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Reproductive Strategy in *Drosophila melanogaster*: Significance of a Genetic Divergence between Temperate and Tropical Populations

J. Boulétreau-Merle[1], R. Allemand[1], Y. Cohet[1], and J.R. David[2]

[1] Laboratoire de Biologie des Populations (associé au C.N.R.S.) Université Claude Bernard, Lyon I, Bât. 403, F-69622-Villeurbanne, France

[2] Laboratoire de Biologie et Génétique Evolutives, C.N.R.S. F-91190 Gif-sur-Yvette, France

Summary. Reproductive capacities of tropical and temperate populations of *D. melanogaster* were compared using three complementary techniques: (1) measure of egg production by females grown in the laboratory under uncrowded conditions and provided as adults with abundant food; (2) study of egg production of flies of unknown ages, collected in nature and then kept in similar conditions; and (3) analysis of ovarian activity of wild females dissected just after their capture.

Tropical populations showed a lower fecundity in the laboratory and this was also observed in laboratory reared adults. On the average, flies also appeared to be older in the tropics than in temperate countries. These data, together with ecological observations showing that tropical populations live in a more predictable and stable environment, suggest that temperate populations are *r*-selected, while tropical ones are *K*-selected. The study of ovarian activity of wild females failed however to confirm this expectation. Tropical flies, which have a lower genetic fecundity, generally appeared to produce more propagules than did temperate flies. Such a contradiction shows how the ideas of *r*- and *K*-selection are difficult to apply to natural populations of *Drosophila*. Population density and interindividual competition are probably not the main selective forces in nature. Attention must also be paid to the necessity of exploring the environment to find resources, to the role of predation and parasitism, and to the occurrence in temperate countries of seasonal fluctuations with different selective pressures on successive generations.

Introduction

It is now well-established that *D. melanogaster*, in spite of its domestic status, shows much genetic divergence between allopatric populations. The best documented cases concern differences between European and Afrotropical populations in morphological biometrical traits (David et al. 1977), physiological traits (David and Bocquet 1975; Allemand and David 1976; Cohet et al. 1980), and allozyme frequencies (David, in preparation). Such differences are interesting for two main reasons:

1. Since *D. melanogaster* is a species native to Africa (Tsacas and Lachaise 1974), the Afrotropical populations can be considered as central or ancestral.

2. The variations occur in a latitudinal, clinal pattern, suggesting some kind of climatic adaptation.

Offprint requests to: J. Boulétreau-Merle

In trying to understand the adaptive significance of morphological variations, we must correlate them with some physiological difference, which itself would be the true target of natural selection. Among numerous biometrical differences observed between European and Afrotropical populations, ovariole number in the ovaries is about 25% higher in France than in Africa (David et al. 1977). Such a systematic difference is especially interesting since, at least in the laboratory, ovariole number is strongly correlated with egg production (David 1970; Cohet and David 1978), so that a divergence in the reproductive capacities of these populations is likely.

Ecological observations show drastic differences between European and Afrotropical populations with respect to their population dynamics and demography. In humid tropical or equatorial countries, climatic conditions are relatively stable all year round: resources are abundant and population is large (Dobzhansky 1950; Lachaise 1974; Vouidibio 1977; and many unpublished observations). In temperate countries, on the other hand, large seasonal variations are observed, usually with a demographic explosion at the end of summer and a bottle-neck during winter (Petit 1969; Ives 1970).

From current evolutionary theory, we expect that temperate populations living in a fluctuating and less predictable environment would be *r*-selected, while tropical populations should be more *K*-selected (MacArthur and Wilson 1967; Pianka 1970; Giesel 1976). Our laboratory results, at first sight, confirmed this expectation and were also in agreement with observations made in Australia on various physiological traits (Parsons 1980a). However, a previous work (Boulétreau 1978) showed that there were no obligatory relationships between the actual reproductive effort of the temperate flies and their genetic potential. A careful analysis of the reproductive capacity of wild flies revealed a much greater complexity, showing the diversity of the selective pressures with which natural populations are faced.

Material and Methods

Adult of the African population were collected by sweeping in the suburbs of Brazzaville (Congo), near Madibou. This population lived in a cultivated area with cassava and various fruit trees. The French population taken for comparison was collected in September with banana baits at Veaux near Avignon, in southern France. Its reproductive potential has already been studied (Boulétreau 1978). Immediately after their capture, some of the females were dissected and checked for their ovarian status: egg chambers in vitellogenesis (stages 8–13 according to King et al. 1956), mature oocytes (stage 14), and ovarioles were

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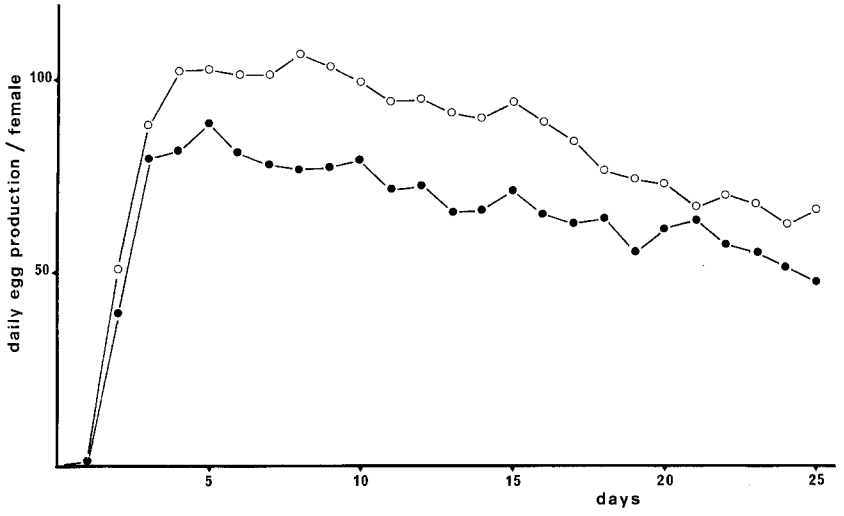

Fig. 1. Daily egg production at 25° C of mated females of the first laboratory generation. ● Tropical population from Brazzaville (Congo); ○ temperate population from Veaux (France)

counted. Another fraction of the collected wild females were brought back to the laboratory and isolated with or without a male in oviposition vials. Their egg production was followed for a least 20 days at 25° C under the best possible feeding conditions and percentage of eggs hatching after 1 day of incubation at 25° C was also measured. Ovariole number was determined at the end of the experiment by dissection. In the case of the French flies, 5 days elapsed between the time of capture and the start of the experiment. This delay was reduced to 3 days in the case of the African population which was, however, studied in France. Other wild-collected adults were distributed in groups of 10 females and 10 males and their longevity measured by checking dead flies every day.

Finally, offspring of the wild-collected females were reared in favourable laboratory conditions: growth on a killed yeast medium at 25° C and low population density. Upon emergence, couples (1♀ 1♂) were isolated in oviposition vials and their egg production was followed over 25 days. Other flies in groups of 10 couples were used for measuring longevity. Since the dissection of wild females produced quite unexpected results, it appeared necessary to extend this analysis to more cases. Two other tropical populations were studied: an African one from Cotonou (Bénin) and another from Guadeloupe (French West Indies). Two other French populations were also considered: another one from Veaux collected in a different season (Boulétreau 1978) and one from Bully near Lyon, collected in October during vintage time.

Results

Genetic Differences Between Laboratory-Reared Females

Egg Production. Studying laboratory-grown flies is convenient for reducing environmental variability and estimating their genetic properties (David 1979). The experiment was done with the offspring of 10 isolated wild African females (isofemale lines). At emergence, 5 couples from each family (total number = 50) were put in oviposition flasks and daily egg production followed for 25 days. The same procedure was used with 12 isofemales lines of the French population (total number = 60).

Egg production curves are given in Fig. 1 and show the classical shape for *D. melanogaster* (David et al. 1974). Starting on the second day, oviposition increases rapidly, reaches a maximum on the fourth or fifth day, and then decreases slowly as females become older. A striking and highly significant difference exists between ordinates of the two curves, egg production being higher in French flies.

The females were dissected at the end of the experiment and the average ovariole numbers and standard errors for the African and French flies were 39.68 ± 0.51 and 48.57 ± 0.60, respectively. This highly significant difference confirms what was previously known and explains the difference in fecundity. When we consider the daily egg production per ovariole, the curves of the two populations are almost identical (Fig. 2).

Egg Viability. The proportion of hatching eggs was checked daily. For the African flies, the percentage of larvae was 93.5% for the first 15 days; 4,4% were unfertilized; 2.1% did not hatch due to embryonic mortality. Over the whole duration (25 days), 91.1% of the eggs produced larvae, 6.7% were unfertilized and 2.2% contained a dead embryo. In the French population, the values were very similar: 96.0% produced larvae during the first 15 days with 1.9% unfertilized eggs and 2.1% dead embryos.

Longevity. The mean longevities of laboratory-reared flies are given in Table 1 and survival curves are shown in Fig. 3. Longevities are a little higher in females than in males, but there is no significant difference between African and French flies.

Study of Wild-Collected Flies in Laboratory Conditions

As indicated under Methods, wild-collected females were brought to the laboratory as rapidly as possible. Each female was isolated either with or without a male and egg production was studied for 20 days.

Egg Production and Hatchability. Daily egg-production curves are given in Fig. 4. All the females, inseminated in the field and then kept for 5 days in groups without males, started to oviposit on the first day of the experiment. The increase of egg production observed during the first 3 days in the couples and in the isolated females was probably due to the decrease of population density, since it is known that isolated females produce more eggs than females in small groups (Boulétreau-Merle 1975). The higher level of egg production observed on

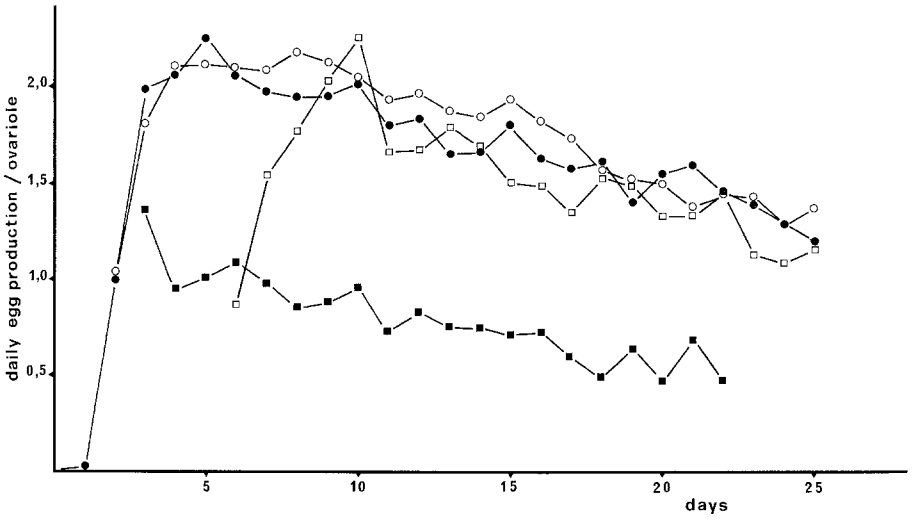

Fig. 2. Daily ovariole production by mated females either wild-collected or of the first laboratory generation. ● First generation and ■ wild females from Brazzaville (Congo). ○ First generation and □ wild females from Veaux (France). (time zero refers either to adult emergence or to the day of capture in nature)

Table 1. Longevity of *D. melanogaster* adults under laboratory conditions at 25° C (*m*: mean in days; *n*: number of adults; *c.v.*: coefficient of variation)

Origin		Females			Males		
		$m \pm \sigma_m$	n	c.v.	$m \pm \sigma_m$	n	c.v.
Laboratory-grown	Africa	62.0±1.6	(75)	22.1	56.1±1.4	(75)	21.1
	France	58.8±1.2	(78)	17.3	54.2±1.2	(75)	19.3
Wild-collected	Africa	16.2±0.5	(80)	36.7	15.3±0.5	(80)	44.1
	France	32.1±1.1	(97)	32.6	33.3±0.7	(219)	31.3

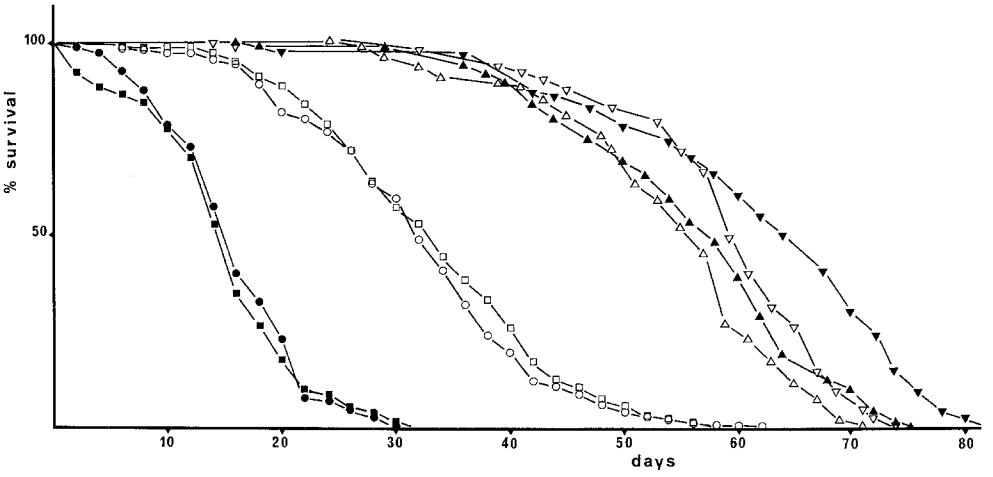

Fig. 3. Survival curves of adults kept in the laboratory at 25° C. Wild-collected males (■) and females (●) from Brazzaville (Congo), Wild-collected males (□) and females (○) from Veaux (France). First laboratory generation males (▲) and females (▼) from Brazzaville. First laboratory generation males (△) and females (▽) from Veaux (age zero corresponds to adult emergence or to the time of collection in nature)

the 4th and 5th days in the couples was due to remating, since repeated copulation is necessary to keep oogenesis at its maximum rate (Boulétreau 1974). This interpretation is confirmed by the analysis of egg hatching. In the case of couples, egg hatchability started at 98% and progressively decreased to 80% at the end of the experiment. This is a classic observation in mated females: periodic copulation during a lifetime provides simultaneously both a sufficient amount of sperm for egg fertilization and also a permanent stimulus for oogenesis (Boulétreau 1974), so the slow decrease is mainly a consequence of ageing. For females kept without males, spermatozoa became progressively exhausted, so that egg hatching was nil on the 12th day. This exhaustion resulted in a lack of stimulation of oogenesis and a return to the physiological state typical of virgin females.

Results are not so clear for African flies. Egg production started at similar levels in the two groups, about 30 eggs day, but then decreased slowly and regularly in an almost linear way. No stimulation due to favourable laboratory conditions was noticeable. Moreover, after the 6th day, lower production was observed in the isolated females, but the difference between the two groups remained very small, about 6 eggs/day, up to the end of experiment. Analysis of egg hatching in the isolated females showed a much slower decrease than in the similar group of French flies: hatching was still above 50% on the 12th day

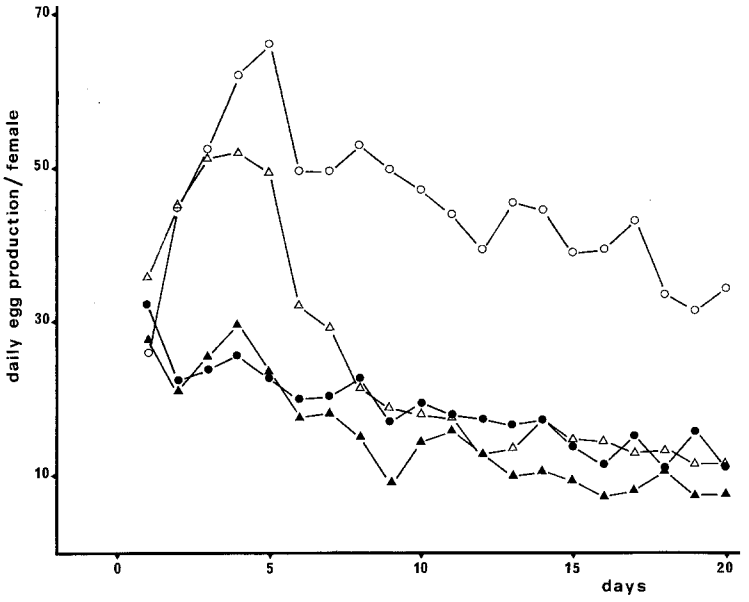

Fig. 4. Daily egg production of wild-collected females in laboratory conditions. Couples (●) and isolated females (▲) from Brazzaville (Congo). Couples (○) and isolated females (△) from Veaux (France) (day zero refers to the beginning of the experiment in the laboratory)

and reached 0 only at the end of experiment. This slower decrease may be explained by the lower egg production resulting in a slower exhaustion of sperm.

Egg Production and Ovariole Number. Wild-collected flies, mainly in tropical countries, are smaller than laboratory-reared ones (David et al. 1980) and this results, in a lower ovariole number. This phenomenon was confirmed in the samples studied here since the average numbers and the standard errors were 33.11 ± 0.73 ($n=110$) and 23.47 ± 0.60 ($n=78$) in French and African flies respectively, values much lower than in their laboratory-reared daughters. It was thus worthwhile to consider egg production in relation to ovariole number. Results for mated flies are shown in Fig. 2.

For wild-caught French females, the curve, after the initial increase of egg production, was practically identical to that of laboratory-grown flies; in the best conditions, each ovariole produced about 2 eggs/day. A large difference characterized the African females, since the rate never exceeded 1.4 eggs/day and, after the second day, remained at a value of about 1. It is known that daily egg production decreases with age. The difference noticed here, associated with the lack of stimulating effect of isolation and the low hatchability of the eggs, strongly suggests that African flies, when collected, were on the average much older than French flies.

Longevity. Survical curves of wild-collected adults are given in Fig. 3 and compared to the curve typical of laboratory-grown flies. Mean values are also given in Table 1.

Wild-collected flies are characterized by a much shorter life expectancy and also a greater variability between individuals, measured by the coefficient of variation. For example, if we compare the French flies, we note that laboratory-grown adults started to die after 35 days, while wild-collected flies started to die significantly after only 20 days. This difference may be explained by assuming that, in the wild sample, a significant part of the population consisted of fairly old flies, thus explaining their early death in the laboratry. However, if this is the only reason for the results, the difference of longevity between the two groups, i.e. about 24 days must represent the mean age at time of collection. Longevity of *Drosophila* adults in nature is, unfortunately, not known but ist is very likely that, at least for summer generations, average life duration is below 24 days (Boulétreau 1978) in a large proportion of young adults. The difference observed is probably also due to a shorter life expectancy of wild flies, perhaps because of deleterious effects of poor larval feeding conditions. Such epigenetic influences upon life duration of adults have been shown after various pre-imaginal treatments (Lints and Lints 1971; Cohet 1975).

For the African population, the difference between wild- and laboratory-collected flies is still more striking, since it amounts to more than 40 days. In this case, it is very unlikely that such a difference corresponds to the mean age of flies in nature. However, it seems legitimate to assume that the mean age in the African natural population was higher than in the corresponding French population, as this is also suggested by the fecundity curves.

Ovarian Development and Oogenesis in Wild Females

Females of the two populations previously studied were dissected and examined for their ovarian development just after capture. Results concerning the numbers of ovarioles, egg chambers in vitellogenesis (stages 8–13), and mature oocytes (stage 14) are given in Table 2 (populations from the Congo and from Veaux in September). Results again show the difference in ovariole number between African and French populations. Much heterogeneity exists between individuals in both populations as regards the number of egg chambers in vitellogenesis and of mature oocytes since the coefficients of variation (not shown) were always very high, close to or above 100%. This very high variability, which seems typical of wild flies, contrasts with the greater homogeneity of the ovarian state of flies grown and studied in the laboratory (Boulétreau, 1978). It reflects age differences between individuals and also the hazards of natural life, such as the difficulties of finding food resources and oviposition sites.

More interesting is the fact that, in spite of a lower ovariole number, the African flies contained somewhat more oocytes in vitellogenesis than French flies and many more mature oocytes in their ovaries. From such data it is difficult to estimate what could be the mean number of eggs deposited each day in nature, for two main reasons. First, we know that mature oocytes may be retained in the ovaries for several days, especially in the

Table 2. Ovarian state of wild females in three tropical (*above*) and three temperate (*below*) French populations (*n*: number of dissected flies)

Origin	Month	*n*	Ovarioles $m \pm \sigma_m$	Vitellogenic stages (1)	Mature oocytes (2)	Total 1+2
Congo	May	50	27.22±0.89	13.60±1.89	22.92±2.58	36.52
Bénin	August	51	29.10±0.84	23.62±2.68	13.86±2.14	37.48
Guadeloupe	February	30	28.53±1.09	16.00±1.96	10.40±2.10	26.10
Veaux	September	220	33.11±0.39	11.84±0.73	5.14±0.52	16.98
Veaux	June	264	31.84±0.81	7.38±0.57	6.00±0.53	13.88
Bully	October	50	34.84±1.04	28.44±1.24	10.52±2.34	38.96

absence of suitable oviposition sites (Van Herrewege 1970). Second, ovarian activity is greatly influenced by temperature (Cohet and David 1978) and the two populations studied differed greatly in this respect: in the Congo the average temperature was 25° C, while it was below 20° C in France. Dissected flies were also examined for their feeding status, i.e. the presence of food in the crop and midgut, and it was found that African flies were better fed than French ones.

From all this information, we can tentatively conclude that African females in nature produced about four times more eggs/day than French ones, and that only half of this difference could be attributed to a temperature effect.

It is paradoxical to conclude that the flies (African) that are both phenotypically and genetically less able to produce eggs were, in nature, producing many more eggs than those with a higher intrinsic capacity. Thus it was interesting to consider other populations from tropical and temperate places: results are also given in Table 2. Studies of two other tropical populations (one African from Bénin, one American from Guadeloupe) broadly confirmed the results obtained from the Congo population: vitellogenic stage were found to be more numerous, but the ovaries contained fewer mature oocytes. If we consider the sum of mature oocytes and vitellogenic stages as an approximate measure of the instantaneous reproductive activity of the population, we find that, in the tropics, this number is equal to or higher than the ovariole number.

Higher variability was observed between the other two French samples. The population of Veaux collected in June showed approximately the same low ovarian activity as in September. However, the Bully population, which was living in a wine cellar with abundant resources, as shown by the repletion of the midgut in almost all flies, exhibited a much higher reproductive effort, comparable to that observed in the tropics.

Discussion and Conclusion

As stated in the Introduction, life conditions encountered by *D. melanogaster* are extremely different in tropical and temperate countries. The environmental stability and availability of resources in the tropics should maintain the population at a high level, close to the maximum carrying capacity, and thus result in *K*-selection. Under a temperate climate, on the other hand, resources are less predictable and often scarce, but sometimes in great excess. Therefore, demographic explosions are followed by population bottle-necks, especially in winter, and *r*-selection should be observed (McArthur and Wilson 1967; Pianka 1970). In agreement with these predictions, the mean age of wild flies was certainly higher in Africa than in France (Fig. 3).

Finding that French populations have a higher genetic fecundity than African flies appears, at first sight, to be one of the very few cases in which the theory of *r-K* selection is verified at a genetic level. More precisely, if we admit with Pianka (1970) the existence of an *r-K* continuum, we could say that French flies are more *r* and less *K* than African ones. However, more careful analysis shows that the real picture is far more complex. First, it is generally assumed that *r*-selection will result in a decrease in individual size (Pianka 1970; Stearns 1976; Barbosa 1977; Taylor and Condra 1980; Parsons 1980b) while in *D. melanogaster*, the French flies, which are bigger (David et al. 1977), also exhibit a higher reproductive capacity. Second, *K*-selection, as suspected to occur in the tropics, should produce an increase of life expectancy, while longevities of laboratory-reared flies were about the same in the two geographic races (Table 1). But the most striking observation, completely contradicting the theory, is that African flies, which are genetically (Fig. 1) and phenotypically (Fig. 4) less able to produce numerous eggs, exhibit in nature a higher reproductive effort than do French flies in spring and summer.

Of course, these differences may be explained by ecological conditions, especially resource availability. In France, at the end of June and during the summer, resources are generally scarce and unequally distributed in a coarse-grained environment. Females are obliged to use much more food for energy production so that, in spite of a higher intrinsic reproductive capacity, the proportion of resources allocated to egg production remains small. In a wine cellar population, on the other hand, as at Bully, food is very abundant, so there is no need for long-range flights and ovarian activity is close to its maximum capacity.

For tropical populations, the small ovariole number does not appear to be a consequence of a simple *K*-selection, favouring females more tolerant to competition, living a longer time, but producing fewer offspring. The tropical populations, which should be selected for stability and survival, are producing on the average the highest number of propagules. The following interpretation may be suggested. During all seasons, natural selection will favour an equilibrium between daily egg production and duration of reproduction. Because of the abundance of resources, ovaries will be generally well-developed and productive females with numerous ovarioles could be handicapped by excessive weight, which would impair their flight capacity and ability to escape predation (spiders, small frogs and lizards etc.). We must also assume that pre-adult mortality is very high, not because the environment is unstable, but mainly because of a higher rate of predation by ants, staphylinid beetles (unpublished data) or parasitoid wasps (Rouault 1979; Carton and Kitano 1981).

Temperate populations are certainly derived from tropical Africa (Tsacas and Lachaise 1974; David and Tsacas 1981) and we must try to explain how this adaptation to a new and colder environment resulted in the genetic divergence observed. We can first mention that, because of its physiological capacity of regulation, a poorly fed female will stop its oogenesis (Van Herrewege 1970) so that having a high ovariole number is not a

handicap when food is rare. When resources are abundant, on the other hand, the capacity to produce more eggs provides a selective advantage. This selection will be much more efficient if pre-adult mortality is low at that time due to desiccation of breeding sites, predation or parasitism. As mentioned above, resources are usually more abundant in France during autumn, and at that time of the year desiccation of the breeding sites is unlikely because of the rainy season and lower temperatures. The influence of predators and parasites is not known but, at least for parasitic wasps, it seems that the losses are much lower in temperate countries than in the tropics (Carton and Kitano 1981).

We may also try to explain the identity of life expectancy in tropical and temperate populations. In the tropics, the average age of *D. melanogaster* adults seems higher than in France during the warm breeding season. This should favour a greater genetic longevity as expected under *K*-selection, but in a temperate country natural populations are faced with the redoubtable task of surviving the winter. At that time of the year, most of the population will die and natural selection certainly favours individuals having the longest life duration.

Since *Drosophila* population cages were invented (L'Héritier and Teissier 1933) numerous studies have been done with this technique, which usually maximizes interindividual competition and should produce *K*-selection. Recently, in *D. pseudoobscura*, Taylor and Condra (1980), by reducing the adult population size at each generation, tried to impose *r*-selection in cages. They were able to increase the rate of development, but not egg production; moreover, the reproductive potential was much higher in the *K*-selected cages. On the whole, the predictions of the theory were only weakly met.

Studies of wild populations of *Drosophila* (Kambysellis and Heed 1971; Boulétreau 1978; Atkinson, 1979; Shorrocks and Charlesworth 1980) have also indicated that competition is probably not the main selective force in nature. The difficulty was pointed out of finding breeding sites and thus the necessity of allocating a significant part of the energy budget to exploration of the environment. The role of differing mortality in larvae and adults has also been emphasized recently (Barclay and Gregory 1981).

In the case of *D. melanogaster*, resources are certainly more dispersed and unpredictable in temperate than in tropical countries, so more energy should be allocated to exploration. Indeed we find that the effective reproductive effort – but not the genetic capacity – is usually larger in the tropics. This can be explained only by assuming that a higher level of mortality occurs in pre-adult stages. Tropical adults, on the other hand, seem to have a higher life expectancy.

Finally, our observations suggest that, in *Drosophila* as in many other animals (Foster 1974; Wilbur et al. 1974; Maiorana 1976; Barbosa 1977), predation and parasitism play a significant role in regulating numbers. Moreover we emphasize the occurrence of changing selective pressures on different developmental stages (larvae vs adults) and on different generations (summer vs winter) in temperate countries.

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