.
Log Rank (Mantel-Cox)	3.07	3	0.38 ^{NS}
Breslow (Generalized Wilcoxon)	2.69	3	0.44 ^{NS}
Tarone-Ware	2.79	3	0.43 ^{NS}

NS- Non- significant at $p < 0.01$ and $p < 0.05$

Table 3. Effects of pyrogallol on the quantity of ACP males of *D. bipectinata.*

Concentration of pyrogallol	Quantity of Acp		
	Unmated male flies	Mated male flies	Transferred (unmated-mated)
Untreated (control)	10.33	7.2	3.13
1 ppm	10.4	7.33	3.07
3 ppm	10.13	7	3.13
5 ppm	10.47	7.2	3.27
F value	8.42*	5.71**	7.55**

* Significant at $p < 0.01$ **Significant at $p < 0.05$

Since the same diet was used, except pyrogallol, the antioxidant at different concentrations added to the culture of *D. bipectinata* suggesting that greater resistance to starvation of treated flies could be attributed to pyrogallol. Our results support the earlier studies on the role of antioxidants in stress management (Tapiwanashe *et al*., 2006). Hence, the increased resistance with an increase in the concentration levels of the antioxidants (known to decrease the oxidative stress) can be inferred as an important factor influencing the resistance to starvation in flies of the treated groups. Stress related studies have been carried out to a large extent in order to study adaptations and counter interactions that may be an effect of changing climatic conditions (Hoffmann and Harshman, 1999) of which starvation resistance is a commonly measured trait (Huey *et al*., 2004), populations of *Drosophila* appear to harbour sufficient genetic variation for starvation resistance, as shown by the quick and high amount of responses to laboratory selection experiments for this trait (Hoffmann and Harshman, 1999; Archer *et al*., 2003; Hoffmann *et al*., 2005).

Studies have shown that mating is not harmful to the female, instead a useful process which could attribute to greater starvation resistance in females (Chapman *et al*., 1995; Wolfner, 1997; Lung *et al*., 2002; Chapman and Davies, 2004). In the present study it was noticed that resistance to starvation was significantly greater in mated females, compared to unmated females in *D. bipectinata* suggesting that females obtained fitness benefits from mating. Our study also supports the work of Brandy *et al.* (2007), where they found that mated females survive starvation longer than unmated ones. This increased resistance to starvation could be attributed to the higher fat reserves stored as triglycerides in mated females to ensure reproductive success, than the leaner unmated ones, with which our results agree. The longer survival in mated females could also be explained by the accessory gland proteins transferred to the female during mating, which can act as a source of protein to survive for longer periods of starvation. Also a decrease in the reproductive stress faced by mated flies can be attributed to the increase in their resistance to starvation in both males and females, hence in this experiment mated females and males from all groups were used to make a comparison between the control and the treated groups in which though there is a reduced reproductive stress in both groups the antioxidants further reduce these stress levels in the treated flies in turn increasing their survival. Uniformity was maintained by choosing both young unmated and mated females and males to rule out the effects of age on the survival of the flies in both groups.

Our results show that the amounts of Acps in the control and the treated groups are slightly similar in both the mated and the unmated flies, with the amount of transfer a little higher in the treated group, showing that the antioxidant has no significant effect on the Acp contents in the fly, as antioxidants are only involved in the oxidative stress reduction. Studies so far have, however, not been focused on studying the effects of antioxidants on proteins or the Acps in the fly. On the other hand new studies now focus on the antioxidant properties of proteins such as albumin (Rafael *et al*., 2010), thus leading us to infer that antioxidants, which are known to lower the oxidative stress and increase the longevity of the fly, also infer an additive property of starvation resistance in flies and increase the ability to survive starvation, when the antioxidant is included in the diet.

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Quantitative assessment of ommatidial distortion in *Drosophila melanogaster.*

Caudron, Quentin,[1] Ceri Lyn-Adams,[2,5] John A.D. Aston,[3] Bruno G. Frenguelli,[2] and Kevin G. Moffat.[2] [1]Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, 08648, USA; [2]School of Life Sciences, University of Warwick, Coventry, CV4 7AL, UK; [3]CRiSM, Department of Statistics, University of Warwick, Coventry, CV4 7AL, UK; [5]Current affiliation: BBSRC, Polaris House, North Star Avenue, Swindon, Wiltshire, SN2 1UH, UK.

Assessing the structural characteristics of an organism's physical appearance can be an important aspect of evaluating the effect of protein-protein interactions. Many biomedical