

Genetics and origin of a *Drosophila melanogaster* population recently introduced to the Seychelles

BY J. R. DAVID AND P. CAPY

Laboratoire de Biologie et Génétique Evolutive du CNRS 91190 Gif-sur-Yvette,
France

(Received 14 April 1982 and in revised form 16 June 1982)

SUMMARY

During an extensive survey of drosophilid fauna in 1977, *D. melanogaster* was not collected in the Seychelles. However, a population was found in 1981 in Victoria city, suggesting a recent introduction of this species. With respect to allozyme frequencies or ethanol tolerance, this population is almost identical to European ones and very different from those living under a similar equatorial climate on the African continent. The frequencies of rare biochemical alleles perhaps suggested that this population was founded by a small number of flies, less than ten inseminated females. For various biometrical traits, the situation was not so clear: according to the trait considered, Seychellian flies are either intermediate between European and African populations or closer to the latter. These data suggest that a few flies, recently introduced from a temperate (European?) country, built up a big population which is now on the way to adapting itself to new tropical conditions. Such an involuntary experiment should afford a unique opportunity to distinguish the respective roles of drift and adaptation in the evolution of *D. melanogaster* geographic races.

1. INTRODUCTION

During its geographic extension and colonization of most parts of the world, *D. melanogaster* has produced various genetic races among which the best characterized are found in the Far East, Europe and tropical Africa (David, Bocquet & Pla, 1976; David, Bocquet & De Scheemaeker-Louis, 1977*a*; David, 1982). Whether this geographic divergence is due to genetic drift or to adaptation to local conditions is still debated. However, differences between Afrotropical and European temperate populations may reflect an adaptation to various ecological conditions (David & Bocquet, 1975*a, b*; David *et al.* 1976, 1977*a*; Allemand & David, 1976; Boulétreau-Merle *et al.* 1982).

D. melanogaster has an Afrotropical origin and has been introduced recently by man to many countries of the world, for example, in America, Australia and many islands (see David & Tsacas, 1981). Islands in which *D. melanogaster* is absent will probably be colonized, sooner or later, by an involuntary introduction. Such events

correspond to an 'ecological experiment', and provide an opportunity to study bottleneck effects, readjustment of the genome, adaptation to a new environment competition with other species and so on. Similar analyses have been already made on various animal species, for example house sparrows in America (Johnston & Selander, 1971), and house mice introduced in islands (Berry & Peters, 1975; Berry, Jakobson & Peters, 1978).

In November 1977, during an extensive survey of the drosophilid fauna of Mahé island in Seychelles archipelago, 35 different species were collected, not including *D. melanogaster* (Tsacas & David, unpublished). In July 1981, during another trip mainly aimed to collect the endemic *D. seychellia* in the tiny island of Cousin, *D. melanogaster* was found quite abundantly in Victoria, the chief town of Mahé. Unexpectedly, this population appeared to be genetically different from those living in equatorial countries of the African mainland and to be much closer to European populations.

2. MATERIAL AND METHODS

D. melanogaster was found only in Victoria and vicinity. One male was collected in the botanical garden, another on Ile aux Cerfs (a few km off Victoria), and the population here studied was collected in the fruit market of Victoria. Adult flies were attracted with banana baits and only two species, *D. melanogaster* and *D. ananassae* were collected in this highly domestic habitat. Each female was used to initiate an isofemale line. Finally, 26 lines were studied. A mixed population was also built up by putting together adults from all the lines into the same bottle.

Morphological traits were measured on the second laboratory generation of 10 isofemale lines, according to previously described techniques (see David *et al.* 1977 *a, b*; David, 1979, for techniques). Fresh weight, thorax and wing lengths, numbers of sternopleural and abdominal chaetae were measured on ten males of each line; ovariole number was determined on samples of ten females. The same trait was not studied in the two sexes of the same line, because such values are highly correlated (David, 1979).

Allozyme frequencies at five polymorphic loci were calculated by sampling two flies from each line. The loci and techniques were the same as those already used when comparing European and Afrotropical populations (David, 1982). Ethanol tolerance was measured on adults of the mixed population according to the technique of David & Bocquet (1975*b*).

3. RESULTS

(a) Allozyme frequencies

Our data (Table 1) are compared to the average frequencies of various European and African populations studied by David (1982). Genetic distances (Nei, 1972) are calculated for each locus and show a constant pattern: for each locus the Seychellian population is close to the European group and very different from the

Table 1 Comparison of allelic frequencies at five polymorphic loci in Seychelles, Europe and tropical Africa

For the Seychelles population, 104 genes were studied at each locus; values for European and African flies correspond respectively to the averages of 7 and 6 different populations (see David, 1982); genetic distances according to Nei (1972).

Locus and alleles	Seychelles	Europe	Africa	Genetic distance		
				S-E	S-A	E-A
Adh S	0.151	0.060	0.916	0.006	1.332	1.867
	0.849	0.940	0.084			
Odh S	0.0	0.029	0.089	0.001	0.005	0.002
	1.0	0.971	0.911			
α Gpdh S	0.491	0.408	0.011	0.014	0.318	0.187
	0.509	0.592	0.989			
Est-6 S ₁ -S ₂	0.047	0.025	0.015	0.001	0.303	0.296
	0.689	0.697	0.317			
	0.264	0.272	0.628			
	0.0	0.005	0.040			
Est-C S	0.0	0.083	0.137	0.005	0.122	0.122
	0.929	0.881	0.551			
	0.071	0.036	0.312			

Afrotropical. For the *Adh* locus, the Seychelles flies are located between European and African ones. For the other loci, the Seychellian population is a little more distant from the African populations than these are distant from European ones.

The general distance including all five loci below, clearly demonstrate the close relationship of European and Seychellian flies:

$$\begin{aligned} \text{Seychelles-Europe: } D &= 0.006, \\ \text{Seychelles-Africa: } D &= 0.351, \\ \text{Europe-Africa: } D &= 0.370. \end{aligned}$$

For 3 loci, one allele at least is lacking in Seychelles: *Odh*^S, *Est-C*^S and *Est-6*^{F₁ · F₂}. Moreover, in European and African populations, two very slow alleles (S₁ and S₂) of *Est-6* are found in most populations. Only one (S₁) was present in Seychelles.

Ethanol tolerance

European *D. melanogaster* populations are about 2.5 times more tolerant to ethanol than are Afrotropical (David & Bocquet, 1975*b*). Ethanol tolerance of the mixed population of Seychelles, in comparison to that of African and European populations, is given in Fig. 1. The tolerance of Seychellian flies is almost identical to that of flies living in Europe and much higher than that typical of tropical populations living on the African mainland.

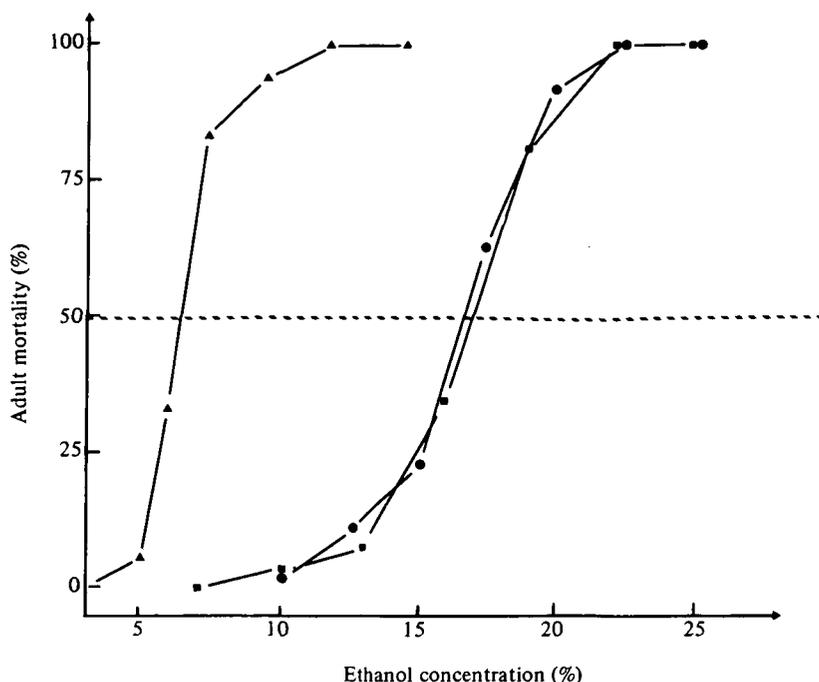


Fig. 1. Comparison of the ethanol tolerance of the African (\blacktriangle), European (\blacksquare) and Seychellian (\bullet) flies. The curves show the percentage of adult mortality on various concentrations of ethanol after two days of treatment (for each point, 80 flies of both sexes were studied). The lethal concentrations 50 are respectively 6.5% (African), 17% (European) and 16.7% (Seychellian).

Table 2 Comparison of biometrical characters of Seychellian flies with populations from France and tropical Africa

Fresh weight expressed in $\text{mg } 10^{-2}$ and lengths in $\text{mm } 10^{-2}$; n number of isofemale lines (Seychelles) or of strains (France or Africa); comparisons are done with the t test; * $P < 0.05$; ** $P < 0.01$.)

Characters	Seychelles	France	Africa	Comparison with	
				France	Africa
Fresh weight (δ)	85.45 \pm 2.21	91.91 \pm 0.73	78.03 \pm 0.94	2.77	3.064**
Wing length (δ)	185.72 \pm 0.95	198.06 \pm 0.79	178.80 \pm 0.85	9.89**	5.33**
Thorax length (δ)	89.74 \pm 0.76	95.23 \pm 0.39	88.74 \pm 0.46	6.39**	1.10
Abdominal chaetae (δ)	35.48 \pm 0.57	35.47 \pm 0.29	31.42 \pm 0.31	0.015	6.13**
Sternopleural chaetae (δ)	16.70 \pm 0.24	18.40 \pm 0.22	16.24 \pm 0.21	5.17**	1.38
Ovarioles (δ)	39.31 \pm 1.14	47.57 \pm 0.45	38.59 \pm 0.60	11.38**	0.866
n	10	30	22		

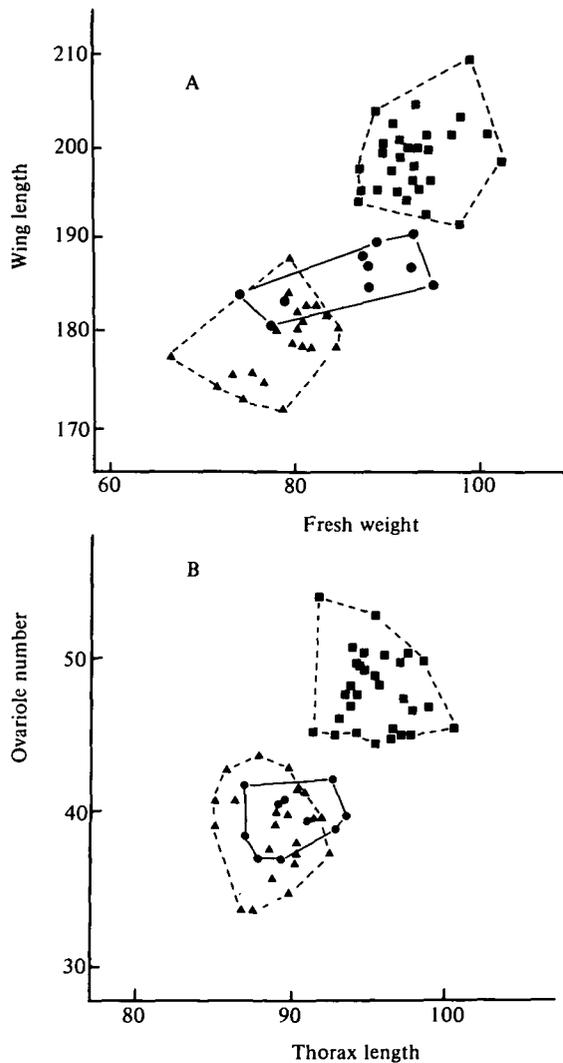


Fig. 2. Correlation diagrams between biometrical traits in African, Seychellian and French flies (for the Seychelles population, each point corresponds to the mean of an isofemale line; for African and French flies, each point is the mean of a recently collected strain founded by several adults). Same symbols as in Fig. 1.

(c) Biometrical traits

The average values of the ten isofemales lines from Seychelles are given in Table 2 and compared to those of 30 different French strains and 22 Afrotropical strains. Such a comparison is legitimate although it involves in one case several isofemale lines from the same population and, in the others, different populations. We know that variations between strains or lines mainly reflect genetic differences and that their magnitudes are similar (David, Fouillet & Arens, 1978; David, 1979).

Table 2 shows that differences between Seychelles populations and others are less clear than for ethanol tolerance. For weight and wing length, for example, the Seychelles population is intermediate between European and African flies (Fig. 2A). The variance among isofemale lines is comparable to that among different African or French populations. For ovariole number and thorax length (Fig. 2B) and also for sternopleural chaetae number, the Seychellian flies are very different from European but not from African ones (see Table 2 for statistical

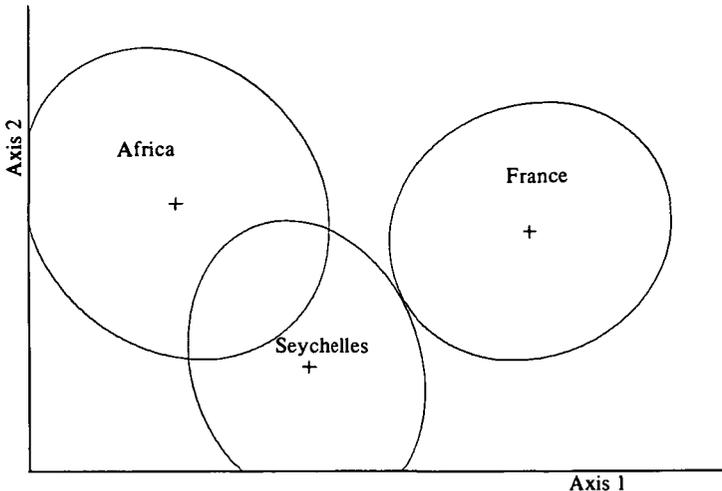


Fig. 3. Discriminant analysis between African, French and Seychellian flies. Each ellipse is calculated for containing 95% of all observations. Axes 1 and 2 explain respectively 80.8% and 19.1% of the total variance. Differences between average points of the 3 groups are highly significant.

significance). Finally, for the number of abdominal chaetae, the reverse is true, since the Seychellian flies are almost identical to European ones. The result of a discriminant analysis (Bartlett, 1938) which maximizes the differences among the 3 groups, is shown in Fig. 3.

We see that, when considering the ellipses which contain 95% of the observed values, African and European populations are well separated on the first axis which contains 80.8% of the whole information. Seychellian flies are closer to the African ones but separated both on the first and second axes. By considering only these two axes, 99.9% of the total variance is explained.

4. DISCUSSION AND CONCLUSION

When did *D. melanogaster* arrive in the Seychelles? The drosophilid fauna of this archipelago was first investigated at the beginning of the 20th century by Lamb (1914) who reported the presence of *D. melanogaster*. However, an extensive survey of Mahé fauna by L. Tsacas and J. David in November 1977 failed to find any

D. melanogaster while its sibling species, *D. simulans*, was discovered in natural habitats. Moreover, a reexamination of the preserved specimens studied by Lamb in 1914 showed that they also belonged to *D. simulans*, a species which was only recognized 5 years later (Sturtevant, 1919). The fact that, in 1981, *D. melanogaster* was found only in domestic habitats in Victoria city is also an argument for a recent involuntary introduction.

Genetic analysis of allozyme frequencies and ethanol tolerance strongly suggests that the founder flies were imported from Europe. Biometrical analysis clearly leads to the rejection of the possibility of a Far East origin (see David *et al.* 1976). Other origins than Europe cannot be excluded, for example American temperate countries, North Africa or Australia. However, the possibility of an introduction from a tropical African country can be rejected. As stated previously (David & Tsacas, 1981); we are badly lacking an extensive description of the genetic properties of *D. melanogaster* populations on a worldwide basis. A detailed list of the places, mainly islands, in which *D. melanogaster* is not yet present, would be particularly welcome.

When a species is introduced into a new place, the most important problem is the number of founder individuals (Mayr, 1963) which is usually unknown. Allozyme frequencies in Seychellian *D. melanogaster* provide some interesting information if we assume an European origin. For alleles which have a high frequency in the initial population, such as those of $\alpha Gpdh$, only a few individuals or even a single inseminated female would be sufficient to produce the polymorphism. Better information on the probable number of founders is provided by rare alleles. If the number of the founder flies is low, we expect that most rare alleles will be lost, while those which will be present should have a higher frequency than in the initial population. Table 1 shows that this is indeed the case: we find three disappearing (Odh^S , $Est-C^S$ and $Est-6^{F_1 \cdot F_2}$) and three increasing (Adh^S , $Est-6S^I$ and $Est-C^V$). If we assume that such variations are due to sampling and not to selection, we may conclude that the Seychelles population was founded by less than 100 haploid genomes. Even 20 genomes (corresponding to only five inseminated females) could have been sufficient.

The morphological analysis is more difficult to interpret, since most of these traits probably have an adaptive value (David & Bocquet, 1975*a, b*; David *et al.* 1977; Boulétreau-Merle *et al.* 1982). Particularly in a tropical environment in which resources are always abundant, the population size is expected to be close to the maximum carrying capacity so that inter-individual competition should result in a genetic decrease in size. Conclusions obtained on Seychellian flies differ according to the trait considered. One possibility is that, since the arrival of the European population, natural selection has succeeded in decreasing the ovariole number, the sternopleural chaetae number and the thorax length, has been less successful in decreasing weight and wing length, and has failed to decrease the number of abdominal chaetae. However, other explanations are possible, for example a non-European origin of the population and also a complex reorganization of the genetic correlations following foundation of the population.

The high ethanol tolerance of the Seychellian flies is also surprising. The high tolerance of European flies is probably due to adaptation to resources containing a high amount of alcohol, such as those found in wine cellars (David & Bocquet, 1975 *b*). Natural populations harbour a large amount of genetic variability for ethanol tolerance and quickly respond to selection (David *et al.* 1977 *a*). The lack of change of tolerance in the Seychelles population suggests that there is no selection against this trait in a tropical environment, as there is no advantage in becoming more sensitive to ethanol when resources containing much alcohol are not available.

The *D. melanogaster* population of the Seychelles island is a remarkable ecological experiment in which a species, which shows long range geographic clines, has been also submitted to a founder effect. More interesting, the bottleneck is accompanied by an important modification of the environmental pressures, because of the transfer from temperate to tropical conditions. With respect to current theories of speciation, geographic clines and founder effects correspond to what Templeton (1980) calls genetic divergence and genetic transience. It seems unlikely that, in a short time, the Seychellian population will evolve toward a new species. From a microevolutionary point of view, it should be, however, highly interesting to study this population in forthcoming years.

We thank M. De Scheemaeker-Louis, E. Pla and J. Sandrin for excellent assistance in this study and P. Hyytia and an unknown referee for valuable comments on the manuscript.

REFERENCES

- ALLEMAND, R. & DAVID, J. R. (1976). The Circadian rhythm of oviposition in *Drosophila melanogaster*: a genetic latitudinal cline in wild populations. *Experientia* **32**, 1403.
- BARTLETT, M. S. (1938). Further aspects of the theory of multiple regression. *Proceedings of the Cambridge Philosophical Society* **34**, 33–40.
- BERRY, R. J. & PETERS, J. (1975). Macquarie island house mice: a genetical isolate on a sub-antarctic island. *Journal of Zoology, London* **176**, 375–389.
- BERRY, R. J., JAKOBSON, M. E. & PETERS, J. (1978). The house mice of the Faroe islands: a study in micro-differentiation. *Journal of Zoology, London* **185**, 73–92.
- BOULÉTREAU-MERLE, J., ALLEMAND, R., COHET, Y. & DAVID, J. R. (1982). Reproductive strategy in *Drosophila melanogaster*: significance of a genetic divergence between temperate and tropical populations. *Oecologia*. (In Press.)
- DAVID, J. R. (1979). Utilization of morphological traits for the analysis of genetic variability in wild populations. *Aquilo, ser. Zoology* **2**, 49–61.
- DAVID, J. R. (1982). Latitudinal variability of *Drosophila melanogaster*: Allozyme frequencies divergence between European and Afrotropical populations. *Biochemical Genetics*. (In the Press.)
- DAVID, J. R. & BOCQUET, C. (1975 *a*). Evolution in a cosmopolitan species: genetic latitudinal clines in *Drosophila melanogaster* wild populations. *Experientia* **31**, 164–166.
- DAVID, J. R. & BOCQUET, C. (1975 *b*). Similarities and differences in latitudinal adaptation of two sibling species. *Nature* **257**, 588–590.
- DAVID, J. R., BOCQUET, C. & De Scheemaeker-Louis, M. (1977 *a*). Genetic latitudinal adaptation of *Drosophila melanogaster*: new discriminative biometrical traits between European and equatorial African populations. *Genetical Research* **30**, 247–255.

- DAVID, J. R., BOCQUET, C., FOUILLET, P. & ARENS, M. F. (1977b). Tolérance génétique à l'alcool chez *Drosophila*: comparaison des effets de la sélection chez *D. melanogaster* et *D. simulans*. *Comptes rendus de l'Académie des Sciences, Paris* **285**, 405–408.
- DAVID, J. R., BOCQUET, C. & PLA, E. (1976). New results on the genetic characteristics of the Far East race of *Drosophila melanogaster*. *Genetical Research* **28**, 253–260.
- DAVID, J. R., FOUILLET, P. & ARENS, M. F. (1978). Utilisation de l'effet fondateur pour mesurer l'hétérogénéité génétique d'une population naturelle: étude de caractères quantitatifs chez *Drosophila melanogaster*. *Comptes rendus hebdomadaires les séances de l'Académie des Sciences, Paris* **286**, 129–132.
- DAVID, J. R. & TSACAS, L. (1981). Cosmopolitan, subcosmopolitan and widespread species: different strategies within the Drosophilid family (Diptera). *Comptes rendu de la Société de biogéographie* **57**, 11–26.
- JOHNSTON, R. F. & SELANDER, R. K. (1971). Evolution in the house sparrows. II. Adaptive differentiation in North American populations. *Evolution* **25**, 1–28.
- LAMB, C. G. (1914). Reports of the Percy Sladen trust expedition to the Indian Ocean in 1905. XV. Diptera: Heteroneuridae, Orthalidae, Trypetidae, Sepsidae, Micropezidae, Drosophilidae, Geomyzidae, Milichidae. *Transactions of the Linnean Society of London, Zoology* **16**, 307–372.
- MAYR, E. (1963). *Animal Species and Evolution*. Cambridge, Mass: Harvard University Press.
- NEI, M. (1972). Genetic distance between populations. *American Naturalist* **106**, 283–290.
- STURTEVANT, A. H. (1919). A new species closely resembling *Drosophila melanogaster*. *Psyche, Cambridge, Mass.* **26**, 153–155.
- TEMPLETON, A. R. (1980). Modes of speciation and inferences based on genetic distances. *Evolution* **34**, 719–729.