Longevity of 68 Species of *Drosophila*[1]

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Abstract. **Adult longevity of *Drosophila* is dependent upon many factors. In this study the differences in longevity caused by species, strain, sex, and mating status were examined for 68 species (89 strains) belonging to the *D. obscura, melanogaster,* and *willistoni* species groups. Both inter- and intra-specific differences in adult longevity were observed. In most species studied, females lived longer than males. In general, the longevity of unmated females exceeded that of mated ones, while the longevity of mated males was greater than that of unmated ones.**

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INTRODUCTION

Adult longevity and aging in *Drosophila* have been widely studied by a number of investigators (Baker et al. 1985, Lamb 1978). A large body of information about longevity and those factors influencing it has accumulated as a result of these studies. Longevity is a component of fitness for a variety of organisms (Hamilton 1966, Sacher 1978). In *Drosophila,* longevity has been considered an adaptive trait genetically controlled by minor genes and epistatic interactions (Bourgois and Lints 1982), as well as a selectable trait under polygenic control (Luckinbill et al. 1988, Luckinbill et al. 1984, Rose 1984).

Environmental factors, both before and during adulthood, have been demonstrated to effect longevity in *Drosophila.* These factors include temperature (Bourgois and Lints 1982, Burcombe and Hollingsworth 1970, Hollingsworth 1969, Lamb 1968, Parsons 1977), nutrition (David et al. 1971, 1983, Hollingsworth and Burcombe 1970, Van Herrewege 1973, 1974, Rockstein and Miquel 1973), dietary antioxidants (Miquel and Economos 1979), ultraviolet and ionizing radiation (Atlan et al. 1969, Felix and Ramirez 1967, Giess et al. 1980, Lamb 1964, 1965, 1966, Gartner 1973, Nöthel 1965, Tribe and Webb 1979a,b,c), photoperiod (Allemand et al. 1973, Pittendrigh and Minis 1972), light density (Northrop 1925), humidity (Pearl and Parker 1922), oxygen tension (Rockstein and Miquel 1973, Thomas et al. 1966, Strehler 1962), population density (Müeller 1987, Pearl et al. 1927), and larval crowding (Clare and Luckinbill 1985, de Miranda and Eggleston 1988, Miller and Thomas 1958).

Differences in longevity have been reported for both inter- and intra-specific variations among the *melanogaster, obscura,* and *virilis* species groups (Felix and Ramirez 1967, Spiess et al. 1952, Durbin and Yoon 1986, 1987). Intra-specific differences include those between strains, sexes, mated and unmated individuals of the same sex (Bilewicz 1953, Kidwell and Malick 1967, Maynard Smith 1958, Fowler and Partridge 1989) and those associated with female fertility (Doane 1960a,b), fecundity (Rose and Charlesworth 1981a,b), and age of reproduction (Rose 1984).

The purpose of this study was to determine the adult longevity of 68 species (89 strains) of the genus *Drosophila* belonging to the *obscura, melanogaster* and *willistoni* species groups. Both inter- and intra-specific differences including those associated with sex and mating status were studied. The results of this study will contribute to the knowledge of the basic biology and evolution of *Drosophila.* The present paper is the first of a two-part series of investigations, the second part of which will focus upon the duration of each developmental stage for members of each of the strains and species used in this investigation.

MATERIALS AND METHODS

Sixty-eight species (89 strains) of the *obscura, melanogaster,* and *willistoni* groups of the genus *Drosophila* were studied for adult longevity. These strains were obtained from the National *Drosophila* Species Resource Center, Bowling Green State University. All strains were laboratory stocks that have been maintained under laboratory conditions for a number of years. Stock vials of each strain contained approximately equal numbers of flies. Rearing conditions were similar for all strains and species.

Newly eclosed adults of each strain were removed from the stock vials daily and separated according to sex by aspiration, without anesthesia which may adversely affect longevity. For each strain studied, ten flies were placed in each of 12 standard food vials (25mm X 95mm) containing fresh cornmeal medium (Yoon 1985). Three categories of vials were prepared for each strain according to sex and mating status: (1) four vials, each containing ten unmated males, (2) four vials, each containing ten virgin females, and (3) four vials, each containing ten flies of mixed sex, considered as mated males and mated females. Each vial was labelled as to species, strain, vial category (sex and mating status), and date of eclosion. These flies were maintained in a room with a temperature of 22 ±1°C, relative humidity 45-50%, and 12D:12L photoperiod, as were the original stocks.

Vials were checked daily for the presence of dead flies. The date of death was recorded for each fly. Visual inspection of the vials was usually adequate to determine the viability of the flies. However, sometimes the vials were shaken lightly to determine whether a fly was dead or just inactive. Care was taken to keep these disturbances to a minimum in order to reduce their possible effects upon longevity. The surviving flies were transferred to

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new vials with fresh cornmeal medium every seven days or as necessary by the condition of the medium.

Longevity was measured as the difference between eclosion date and date of death. Within each strain, the mean longevity was determined by sex (Table 1) and mating status (Table 3). The mean longevity of each species was determined by pooling data from all flies of that species across strain, sex, and mating status (Table 2). The results were analyzed by species, strain, sex, and mating status with the Kruskal-Wallis (Chi-Square approximation) and Student-Newman-Keuls (multiple range) statistical test (Zar 1984) using SAS (Statistical Analysis System, SAS Institute, Inc. 1982, 1985). Significance was ascribed at the $p<0.05$ level.

Table 1.
Longevity of Drosophila *(with respect to strain and sex differences)*

Group	Subgroup	Species†	Strain	Sex	N	Mean Longevity (days)††	Range (days)	P>χ^2	
Obscura	Obscura	ambigua*	England	♂	61	26.0 ± 2.4	3-70	0.74	NS
				♀	55	25.3 ± 1.7	7-61		
			Port Coquitlam, Canada	♂	58	20.9 ± 2.0	6-66	0.99	NS
				♀	60	27.3 ± 3.2	3-78		
		miranda*	14011-0101	♂	44	29.5 ± 1.9	5-54	0.0147	SIG
				♀	53	37.5 ± 2.6	4-89		
			Mather, California	♂	61	34.5 ± 2.2	4-71	0.0001	SIG
				♀	57	21.7 ± 1.9	3-52		
		persimilis***	Quesnel, Canada	♂	44	13.6 ± 1.3	2-37	0.004	SIG
				♀	52	19.0 ± 1.5	4-74		
			Cold Creek, California	♂	56	31.5 ± 2.2	2-62	0.008	SIG
				♀	48	42.1 ± 3.0	4-81		
		pseudoobscura***	Tucson, Arizona	♂	47	39.6 ± 2.6	8-70	0.0001	SIG
				♀	60	54.4 ± 1.9	17-79		
			Simapan, Hidalgo, Mexico	♂	41	31.1 ± 2.7	5-69	0.012	SIG
				♀	53	40.3 ± 2.1	4-74		
		subobscura**	Norway	♂	59	15.8 ± 1.1	6-41	0.0051	SIG
				♀	60	22.7 ± 1.7	5-53		
			Cave Junction, Oregon	♂	62	16.2 ± 1.4	3-45	0.052	NS
				♀	49	13.7 ± 1.7	3-61		
	Affinis	affinis	Crystal Lake, Nebraska	♂	57	40.3 ± 3.0	3-82	0.35	NS
				♀	62	36.8 ± 2.9	7-82		
		alonquin	Halstad, Minnesota	♂	61	22.6 ± 1.4	7-56	0.59	NS
				♀	57	23.6 ± 1.5	5-52		
			Lincoln, Nebraska	♂	66	25.2 ± 1.8	6-67	0.82	NS
				♀	66	26.4 ± 2.0	2-68		
		azteca	Chipancingo, Mexico	♂	47	21.3 ± 2.2	4-67	0.004	SIG
				♀	47	34.2 ± 3.1	3-73		
		bifasciata	Akan-Ko, Japan	♂	65	27.8 ± 1.8	3-57	0.72	NS
				♀	58	28.8 ± 2.0	3-90		
		tolteca	Coroico, Bolivia	♂	56	29.5 ± 2.0	8-67	0.0001	SIG
				♀	51	57.7 ± 1.8	16-80		
Melanogaster	Melanogaster	melanogaster***	Oahu, Hawaii	♂	65	51.5 ± 2.8	9-100	0.78	NS
				♀	48	53.3 ± 2.4	16-86		
			Ica, Peru	♂	74	63.3 ± 2.3	16-145	0.61	NS
				♀	46	62.1 ± 2.8	14-98		
		mauritiana	Rivere Noire, Mauritius	♂	58	43.1 ± 1.5	17-65	0.10	NS
				♀	54	47.7 ± 2.1	16-101		

Table 1. (continued)

Group	Subgroup	Species†	Strain	Sex	N	Mean Longevity (days)††	Range (days)	$P>\chi^2$	
		simulans	Kenscoff, Haiti	♂	62	53.5 ± 2.6	13-87	0.24	NS
				♀	53	52.0 ± 3.6	15-132		
			Georgetown, Guyana	♂	51	54.8 ± 2.9	9-87	0.40	NS
				♀	58	53.5 ± 2.3	10-102		
		yakuba	Ivory Coast, Africa	♂	64	34.0 ± 1.6	10-83	0.0004	SIG
				♀	49	42.0 ± 1.8	18-82		
	Takahashii	takashashii	Nepal, Asia	♂	69	41.2 ± 1.7	14-85	0.0075	SIG
				♀	55	51.5 ± 2.9	14-116		
			Karale, South India	♂	48	42.6 ± 1.6	18-64	0.54	NS
				♀	62	43.9 ± 1.8	16-73		
		prostipennis	Wulai, Taiwan	♂	59	44.0 ± 2.0	18-87	0.007	SIG
				♀	58	51.5 ± 2.1	11-82		
		lutescens	Mito, Honshu, Japan	♂	58	40.2 ± 2.8	10-109	0.0001	SIG
				♀	56	80.5 ± 3.3	20-139		
		paralutea	Khao Yai, Thailand	♂	60	38.4 ± 1.9	9-71	0.0001	SIG
				♀	55	50.0 ± 1.5	25-66		
		pseudotakahashii	Goroka, New Guinea	♂	58	51.6 ± 2.6	13-87	0.24	NS
				♀	51	56.1 ± 2.4	16-101		
		trilutea	Ali-Shan, Taiwan	♂	41	33.4 ± 1.7	9-51	0.72	NS
				♀	47	33.2 ± 1.5	9-53		
	Suzukii	lucipennis*	Chi-Tou, Taiwan	♂	33	27.1 ± 2.7	6-61	0.001	SIG
				♀	81	38.1 ± 1.9	7-76		
			Wulai, Taiwan	♂	46	30.7 ± 2.1	7-60	0.0001	SIG
				♀	60	45.1 ± 1.8	16-75		
		mimetica	Kuala Lumpur, Malaysia	♂	59	35.3 ± 2.2	12-82	0.44	NS
				♀	54	34.9 ± 2.1	1-70		
		pulchrella	Kirishima, Japan	♂	60	37.4 ± 2.0	15-92	0.49	NS
				♀	58	34.7 ± 1.6	13-62		
		rajasekari**	Ari Ksatr, Cambodia (4023-036)	♂	64	54.1 ± 1.5	16-74	0.35	NS
				♀	53	55.8 ± 2.4	14-80		
			" " (4023-036.1)	♂	53	41.3 ± 1.7	10-70	0.0001	SIG
				♀	59	54.3 ± 1.8	6-80		
	Ananassae	ananassae	Tamazunchale, Mexico (0371)	♂	51	84.3 ± 3.3	10-140	0.0001	SIG
				♀	55	68.6 ± 2.7	14-122		
			" " (0371.1)	♂	47	71.5 ± 2.5	11-105	0.87	NS
				♀	59	71.9 ± 2.6	17-107		
		bipectinata*	Patan, Nepal	♂	62	53.0 ± 2.1	16-85	0.50	NS
				♀	57	51.0 ± 2.2	10-74		
			Cabuyao, Laguna, Luzon, Philippines	♂	56	53.5 ± 3.0	11-90	0.056	NS
				♀	54	65.2 ± 3.6	21-148		
		malerkotliana***	Mysore, India	♂	69	75.4 ± 3.0	12-141	0.42	NS
				♀	67	74.0 ± 2.5	22-128		
			Samut, Songkhram, Thailand	♂	61	62.5 ± 2.3	20-105	0.40	NS
				♀	63	60.0 ± 2.5	11-117		
		parabipectinata	Ari Ksatr, Cambodia	♂	48	61.2 ± 3.0	16-92	0.0006	SIG
				♀	62	76.8 ± 2.8	24-159		
			Los Banos, Luzon, Philippines	♂	61	67.4 ± 2.7	11-112	0.72	NS
				♀	63	67.1 ± 3.2	15-152		

Table 1. (continued)

Group	Subgroup	Species†	Strain	Sex	N	Mean Longevity (days)††	Range (days)	P>χ^2	
		pseudoananassae nigrens	Samut Songkhram, Thailand	♂	60	63.9 ± 2.5	17-98	0.96	NS
				♀	52	62.3 ± 2.6	8-96		
		pseudoananassae pseudoananassae	Chiang Mai, Thailand	♂	52	59.0 ± 2.9	17-101	0.17	NS
				♀	62	53.5 ± 1.9	12-81		
	Ficusphila	ficusphila***	Khan-ing Tong, Taiwan (0441)	♂	41	26.2 ± 2.1	6-55	0.004	SIG
				♀	53	35.1 ± 1.8	7-69		
			“ “ “ (0441.1)	♂	52	51.3 ± 3.2	12-134	0.0001	SIG
				♀	59	67.6 ± 2.5	14-108		
	Eugracilis	eugracilis***	Popondetta, Papua, New Guinea	♂	42	36.0 ± 1.7	6-56	0.0001	SIG
				♀	64	53.9 ± 1.6	11-76		
			Palawan, Philippines	♂	59	30.1 ± 0.9	13-56	0.0001	SIG
				♀	56	43.4 ± 1.6	21-77		
	Montium	auraria*	Kirishima, Japan	♂	46	39.0 ± 2.3	13-76	0.0007	SIG
				♀	53	56.7 ± 3.6	11-92		
			Noppora, Japan	♂	54	27.3 ± 1.3	9-52	0.0001	SIG
				♀	60	51.4 ± 2.4	19-92		
		baimaii	Kuala Lumpur, Malaysia	♂	65	43.2 ± 1.6	17-65	0.0001	SIG
				♀	60	67.3 ± 3.	8-108		
			Khao Yai, Thailand	♂	56	42.2 ± 2.0	9-73	0.0001	SIG
				♀	60	72.1 ± 2.7	11-101		
		barbarae*	Kuala Lumpur, (4028-0491) Malaysia	♂	59	43.1 ± 1.8	12-73	0.0001	SIG
				♀	62	61.1 ± 2.5	9-101		
			“ “ (4028-0491.1)	♂	43	40.0 ± 2.1	12-63	0.0001	SIG
				♀	53	52.5 ± 1.9	7-76		
		biauraria	Ka-ari, Korea	♂	52	46.8 ± 2.8	6-99	0.05	SIG
				♀	48	57.9 ± 4.3	6-120		
		bicornuta	Ken-ting, Taiwan	♂	50	51.0 ± 1.6	34-85	0.0005	SIG
				♀	59	61.4 ± 2.5	20-91		
		birchii	Cairns, Australia	♂	61	39.1 ± 1.4	17-59	0.0006	SIG
				♀	55	47.3 ± 2.4	20-79		
		jambulina	Bon Chakkarat, Thailand	♂	44	50.9 ± 2.7	11-84	0.19	NS
				♀	67	56.4 ± 2.9	13-104		
			Changwat, Thailand	♂	66	46.3 ± 2.3	11-90	0.0003	SIG
				♀	48	67.8 ± 4.6	13-153		
		kanapiae	Tagaytay, Luzon, Philippines	♂	44	33.3 ± 1.4	12-49	0.06	NS
				♀	66	37.5 ± 1.2	18-62		
		khaoyana	Khao Yai, Thailand	♂	60	31.4 ± 1.6	10-56	0.0001	SIG
				♀	60	51.1 ± 2.3	16-88		
		kikkawai	Leticia, Columbia	♂	54	38.7 ± 1.7	8-59	0.0002	SIG
				♀	53	49.1 ± 2.2	10-78		
		lacteicornis	Okinawa, Japan	♂	64	50.8 ± 2.1	13-114	0.005	SIG
				♀	60	59.3 ± 2.2	13-106		
		lini	Yun-shui, Taiwan	♂	55	44.4 ± 2.2	10-86	0.0001	SIG
				♀	64	61.4 ± 2.9	11-99		
		diplacantha	Bafut, Ngemba, Cameroun	♂	61	55.8 ± 2.0	16-98	0.0001	SIG
				♀	58	70.0 ± 2.9	15-100		
		mayri	Lae, New Guinea	♂	56	31.9 ± 1.7	12-70	0.0001	SIG
				♀	62	52.4 ± 1.9	8-75		

Table 1. (continued)

Group	Subgroup	Species†	Strain	Sex	N	Mean Longevity (days)++	Range (days)	$P>\chi^2$	
		nikananu	Ivory Coast, Africa	♂	55	35.5 ± 1.3	14-53	0.0013	SIG
				♀	64	41.5 ± 1.7	6-69		
		orosa	Khao Yai, Thailand	♂	68	29.1 ± 1.4	9-62	0.0001	SIG
				♀	51	41.9 ± 2.5	6-74		
		parvula	Kuala Lumpur, Malaysia	♂	56	32.0 ± 1.5	8-60	0.54	NS
				♀	58	32.3 ± 0.9	17-48		
		pennae	Garoka, New Guinea	♂	49	24.5 ± 1.8	7-57	0.029	SIG
				♀	59	30.0 ± 1.8	7-66		
		punjabiensis	Kuala Lumpur, Malaysia	♂	65	35.3 ± 1.5	12-74	0.007	SIG
				♀	58	42.4 ± 1.9	12-89		
		quadraria	Chi Tou, Taiwan	♂	44	40.5 ± 2.5	16-86	0.21	NS
				♀	58	42.7 ± 1.6	12-72		
		ponera	Isle de la Reunion	♂	64	21.0 ± 1.6	3-57	0.08	NS
				♀	62	26.1 ± 2.1	3-73		
		rufa	Hangchow, China	♂	54	37.0 ± 1.7	16-65	0.12	NS
				♀	50	41.4 ± 2.2	10-88		
		seguyi	Salisbury, Rhodesia (Zimbabwe)	♂	52	54.1 ± 3.5	6-119	0.43	NS
				♀	53	57.8 ± 3.4	10-98		
		serrata	Queensland, Australia	♂	61	49.2 ± 2.5	10-103	0.0001	SIG
				♀	58	72.9 ± 3.4	17-115		
		triauraria	Hangchow, China	♂	52	32.2 ± 0.9	8-52	0.0001	SIG
				♀	62	53.1 ± 2.1	15-89		
		tsacasi	Ivory Coast, Africa	♂	57	29.9 ± 1.2	12-52	0.0001	SIG
				♀	62	42.0 ± 1.9	9-67		
		vulcana	Mount Selinda, Rhodesia (Zimbabwe)	♂	62	28.7 ± 1.1	7-49	0.0001	SIG
				♀	62	53.9 ± 2.6	5-106		
Willistoni	Willistoni	capricorni	Palmira, Columbia	♂	58	39.2 ± 1.1	14-60	0.0001	SIG
				♀	60	44.3 ± 1.1	12-72		
		equinoxalis	La Hina, Honduras	♂	46	53.6 ± 2.2	15-95	0.0003	SIG
				♀	61	71.1 ± 3.3	15-111		
		fumipennis	Bucaramanga, Columbia	♂	59	45.2 ± 2.8	6-89	0.0001	SIG
				♀	69	70.0 ± 3.0	20-137		
		nebulosa	Facultad de Agronomia, Palmira, Columbia	♂	67	24.4 ± 1.1	5-61	0.0001	SIG
				♀	53	44.7 ± 2.5	10-111		
		paulistorum	Mesitas	♂	63	48.4 ± 1.8	15-79	0.015	SIG
				♀	66	58.8 ± 2.9	14-104		
		sucinea	Medellin, Columbia	♂	47	37.0 ± 1.1	17-53	0.0003	SIG
				♀	45	48.2 ± 2.6	15-77		
		tropicalis	Institutio Tropical, San Salvador, El Salvador	♂	63	34.0 ± 1.2	7-64	0.0001	SIG
				♀	62	47.7 ± 2.1	8-79		
		willistoni	Santa Mara de Ostuna, Nicaragua	♂	48	35.0 ± 2.2	6-66	0.25	NS
				♀	64	56.2 ± 2.6	8-123		
		willistoni-like	Institutio Tropical, Sal Salvador, El Salvador	♂	51	52.8 ± 2.6	11-89	0.25	NS
				♀	51	57.3 ± 2.6	14-99		

† Significant difference betweeen strains within species based upon Kruskal-Wallis Test (χ^2 approximation)

- * $p \leq 0.05$
- ** $p \leq 0.001$
- *** $p \leq 0.0001$

++ Longevity = Mean days from eclosion to death ± standard error of mean.

p= Probability of greater χ^2 based upon Kruskal-Wallis Test (χ^2 approximation)

NS = no significant difference between sexes within strain

SIG = significant difference between sexes within strain

Table 2.
Longevity of Drosophila *species*

Group	Subgroup	Species	N	Longevity (days)[*]	Range (days)
Obscura	Obscura	ambigua	234	24.9 ± 1.2 A[**]	3-78
		miranda	215	30.8 ± 1.2	3-89
		persimilis	200	26.9 ± 1.3 A	2-81
		pseudoobscura	201	42.5 ± 1.3	4-79
		subobscura	230	17.3 ± 0.8	3-61
	Affinis	affinis	119	38.5 ± 2.1	3-82
		alonquin	250	24.5 ± 0.9 B	2-68
		azteca	94	27.7 ± 2.0 B	3-73
		bifasciata	123	28.3 ± 1.3 B	3-90
		tolteca	107	42.9 ± 1.9	8-80
Melanogaster	Melanogaster	melanogaster	233	57.7 ± 1.3	9-145
		mauritiana	112	45.3 ± 1.3	16-101
		simulans	224	53.4 ± 1.4	9-132
		yakuba	113	37.5 ± 1.2	10-83
	Takashashii	takahashii	234	44.6 ± 1.0 D	14-116
		prostipennis	117	47.5 ± 1.5 D	11-87
		lutescens	114	60.0 ± 2.9	10-139
		paralutea	115	43.9 ± 1.3 D	9-71
		pseudotakahashii	109	53.7 ± 1.8	13-101
		trilutea	88	33.3 ± 1.1	9-53
	Suzukii	lucipennis	220	36.8 ± 1.1 E	6-76
		mimetica	113	35.1 ± 1.5 E	1-82
		pulchrella	118	36.1 ± 1.3 E	13-92
		rajasekari	229	51.6 ± 1.0	6-80
	Ananassae	ananassae	212	73.9 ± 1.4	10-140
		bipectinata	229	55.5 ± 1.4	10-148
		malerkotliana	260	68.3 ± 1.4 F	11-141
		parabipectinata	234	68.5 ± 1.5 F	11-159
		pseudoananassae nigrens	112	63.2 ± 1.8	8-98
		pseudoananassae pseudoananassae	114	60.0 ± 1.7	12-101
	Ficusphila	ficusphila	205	46.8 ± 1.7	6-134
	Eugracilis	eugracilis	221	41.5 ± 1.0	6-77
	Montium	auraria	213	43.9 ± 1.5 J	9-92
		baimaii	232	56.7 ± 1.5 GHI	8-108
		barbarae	217	49.9 ± 1.2 I	7-101

Table 2. (continued)

Group	Subgroup	Species	N	Longevity (days)*	Range (days)
		biauraria	100	52.1 ± 2.6 I	6-120
		bicornuta	109	56.6 ± 1.6 GHI	20-91
		birchii	116	43.0 ± 1.4 JK	17-79
		jambulina	225	54.8 ± 1.6 HI	11-153
		kanapiae	110	35.8 ± 0.9 KLM	12-62
		khaoyana	120	41.2 ± 1.7 JKL	10-88
		kikkawai	107	43.8 ± 1.5 J	8-78
		lacteicornis	127	55.0 ± 1.5 HI	13-114
		lini	119	53.5 ± 2.0 I	10-99
		diplacantha	119	62.5 ± 1.9 G	15-100
		mayri	118	42.7 ± 1.6 JK	8-75
		nikananu	119	39.7 ± 1.1 JKLM	6-69
		orosa	119	34.6 ± 1.5 LM	6-74
		parvula	114	32.2 ± 0.9 M	8-60
		pennae	108	27.5 ± 1.3 N	7-66
		punjabiensis	123	38.8 ± 1.3 JKLM	12-89
		quadraria	102	41.7 ± 1.4 JKL	12-86
		ponera	126	23.6 ± 1.3 N	3-73
		rufa	104	39.0 ± 1.4 JKL	10-88
		seguyi	105	55.9 ± 2.4 HI	6-119
		serrata	119	60.7 ± 2.4 GH	10-119
		triauraria	114	43.6 ± 1.6 J	8-89
		tsacasi	119	36.2 ± 1.3 JKLM	9-67
		vulcana	124	41.3 ± 1.9 JKL	5-106
Willistoni	Willistoni	capricorni	118	41.7 ± 1.0 P	12-72
		equinoxialis	107	63.6 ± 2.2	15-111
		fumipennis	128	58.3 ± 2.3 O	6-137
		nebulosa	121	33.5 ± 1.6	5-111
		paulistorum	129	53.7 ± 1.8 O	14-104
		sucinea	92	42.5 ± 1.5 P	15-77
		tropicalis	125	40.7 ± 1.4 P	7-79
		willistoni	112	47.1 ± 2.0 P	6-123
		willistoni-like	112	55.3 ± 1.8 O	11-99

* x ± S.E.

** within each subgroup, species with the same letter are not significantly different at $P \leq 0.05$ (based on Student-Newman-Keuls test)

Table 3.
Longevity of Drosophila *with special regard to mating status.*

Group	Subgroup	Species	Strain	Sex	Mating[†] Status	N	Longevity[**]	Range	Prob >χ^2	$
Obscura	Obscura	ambigua	England	♂	V	38	28.0 ± 3.0	6-70	0.276	NS
				♂	M	23	22.7 ± 3.8	3-54		
				♀	V	29	26.2 ± 2.4	8-61	0.62	NS
				♀	M	26	24.4 ± 2.6	7-47		
			Port Coquitlam, Canada	♂	V	49	18.9 ± 1.6	7-54	0.63	NS
				♂	M	9	31.6 ± 8.6	6-66		
				♀	V	39	25.1 ± 3.7	3-78	0.74	NS
				♀	M	21	31.4 ± 5.9	3-70		
		miranda	(14011-0101)	♂	V	11	18.9 ± 2.4	7-31	0.0006	**
				♂	M	33	33.0 ± 2.0	5-54		
				♀	V	20	44.6 ± 2.8	14-60	0.0028	*
				♀	M	33	33.3 ± 3.6	4-89		
			Mather, California	♂	V	50	33.1 ± 2.2	4-63	0.27	NS
				♂	M	11	40.7 ± 6.2	12-71		
				♀	V	50	22.5 ± 2.0	3-52	0.14	NS
				♀	M	7	16.1 ± 3.6	3-27		
		persimilis	Quesnel, Canada	♂	V	19	16.9 ± 1.8	9-37	0.006	*
				♂	M	25	11.0 ± 1.7	2-34		
				♀	V	30	17.4 ± 1.1	6-33	0.68	NS
				♀	M	22	21.3 ± 3.3	4-74		
			Cold Creek, California	♂	V	42	30.1 ± 2.6	2-62	0.23	NS
				♂	M	14	35.6 ± 3.7	9-60		
				♀	V	42	43.3 ± 3.4	4-81	0.27	NS
				♀	M	6	33.8 ± 2.6	26-42		
		pseudoobscura	Tucson, Arizona	♂	V	28	42.3 ± 3.3	9-70	0.30	NS
				♂	M	19	35.7 ± 4.1	8-63		
				♀	V	38	53.4 ± 2.6	17-79	0.70	NS
				♀	M	22	56.1 ± 2.3	31-72		
			Simapan, Hidalga, Mexico	♂	V	21	32.9 ± 3.7	7-69	0.46	NS
				♂	M	20	29.2 ± 4.0	5-65		
				♀	V	20	40.0 ± 2.6	24-61	0.92	NS
				♀	M	33	40.5 ± 3.0	4-74		
		subobscura	Norway	♂	V	40	16.3 ± 1.4	6-41	0.84	NS
				♂	M	19	14.7 ± 1.7	8-32		
				♀	V	39	21.0 ± 2.1	8-53	0.32	NS
				♀	M	21	25.9 ± 2.8	5-42		
			Cave Junction, Oregon	♂	V	31	13.8 ± 1.5	3-45	0.24	NS
				♂	M	31	18.6 ± 2.2	3-45		
				♀	V	25	11.9 ± 2.4	3-61	0.31	NS
				♀	M	24	15.5 ± 2.4	3-39		
	Affinis	affinis	Crystal Lake, Hastings, Nebraska	♂	V	40	30.4 ± 2.7	3-71	0.0001	***
				♂	M	17	63.5 ± 3.9	15-82		
				♀	V	40	30.3 ± 3.6	7-82	0.0022	*
				♀	M	22	48.5 ± 4.1	11-78		
		alonquin	Halstad, Minnesota	♂	V	40	20.8 ± 1.5	10-45	0.13	NS
				♂	M	21	26.1 ± 3.0	7-56		
				♀	V	38	24.1 ± 2.0	6-52	0.59	NS
				♀	M	19	22.6 ± 2.2	5-40		
			Lincoln, Nebraska	♂	V	31	20.9 ± 1.8	6-48	0.10	NS
				♂	M	35	29.1 ± 2.9	7-67		
				♀	V	19	28.1 ± 3.4	4-59	0.45	NS
				♀	M	47	25.7 ± 2.4	2-68		
		azteca	Chipancingo, Mexico	♂	V	40	19.7 ± 2.1	4-47	0.06	NS
				♂	M	7	30.4 ± 8.0	14-67		
				♀	V	46	34.7 ± 3.1	3-73	0.25	NS
				♀	M	1	11	11-11		
		bifasciata	Akan-Ko, Japan	♂	V	10	20.7 ± 2.6	7-41	0.08	NS
				♂	M	55	29.1 ± 2.1	3-57		
				♀	V	10	43.2 ± 3.0	25-60	0.0003	**
				♀	M	48	25.7 ± 2.1	3-90		

Table 3. (continued)

Group	Subgroup	Species	Strain	Sex	Mating[1] Status	N	Longevity**	Range	Prob >χ^2	$
		tolteca	Cordico, Bolivia	♂	V	40	32.5 ± 2.1	13-64	0.0027	*
				♂	M	16	22.2 ± 4.1	8-67		
				♀	V	39	60.4 ± 1.8	28-80	0.01	*
				♀	M	12	48.8 ± 4.3	16-69		
Melanogaster	Melanogaster	melanogaster	Oahu, Hawaii	♂	V	48	49.1 ± 3.5	9-95	0.02	NS
				♂	M	17	58.6 ± 3.9	24-100		
				♀	V	32	56.2 ± 2.9	25-86	0.10	NS
				♀	M	16	47.5 ± 3.9	16-69		
			Ica, Peru	♂	V	52	67.5 ± 1.6	34-91	0.0001	***
				♂	M	22	53.6 ± 6.2	16-145		
				♀	V	10	70.3 ± 1.4	65-80	0.25	NS
				♀	M	36	59.8 ± 3.5	14-98		
		mauritiana	Rivere Noire, Mauritius	♂	V	17	43.4 ± 3.0	17-65	0.10	NS
				♂	M	41	43.0 ± 1.8	20-65		
				♀	V	20	54.9 ± 2.3	30-70	0.0024	*
				♀	M	34	43.5 ± 2.9	16-101		
		simulans	Kenscoff, Haiti	♂	V	38	51.2 ± 3.3	13-87	0.21	NS
				♂	M	24	57.3 ± 4.1	14-79		
				♀	V	31	40.2 ± 2.3	15-68	0.0002	**
				♀	M	22	68.6 ± 6.7	17-132		
			Georgetown, Guyana	♂	V	33	57.3 ± 3.9	9-87	0.12	NS
				♂	M	18	50.2 ± 3.7	24-77		
				♀	V	37	52.1 ± 2.4	10-80	0.95	NS
				♀	M	21	55.9 ± 4.9	24-102		
		yakuba	Ivory Coast, Africa	♂	V	41	31.5 ± 1.7	10-56	0.06	NS
				♂	M	23	38.1 ± 2.9	18-83		
				♀	V	30	40.6 ± 1.9	26-74	0.13	NS
				♀	M	19	44.4 ± 3.4	18-82		
	Takahashii	takahashii	Nepal, Asia	♂	V	39	38.9 ± 1.8	14-71	0.14	NS
				♂	M	30	44.2 ± 2.9	20-85		
				♀	V	36	47.9 ± 3.3	16-89	0.09	NS
				♀	M	19	58.3 ± 5.4	14-116		
			Karale, South India	♂	V	33	41.4 ± 2.1	18-59	0.42	NS
				♂	M	15	45.3 ± 2.3	31-64		
				♀	V	40	41.4 ± 2.3	16-64	0.08	NS
				♀	M	22	48.5 ± 2.5	29-73		
		prostipennis	Wulai, Taiwan	♂	V	47	41.5 ± 2.2	18-87	0.0044	*
				♂	M	12	53.7 ± 2.8	32-71		
				♀	V	19	46.2 ± 4.7	17-81	0.26	NS
				♀	M	39	53.5 ± 2.1	11-82		
		utescens	Mito, Honshu, Japan	♂	V	47	36.3 ± 2.9	13-109	0.003	*
				♂	M	11	56.9 ± 6.2	10-74		
				♀	V	45	81.6 ± 3.6	25-139	0.63	NS
				♀	M	11	76.3 ± 8.0	20-108		
		paralutea	Khao Yai, Thailand	♂	V	49	34.6 ± 1.8	9-62	0.0001	***
				♂	M	11	55.7 ± 3.6	28-71		
				♀	V	50	49.1 ± 1.6	25-66	0.07	NS
				♀	M	5	58.4 ± 3.6	51-63		
		pseudotakahashii	Goroka, New Guinea	♂	V	30	46.1 ± 3.6	19-81	0.0429	*
				♂	M	28	57.4 ± 3.5	13-87		
				♀	V	36	63.0 ± 2.1	28-101	0.0001	***
				♀	M	15	39.7 ± 3.7	16-56		
		trilutea	Ali-Shan, Taiwan	♂	V	5	31.4 ± 4.9	14.39	0.81	NS
				♂	M	36	33.6 ± 1.8	9-51		
				♀	V					
				♀	M	47	33.2 ± 1.5	9-53		
	Suzukii	lucipennis	Chi-Tou, Taiwan	♂	V	17	28.0 ± 3.8	10-56	0.73	NS
				♂	M	16	26.1 ± 4.1	-61		
				♀	V	51	38.3 ± 2.4	16-76	0.80	NS
				♀	M	30	37.9 ± 3.3	7-72		
			Wulai, Taiwan	♂	V	21	25.7 ± 2.6	7-60	0.0028	*
				♂	M	19	37.7 ± 2.8	15-56		
				♀	V	41	42.0 ± 2.2	16-75	0.0091	*
				♀	M	19	51.7 ± 2.7	31-69		

Table 3. (continued)

Group	Subgroup	Species	Strain	Sex	Mating† Status	N	Longevity††	Range	Prob $>\chi^2$	$
		mimetica	Kuala Lumpur, Malaysia	♂	V	10	27.0 ± 2.3	17-38	0.08	NS
				♂	M	49	37.0 ± 2.5	12-82		
				♀	V	36	31.6 ± 2.2	1-57		
				♀	M	18	41.7 ± 4.3	12-70	0.06	NS
		pulchrella	Kirishima, Japan	♂	V	30	31.1 ± 2.7	15-66	0.0052	*
				♂	M	30	43.8 ± 2.5	28-92		
				♀	V	22	32.3 ± 3.1	13-62	0.28	NS
				♀	M	36	36.2 ± 1.7	13-55		
		rejasekari	Ari Ksatr, Cambodia (4023-036)	♂	V	54	56.6 ± 1.4	26-74	0.0008	**
				♂	M	10	40.2 ± 4.1	16-67		
				♀	V	42	57.0 ± 2.8	14-80	0.36	NS
				♀	M	11	51.1 ± 4.7	28-77		
			Ari Ksatr, Cambodia (4023-036.1)	♂	V	29	35.0 ± 1.9	10-55	0.0001	***
				♂	M	24	48.9 ± 2.1	26-70		
				♀	V	39	59.9 ± 1.8	29-80	0.0001	***
				♀	M	20	43.4 ± 2.8	6-63		
	Ananassae	ananassae	Tamazunchale S.L.P. Mexico (0371)	♂	V	13	91.1 ± 4.0	67-120	0.20	NS
				♂	M	38	82.0 ± 4.2	10-140		
				♀	V					
				♀	M	55	68.6 ± 2.7	14-122		
			Tamazunchale S.L.P. Mexico (0371.1)	♂	V					
				♂	M	47	71.5 ± 2.5	11-105		
				♀	V	1	63	63-63	0.50	NS
				♀	M	58	72 ± 2.6	17-107		
		bipectinata	Patan, Napal	♂	V	16	55.7 ± 4.1	16-73	0.41	NS
				♂	M	46	52.0 ± 2.5	23-85		
				♀	V	10	59.5 ± 1.1	53-66	0.12	NS
				♀	M	47	49.2 ± 2.6	10-74		
			Cabuyao, Laguna, Luzon	♂	V	35	46.0 ± 3.8	11-87	0.0018	*
				♂	M	21	66.0 ± 3.7	29-90		
				♀	V	39	67.5 ± 4.2	21-148	0.22	NS
				♀	M	15	59.3 ± 7.2	27-131		
		malerkoliana	Mysore, India	♂	V	44	72.5 ± 3.8	12-110	0.36	NS
				♂	M	25	80.6 ± 4.6	39-141		
				♀	V	19	72.5 ± 3.5	36-96	0.99	NS
				♀	M	48	74.5 ± 3.2	22-128		
			Samut, Songkhram, Thailand	♂	V	20	60.7 ± 3.5	20-75	0.76	NS
				♂	M	41	62.5 ± 2.9	21-105		
				♀	V	18	63.6 ± 3.5	22-78	0.33	NS
				♀	M	45	58.4 ± 3.2	11-117		
		parabipectinata	Ari Ksatr, Cambodia	♂	V	26	60.7 ± 4.5	16-92	0.7	NS
				♂	M	22	61.9 ± 3.7	17-83		
				♀	V	20	87.5 ± 4.1	46-123	0.0003	**
				♀	M	42	71.7 ± 3.4	24-159		
			Los Banos, Luzon, Philippines	♂	V	34	66.3 ± 3.9	11-109	0.65	NS
				♂	M	27	68.7 ± 3.8	25-112		
				♀	V	20	67.7 ± 6.6	15-118	0.92	NS
				♀	M	43	66.9 ± 3.6	17-152		
		pseudoananassae nigrens	Samut, Songkhram, Thailand	♂	V	19	63.7 ± 5.1	19-87	0.56	NS
				♂	M	41	64.0 ± 2.8	17-98		
				♀	V	16	63.9 ± 5.1	8-92	0.77	NS
				♀	M	36	61.6 ± 3.1	22-96		
		pseudoananassae pseudoananassae	Chiang Mai, Thailand	♂	V	29	56.8 ± 4.2	17-101	0.31	NS
				♂	M	23	61.7 ± 3.7	24-94		
				♀	V	38	54.6 ± 2.2	30-81	0.77	NS
				♀	M	24	51.7 ± 3.4	12-81		
	Ficusphila	ficusphila	Khan-ing Tong, Taiwan (0441)	♂	V	5	12.4 ± 2.2	6-18	0.0177	*
				♂	M	36	28.2 ± 2.2	7-55		
				♀	V	5	26.6 ± 1.5	23-30	0.0513	NS
				♀	M	48	36.0 ± 1.9	7-69		
			Khan-ing Tong, Taiwan (0441.1)	♂	V	29	44.6 ± 3.6	12-86	0.0040	*
				♂	M	23	60.0 ± 5.1	13-134		
				♀	V	19	53.8 ± 3.6	14-80	0.0001	***
				♀	M	40	74.1 ± 2.7	34-108		

Table 3. (continued)

Group	Subgroup	Species	Strain	Sex	Mating† Status	N	Longevity**	Range	Prob >χ^2	$
	Eugracilis	eugracilis	Popondetta, Papua, New Guinea	♂	V	23	34.8 ± 2.2	6-49	0.45	NS
				♂	M	19	37.5 ± 2.6	19-56		
				♀	V	45	54.3 ± 1.7	11-69	0.99	NS
				♀	M	19	53.0 ± 3.6	11-76		
			Palawan, Philippines	♂	V	38	29.6 ± 0.9	22-39	0.38	NS
				♂	M	21	31.0 ± 2.1	13-56		
				♀	V	37	45.3 ± 1.6	21-62	0.0208	*
				♀	M	19	39.8 ± 3.5	25-77		
	Montium	auraria	Kirishima, Japan	♂	V	31	40.3 ± 2.8	14-69	0.31	NS
				♂	M	15	36.5 ± 4.4	13-76		
				♀	V	45	62.6 ± 3.5	15-92	0.0001	***
				♀	M	8	23.5 ± 4.5	11-52		
			Nopporo, Japam	♂	V	32	25.9 ± 1.6	9-52	0.36	NS
				♂	M	22	29.2 ± 2.2	13-51		
				♀	V	50	53.5 ± 2.6	21-92	0.04	*
				♀	M	10	40.6 ± 5.6	19-68		
		baimaii	Kuala Lumpur, Malaysia	♂	V	40	39.8 ± 1.8	17-65	0.0003	**
				♂	M	16	51.8 ± 2.0	33-65		
				♀	V	39	68.4 ± 4.4	8-108	0.32	NS
				♀	M	21	65.3 ± 3.5	31-92		
			Khao Yai, Thailand	♂	V	16	39.6 ± 4.0	9-68	0.61	NS
				♂	M	40	43.2 ± 2.3	20-73		
				♀	V	37	77.7 ± 2.4	29-100	0.0479	*
				♀	M	23	63.0 ± 5.5	11-95		
		barbarae	Kuala Lumpur, Malaysia (4028-0491)	♂	V	40	41.7 ± 2.1	12-71	0.23	NS
				♂	M	19	46.0 ± 3.5	15-73		
				♀	V	51	65.3 ± 2.6	9-101	0.0002	**
				♀	M	11	41.5 ± 4.0	15-69		
			Kuala Lumpur, Malaysia (4028-0491.1)	♂	V	10	28.0 ± 3.4	13-4	0.0038	*
				♂	M	33	43.2 ± 2.3	12-63		
				♀	V	19	56.0 ± 3.4	7-74	0.11	NS
				♀	M	34	51.0 ± 2.3	20-76		
		biauraria	Ka-ari, Korea	♂	V	34	45.2 ± 3.5	6-99	0.28	NS
				♂	M	18	49.7 ± 4.6	10-76		
				♀	V	29	51.1 ± 5.1	6-102	0.0511	NS
				♀	M	19	68.2 ± 6.9	10-120		
		bicornuta	Ken-ting, Taiwan	♂	V	8	40.4 ± 2.1	34-47	0.0011	*
				♂	M	42	53.0 ± 1.6	36-85		
				♀	V					
				♀	M	59	61.4 ± 2.5	20-91		
		birchii	Cairns, Australia	♂	V	10	42.4 ± 4.4	17-57	0.2143	NS
				♂	M	51	38.5 ± 1.4	21-59		
				♀	V	16	37.4 ± 4.9	20-69	0.0099	*
				♀	M	39	51.4 ± 2.6	21-79		
		jambulina	Bon Chakkrarat, Thailand	♂	V	8	36.9 ± 6.6	11-66	0.0284	*
				♂	M	36	54.0 ± 2.8	22-84		
				♀	V	37	56.8 ± 4.1	13-102	0.85	NS
				♀	M	30	56.0 ± 4.1	16-104		
			Changwat, Thailand	♂	V	28	41.6 ± 4.0	11-86	0.13	NS
				♂	M	28	49.8 ± 2.7	21-90		
				♀	V	11	65.2 ± 7.0	28-91	0.79	NS
				♀	M	37	68.6 ± 5.7	13-153		
		kanapiae	Tagaytay, Luzon, Philippines	♂	V					
				♂	M	44	33.3 ± 1.4	12-49		
				♀	V	30	36.6 ± 1.5	25-54	0.50	NS
				♀	M	36	38.2 ± 1.8	18-62		
		khaoyana	Khao Yai, Thailand	♂	V	52	31.2 ± 1.7	10-56	0.96	NS
				♂	M	8	32.4 ± 4.9	14-52		
				♀	V	49	52.9 ± 2.6	16-88	0.0398	*
				♀	M	11	43.4 ± 2.6	26-52		
		kikkawai	Leticia, Columbia	♂	V	33	42.2 ± 1.6	15-59	0.0224	*
				♂	M	21	33.2 ± 3.2	8-59		
				♀	V	36	54.9 ± 2.3	10-78	0.0001	***
				♀	M	17	36.8 ± 3.3	15-55		

Table 3. (continued)

Group	Subgroup	Species	Strain	Sex	Mating† Status	N	Longevity^{++}	Range	Prob >χ^2	$
		lacteicornis	Okinawa, Japan	♂	V	40	50.3 ± 2.7	13-114	0.8027	NS
				♂	M	24	51.8 ± 3.2	25-88		
				♀	V	12	60.6 ± 4.1	39-92	0.73	NS
				♀	M	48	59.1 ± 2.6	13-106		
		lini	Yun-Shui, Taiwan	♂	V	18	39.8 ± 3.5	24-63	0.1202	NS
				♂	M	37	46.6 ± 2.7	10-86		
				♀	V	41	69.2 ± 3.2	21-99	0.0010	**
				♀	M	23	47.4 ± 4.5	11-81		
		diplacantha	Bafut Ngemba, Cameroun	♂	V	40	54.7 ± 2.5	16-82	0.59	NS
				♂	M	21	57.9 ± 3.5	17-98		
				♀	V	38	74.0 ± 2.8	18-100	0.0983	NS
				♀	M	20	61.4 ± 6.1	15-100		
		mayri	Lae, New Guinea	♂	V	28	25.6 ± 1.0	12-34	0.0008	**
				♂	M	28	38.2 ± 2.8	13-70		
				♀	V	19	57.4 ± 3.1	10-68	0.0106	*
				♀	M	43	50.3 ± 2.2	8-75		
		nikananu	Ivory Coast, Africa	♂	V	28	34.4 ± 1.7	14-51	0.3117	NS
				♂	M	27	36.6 ± 1.8	16-53		
				♀	V	41	45.2 ± 1.4	24-69	0.0278	*
				♀	M	23	35.0 ± 2.6	6-64		
		orosa	Khao Yai, Thailand	♂	V	42	27.5 ± 1.7	9-62	0.2476	NS
				♂	M	26	31.8 ± 2.5	13-58		
				♀	V	29	45.4 ± 3.1	6-74	0.1099	NS
				♀	M	22	37.1 ± 3.9	9-72		
		parvula	Kuala Lumpur, Malaysia	♂	V	18	28.9 ± 2.4	15-53	0.28	NS
				♂	M	38	33.1 ± 1.9	8-60		
				♀	V	10	28.4 ± 1.8	18-38	0.0382	*
				♀	M	48	33.2 ± 1.0	17-48		
		pennae	Garoka, New Guinea	♂	V	31	19.5 ± 1.9	7-39	0.0004	**
				♂	M	18	33.2 ± 2.6	10-57		
				♀	V	39	35.5 ± 1.8	16-66	0.0001	***
				♀	M	20	19.2 ± 2.5	7-41		
		punjabiensis	Kuala Lumpur, Malaysia	♂	V	30	33.6 ± 2.4	12-71	0.34	NS
				♂	M	35	37.2 ± 2.0	17-74		
				♀	V					
				♀	M	58	42.4 ± 1.9	12-89		
		quadraria	Chi Tou, Taiwan	♂	V	20	35.1 ± 3.1	16-70	0.09	NS
				♂	M	24	45.0 ± 3.7	19-89		
				♀	V	24	44.5 ± 1.6	27-60	0.52	NS
				♀	M	34	41.4 ± 2.5	12-72		
		ponera	Isle de la Reunion	♂	V	37	19.0 ± 2.2	3-55	0.02	*
				♂	M	27	24.0 ± 2.3	6-57		
				♀	V	21	33.1 ± 3.3	4-57	0.02	*
				♀	M	41	22.5 ± 2.5	3-73		
		rufa	Hangchow, China	♂	V	38	33.2 ± 1.8	16-65	0.0025	*
				♂	M	16	45.4 ± 3.2	25-65		
				♀	V	26	43.2 ± 3.6	10-88	0.64	NS
				♀	M	24	39.5 ± 2.6	16-66		
		seguyi	Salisbury, Rhodesia	♂	V	30	52.3 ± 4.6	6-96	0.52	NS
				♂	M	22	56.5 ± 5.2	11-119		
				♀	V	29	75.2 ± 2.8	29-88	0.0001	***
				♀	M	24	36.6 ± 3.2	10-64		
		serrata	Queensland, Australia	♂	V					
				♂	M	61	49.2 ± 2.5	10-103		
				♀	V					
				♀	M	58	72.9 ± 3.5	17-115		
		triauraria	Hangchow, China	♂	V	39	30.9 ± 2.0	8-50	0.0124	*
				♂	M	13	36.1 ± 1.8	31-52		
				♀	V	40	60.6 ± 2.2	33-87	0.0001	***
				♀	M	22	39.5 ± 2.6	15-63		
		tsacasi	Ivory Coast, Africa	♂	V	30	28.0 ± 1.4	15-43	0.10	NS
				♂	M	27	32.0 ± 1.9	12-52		
				♀	V	10	59.0 ± 1.9	45-67	0.0001	***
				♀	M	52	38.7 ± 1.9	9-66		

Table 3. (continued)

Group	Subgroup	Species	Strain	Sex	Mating† Status	N	Longevity++	Range	Prob >χ^2	$
		vulcana	Mount Selinda, Rhodesia	♂	V	47	26.9 ± 1.2	7-44	0.0034	*
				♂	M	15	34.7 ± 2.2	21-49		
				♀	V	29	61.7 ± 3.7	24-106	0.0108	*
				♀	M	33	47.1 ± 3.2	5-80		
Willistoni	Willistoni	capricorni	Palmira, Columbia	♂	V	30	40.5 ± 1.1	30-56	0.88	NS
				♂	M	28	37.7 ± 2.1	14-60		
				♀	V	9	44.1 ± 1.6	38-52	0.53	NS
				♀	M	51	44.3 ± 1.7	12-72		
		equiroxalis	La Hina, Honduras	♂	V	20	61.8 ± 3.2	38-95	0.0009	***
				♂	M	26	47.3 ± 2.2	15-75		
				♀	V	20	73.1 ± 5.7	27-111	0.80	NS
				♀	M	41	70.2 ± 4.0	15-111		
		fumipennis	Bucaramanga, Columbia	♂	V					
				♂	M	59	45.1 ± 2.8	6-89		
				♀	V	10	50.2 ± 6.2	21-72	0.0044	*
				♀	M	59	72.9 ± 3.1	20-137		
		nebulosa	Facultad de Agronomia, Palmira, Columbia	♂	V	10	21.0 ± 1.4	14-26	0.12	NS
				♂	M	57	25.0 ± 1.3	5-61		
				♀	V	10	43.5 ± 3.2	28-60	0.78	NS
				♀	M	43	44.9 ± 3.0	10-111		
		paulistorum	Mesitas	♂	V					
				♂	M	63	48.4 ± 1.8	15-79		
				♀	V					
				♀	M	66	58.8 ± 2.9	14-104		
		sucinea	Medellin, Columbia	♂	V	17	35.5 ± 1.6	17-41	0.48	NS
				♂	M	30	37.9 ± 1.4	21-53		
				♀	V	21	54.9 ± 3.8	21-77	0.0112	*
				♀	M	24	42.5 ± 3.3	15-75		
		tropicalis	Instituto Tropical, San Salvador, El Salvador	♂	V	20	37.4 ± 1.7	29-64	0.18	NS
				♂	M	43	32.4 ± 1.6	7-59		
				♀	V					
				♀	M	62	47.7 ± 2.1	8-79		
		willistoni	Santa Maria de Ostuna, Nicaragua	♂	V	19	32.7 ± 3.6	6-66	0.65	NS
				♂	M	29	36.6 ± 2.7	15-55		
				♀	V	20	59.8 ± 3.2	41-82	0.27	NS
				♀	M	44	54.5 ± 3.4	8-123		
		willistoni-like	Instituto Tropical, San Salvador, El Salvador	♂	V					
				♂	M	51	52.8 ± 2.6	11-89		
				♀	V	24	59.4 ± 4.8	14-99	0.48	NS
				♀	M	27	55.9 ± 2.9	28-88		

† V = unmated
M = mated
++ Longevity = mean days from eclosion to death ± standard error of mean

$ Based upon Kruskal-Wallis Test (χ^2 approximation)
* $p \leq 0.005$
** $p \leq 0.001$
*** $p \leq 0.0001$

RESULTS

Adult longevity of the *Drosophila* thus far studied (89 strains of 68 species) varied with respect to species, strain, sex, and mating status (Tables 1, 2, and 3) ranging from an average longevity of 11 days for mated males of the Quesnel, Canada strain of *D. persimilis* to 91 days for unmated males of the Tamazunchale, San Luis Potosi, Mexico strain of *D. ananassae*. The longest-lived individual fly was a female of the Chanwat, Thailand strain of *D. jambulina,* a member of the *montium* subgroup, which lived 153 days (Table 3). When males and females of either mating status (mated vs. unmated) were combined, statistically significant differences were found between species within all subgroups examined (Table 2, Figs. 1 and 2). Significant differences in longevity were found between strains of 14 of the 21 species for which two strains were studied (Table 1). It is interesting to note that significant between-strain differences were found for all five species examined in the *obscura* subgroup.

In general, females lived longer than males. Statistically significant differences in longevity between the sexes were found in 55 of the 89 strains thus far studied (Table 1). Of these, females had higher longevity in 53 strains, while males had higher longevity in only 2 strains: the Mather, CA strain of *D. miranda* and the Tamazunchale, S.L.P., Mexico strain of *D. ananassae*. In both of these strains, the extent to which males outlived females was highly significant ($p<0.0001$).

Significant differences in adult longevity were found between the sexes in all strains examined in four out of the five species of the *obscura* subgroup. It is of interest to note that in all but the Mather, CA strain of *D. miranda,*

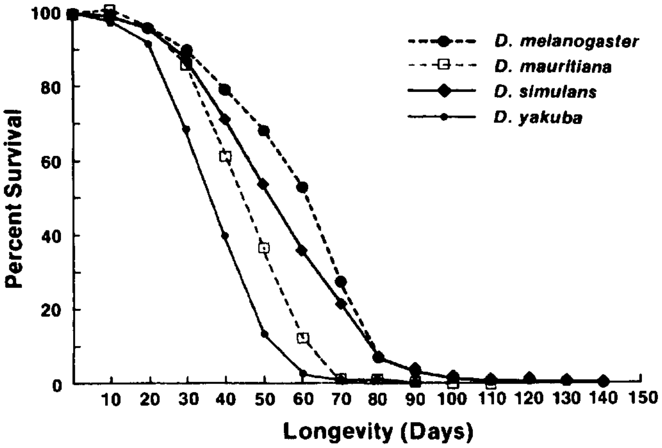

FIGURE 1. Longevity of *Drosophila* (the *melanogaster* subgroup).

female longevity exceeded that of the male. Significant differences in longevity were found between the sexes in only one of the species of the *melanogaster* subgroup, *D. yakuba*. Within the *montium* subgroup, significant between-sex differences in longevity were found in 24 of the 31 strains examined. Within the *willistoni* subgroup, females significantly outlived males in eight of the nine species studied.

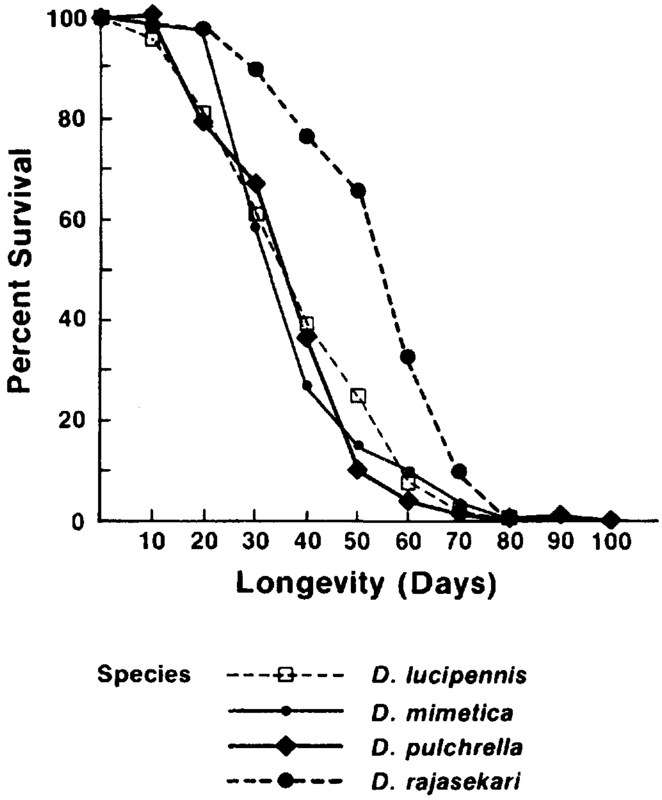

FIGURE 2. Longevity of *Drosophila* (the *suzukii* subgroup).

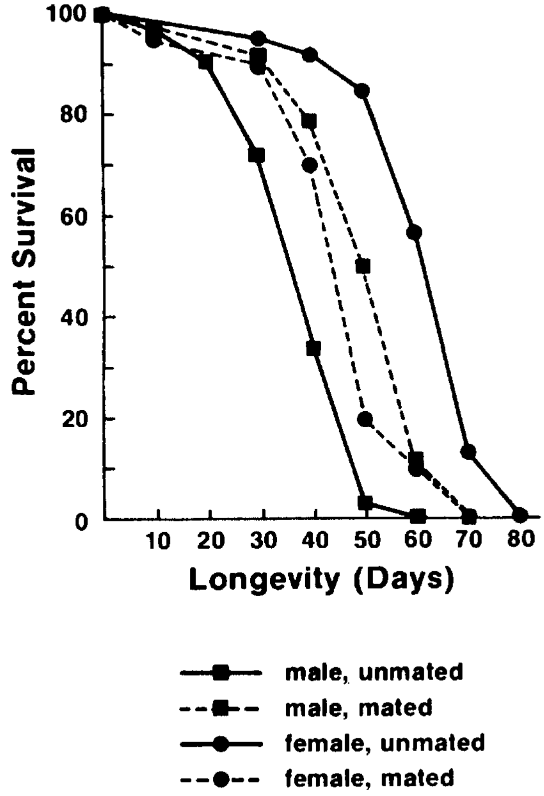

FIGURE 3. Longevity of *D. rajasekari*, with special regard to mating status.

In addition to differences in adult longevity related to species, strain, and sex, differences were found between mated and unmated flies of the same sex in several of the strains studied. Among females, unmated females lived significantly longer in 24 strains when compared with mated females, while in seven strains, mated females lived longer than their unmated counterparts. Among males, the situation is reversed. In 21 strains, mated males lived significantly longer than unmated males, while in seven strains, unmated males lived longer than mated ones (Table 3 and Fig. 3).

DISCUSSION

The genus *Drosophila* has been considered an ideal organism for studies of aging and adult longevity for a variety of reasons. More is known about its genetics than that of any other multicellular eukaryotic organism. A large body of gerontological research has been performed utilizing this organism, yielding a large body of data about its longevity and those factors that influence it. These factors include those associated with species, strain, sex (Durbin and Yoon 1986, 1987, Schnebel and Grossfield 1983), mating status (mated vs. unmated) (Kidwell and Malick 1967, Maynard Smith 1959), female fecundity and fertility (Doane 1960a,b, Giess et al. 1980, Hiraizumi 1985, Maynard Smith 1958, Spiess et al. 1952, Kidwell and Malick 1967), age of reproduction (Rose 1984, Luckinbill et al. 1984), genetic background (Baird and Liszczynskyj 1985, Bozuk 1978, Clark and Gould 1970, Clare and Luckinbill 1985, Gonzalez 1923, Gould and Clark 1983, Hiraizumi 1985, Hughes and Clark 1988, Kidwell and Malick 1967, Levine 1952, Lints 1983, Marinkoavic and Wattiaux 1967, Ohnishi and Moriwaki 1956, Parsons 1978, Roberts and Iredale 1985, Sondhi 1968, Spiess et al. 1952), and environmental factors. The present study contributes new data to this body of knowledge.

Maynard Smith (1962) has defined aging as "those (processes) which render individuals more susceptible as they grow older to the various factors, intrinsic or extrinsic, which may cause death". Historically, two methods have been used to show that aging changes occur in a species: the direct method and the "life table" method (Lamb 1978). In the direct method, deteriorative changes, in particular, physiological, biochemical or morphological functions, are measured in individuals of different ages (Bourgois and Lints 1982, Driver and Lamb 1980, Massie and Kogut 1987, Miquel et al. 1980, Schnebel and Grossfield 1988, Webster et al. 1980). In the "life table" method, the age of death is determined for a population of similar individuals. The force of mortality (the number of individuals dying in a specified time interval divided by the number of individuals alive at the onset of that time interval), the percent survival, or the percent dead is plotted against time (Clare and Luckinbill 1985, Luckinbill and Clare 1986, Doane 1960a,b, Durbin and Yoon 1986, 1987, Hollingsworth 1969, Kimura 1988, Levine 1952, Rose 1984, Spiess et al. 1952). In the present study, the "life table" method (Figs. 1-3) was used in order to broaden the base of data pertaining to the biology and genetics of these species, many of which have heretofore never been used in aging or longevity research.

Each subgroup used in this investigation was tested to determine if there were any significant differences in average longevity among species (Table 2). Within some subgroups, there was no significant difference in average adult longevity for two or more species studied. For instance, within the *affinis* subgroup, there was no difference in mean adult longevity among *D. algonquin, D. azteca,* and *D. bifasciata.* These species, however, had mean adult longevities significantly different from the other two members of this subgroup. In the *D. obscura* subgroup, no significant difference in mean adult longevity was found between two of the five species of the subgroup, while within the *D. suzukii* subgroup, no significant differences were found between three of its four species.

The *montium* subgroup has been divided into at least five complexes: the *nikananu, bakoue, kikkawai, auraria* and *serrata* complexes (Lemeunier et al. 1986). All four species of the *auraria* complex were included in the present study. Of these, there were no significant differences in adult longevity among three of four species of this complex: *D. quadraria* (41.7d), *D. triauraria* (43.6d), and *D. auraria* (43.9d). However, the adult longevity of each of these species is significantly different from that of *D. biauraria* (52.1d), the fourth species within this complex. It is of interest to point out that our longevity results from the *auraria* complex are consistent with data from isozyme variation studies (Ohnishi et al. 1983a,b, Lee 1974, 1980), which indicate that *D. quadraria, D. triauraria* and *D. auraria* are more closely related to each other than any one of them is to *D. biauraria.* Among the members of the *bakoue* complex within the *montium* subgroup, three species (*D. seguyi, D. tsacasi,* and *D. vulcana*) were analyzed in this experiment. It should be noted that the mean adult longevity of *D. seguyi* (55.9d) was significantly different from that of the other two species, *D. tsacasi* (36.2d) and *D. vulcana* (41.3d), for which no significant difference was observed.

In the present study, intra-specific differences were studied at the strain, sex, and mating status (mated vs. unmated) level. Of 21 species studied, significant inter-strain differences were found in 14 species, some of which may be attributed to sex (Table 1) or mating status (Table 3). In some species studied, the laboratory-derived strains used were from different geographic locations, having climatic differences that may have imposed a selective advantage on those traits which influence, either directly or indirectly, adult longevity.

Significant differences in adult longevity were found between the sexes in approximately half of the species included in this investigation. As previously stated, in most of these (52 of 54), females lived significantly longer than males. Several authors have reported a variety of findings with respect to between-sex differences in *Drosophila.* For instance, Maynard Smith (1958) found significant differences between the sexes of most of the populations of *D. subobscura* that he studied. These differences, however, were reported to be in either direction. In general, he found that outbred flies lived longer than inbred ones, and that important genetic factors affect the adult longevity of male and female flies differently. The present data are consistent with his findings: Females (22.7d) of the Norway strain of this species lived significantly longer than males (15.8d, $p=0.005$) (Table 1), while in the Cave Junction, OR strain the situation was reversed, with males living longer than females, although not significantly so. We found no significant differences between the sexes of either strain of *D. melanogaster* examined. This contrasts with some of the data in the literature. For instance, Kidwell and Malick (1967) reported that the mean adult longevity of 58.8d for females of this species was significantly higher than that of the males at 44.2d.

In several of the strains that were examined, significant differences were found between flies of different mating status. Specifically, there was a general tendency for unmated females to live longer than mated ones and mated males to live longer than their unmated counterparts. Although no generalizations across species or across strains can be made on the basis of these data, this general tendency is consistent with the findings of a number of investigators with respect to female longevity. Several authors have suggested that female adult longevity may be inversely related to egg production, the rate of which increases after mating in *Drosophila.* For instance, Speiss et al. (1952) found that mated *D. persimilis* females with the Klamath (KL/KL) gene arrangement lived longer and laid fewer eggs per unit time at all ages than did mated females with the Whitney (WT/WT) gene arrangement. In a study by Bilewicz (1953) using *D. melanogaster,* unmated females lived approximately twice as long as mated ones. In the present study, unmated females of both strains of *D. melanogaster* examined lived longer than their mated counterparts, although these differences were not statistically significant (possibly as a result of small sample size). An inverse relationship between adult longevity and egg laying was shown by Maynard Smith (1958) and Lamb (1964) for *D. subobscura* (for which no significant difference relative to mating status was found in this study), and Nöthel (1965), Doane (1960a,b), and Rose and

Charlesworth (1981a,b) for *D. melanogaster*. Some of these studies used sterilized or genetically produced "ovaryless" flies. However, their published data are not without contradiction (Kidwell and Malick 1967, Lints and Lints 1969, Schnebel and Grossfield 1988).

The general tendency for unmated females to live longer than mated ones in a number of the strains thus far examined is consistent with Pearl's (1928) "rate of living" hypothesis. Pearl proposed that longevity is a function of two factors: (1) the constitution of the animal, which is genetically determined, and (2) the rate of energy expenditure during life. For animals with similar constitutions, "the length of life is inversely proportional to the rate of living". The increased egg production associated with mating places an increased burden upon the metabolic resources of the individual female. Under certain conditions of environment and genetic background, this may render the mated female more susceptible to accelerated aging. However, Fowler and Partridge (1989) recently suggested an alternate explanation. They demonstrated that frequent mating, per se, results in a decrease in female adult longevity even in flies that have the same rates of egg-production and fertility. Future studies of the egg laying patterns of mated and unmated females of the strains used in the present investigation might increase our understanding of this phenomenon.

Among males of the strains used in this study, the situation was reversed. In 24 strains, mated males lived significantly longer than unmated ones, while in five strains unmated males lived longer than mated ones. No significant differences were found between mated and unmated males in the remainder of the strains used in this investigation. The effect of mating status on male adult longevity has not, to the best of our knowledge, been extensively studied in *Drosophila*.

Sex and mating status have been shown to be variables associated with longevity in some strains of *Drosophila*. However, these are but two of a variety of factors that may influence adult longevity. The flies used in this investigation are all laboratory stock, most of which have been maintained in standard food vials (25mm X 95mm) for a number of years. As a result, they may no longer have the same genetic composition as that of members of the original populations from which they were bred. This phenomenon could potentially have occurred in at least two ways: (1) inbreeding depression could occur as a result of the relatively small population size (bottlenecks) maintained in the laboratory for many years and (2) flies raised under such conditions experience quite different selective pressures than do those in the wild. These artificial selective pressures may have resulted in an alteration of gene frequencies within any of the strains employed in this investigation. Therefore, care should be taken when applying these results from laboratory to natural populations.

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