

## Ivory coastにおけるDrosophila teissieriおよびD.Yakubaの地理的高度に対応した産卵力の連続的または段階的勾配

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## Alternative Smooth or Stepped Altitudinal Cline of Fecundity in *Drosophila teissieri* and *D. yakuba* in the Ivory Coast

Janine DEVAUX and Daniel LACHAISE

Laboratoire de Biologie et Génétique Evolutives C.N.R.S.  
91198 Gif-sur-Yvette cedex, France

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### ABSTRACT

*Drosophila teissieri* and *D. yakuba* are two closely related species within the *melanogaster* species subgroup. They both live sympatrically in the Ivory Coast but in different places the ratio of their abundance is strikingly reversed. Alternative smooth or stepped cline of fecundity is observed in *D. teissieri* and *D. yakuba* respectively via an altitudinal transect in the Ivory Coast including lowland savannas of Lamto and various elevations and habitats (rainforest versus high-altitude grassland) on Mt Nimba. Crosses of parents of similar origin and, hence, altitude versus crosses of parents of different origin were conducted in order to assess the genetic basis of the differences observed. Allopatric pairs gave intermediate fecundities compared to either relevant sympatric pairs. Some cases of heterosis are observed that are dependent of the direction of cross. Fecundity uniquely and gradually increases with altitude irrespective of the habitat in *D. teissieri* while decreases, although with a strong stepwise inverse shift due to dramatic habitat change, in *D. yakuba*.

### 1. INTRODUCTION

Comparing populations of two closely related species of *Drosophila* living at different altitudes over a short distance is a good opportunity for testing altitude related selective forces. Dobzhansky (1943; 1948) was first to show some forty years ago that populations of *Drosophila pseudoobscura* and *D. persimilis* living at different altitudes in the mountains of California differed in the frequency of certain chromosomal arrangements. Since then, a variety of genetic and phenotypic factors have been shown to correlate, more or less independently of each other, with altitude. Some examples are chromosomal arrangements (Stalker and Carson, 1948; Levitan, 1978), allozymic frequencies (Pipkin *et al.*, 1976); morphology, duration of development and preadult mortality (Louis *et al.*, 1982). Although the question of whether or not altitudinal changes result in a selection gradient is old, it has still not been clearly answered.

Endler (1977) argued that when one finds a stepped cline in a continuous natural population, the most obvious causal factor to look for is a spatially abrupt environmental factor. Moreover, when this exists, as on Mount Nimba in the Ivory Coast, there is a good expectation of finding a stepped cline in organisms,

especially in invertebrates like *Drosophila*; we have found such a clinal variation in *Drosophila* populations living on Mt Nimba.

Mount Nimba is the easternmost block of the Guinean mountains in West Africa, our other site, the Lamto savannas, lies some 400 km to the east in lowland Ivory Coast. Mt Nimba is a narrow and linear montane barrier that lies SW-NE and rising from the surrounding lowlands of Guinea, Ivory Coast and Liberia. Its abrupt slopes are lined by a rainforest belt up to 900 m and its ridge is covered with graminaceous grassland. The lowland rainforest of western Ivory Coast is 1000 meters below. Although this mountain is not higher than 1752 m and has only a reduced number of vegetational belts, it provides dramatic changes in physical conditions with respect to altitude: i.e. rainfall, mean seasonal temperature, daily temperature regime, relative humidity, see next section for details (Lamotte, 1949, 1958, 1959; Schnell, 1952; Leclerc *et al.*, 1955; Lamotte and Roy, 1962).

Superimposed on this particularly stressful environment there is an interesting situation in the Ivory Coast: the two closely related species of the *Drosophila melanogaster* species subgroup *Drosophila teissieri* and *D. yakuba*, although coexisting, show to some extent habitat partitioning if their relative frequencies are considered. *Drosophila yakuba* shows a marked abundance in the two open habitats, that is Lamto lowlands and Nimba montane grassland while *D. teissieri* is more abundant in-between in the submontane forest belt of Mt Nimba. There, the absolute number of *D. teissieri* collected increases with altitude and with the approximate abundance of its main breeding site *Parinari excelsa* (Rosaceae). The open space species *D. yakuba* is exceedingly rare in the submontane forest and re-appears in the *Loudetia* montane grassland. This situation where *D. teissieri* is far more abundant than *D. yakuba* is quite unique and contrasts with what occurs elsewhere in Africa more especially in East African mountains where the reverse distributional pattern is observed (Lachaise *et al.*, 1987).

Thus we have two species of *Drosophila* phylogenetically very close (Lemeunier *et al.*, 1986; Lee and Watanabe, 1987), but ecologically very different from one another which nevertheless live sympatrically, although with unevenly sized populations (Lachaise *et al.*, 1987) and are therefore faced with similar dramatic changes of a specific tropical environment. The question can be raised of whether or not they have physiologically responded in a convergent manner and if so whether or not there is an underlying genetic basis to this. We have analyzed comparatively the influence of altitude and, hence, habitat on fecundity in both species. Fecundity is chosen because of its direct concern with fitness.

## 2. MATERIALS AND METHODS

*The stressful climatic conditions of Mt Nimba:* Rainfall ranges from 1.2–2.0 m at 500 meters to 2–3 m at 1650 meters. In the dry season the mean temperature

is around 21°C on the ridges (vs. 25°C in lowlands); in April–May it increases to 24°C (vs. 28°C in lowland); it then decreases rapidly and stabilizes around 15°C (vs. 21.5°C in lowland) throughout the rainy season. Both mean temperature and daily variations decrease noticeably with altitude. But the extent of the daily variation of temperature remains large in the montane grassland ranging from a minimum of 10–12°C (dry season night) to a maximum of 27°C (dry season afternoon); in the rainy season there is no more than a few degrees difference (from 14 to 16°C). The dry season lasts no longer than 3 months and the relative humidity minima are far below (as low as 15%) the lowland values. In contrast, throughout the wet season the montane grassland is covered quite continuously in clouds and drizzle and the relative humidity is close to saturation (Lamotte, loc. cit.).

*Strains and experiments:* *Drosophila teissieri* was represented by five strains: Lamto 200 m (Gif 140–5); Nimba 650 m (Gif 192–2); Nimba 750 m (Gif 192–3); Nimba 850 m (Gif 192–4); Nimba 1300 m (Gif 192–5); and *D. yakuba* by three strains: Lamto 200 m (Gif 142–6); Nimba 850 m (Gif 192–6); Nimba 1300 m (Gif 192–7). All of the Nimba strains were collected simultaneously in April, but the Lamto strains were collected in October (*D. teissieri*) or November (*D. yakuba*). All the strains were founded by more than one wild-caught inseminated female. Experiments were done on the second generation Nimba strains but on older Lamto strains. Between-population crosses were conducted in parallel in both species with one male and one female of either the same (sympatric pair) or of different (allopatric pair) origins. Hence, there were 5 sympatric crosses in *D. teissieri* corresponding to the five strains and 20 allopatric crosses resulting from all the different pairwise combinations between these five strains and including both directions of cross. Similarly in *D. yakuba* there were 3 sympatric and 6 allopatric crosses. Each cross was repeated at least four times except two cases in *D. teissieri* and one in *D. yakuba* where a single cross was made. Parents were transferred daily to fresh tubes of standard axenic medium until the death of the female and old tubes were examined daily for emergences which were scored. Fecundity corresponds here to the number of offsprings reaching maturity from a single female. All crosses were done at 25°C.

### 3. RESULTS AND DISCUSSION

The results are summarized in Figure 1. There is a large between-species difference in fecundity which is, in general, considerably higher in *Drosophila yakuba* than in *D. teissieri* in most habitats. However, it should be noticed that the fecundity value of both species match rather closely in the montane grassland of Mt Nimba. Since every data corresponds to four females and fecundity shows noticeable between-individual variability, the standard error is quite large. As a consequence, the fecundity values of the sympatric pairs of *D. teissieri* popula-

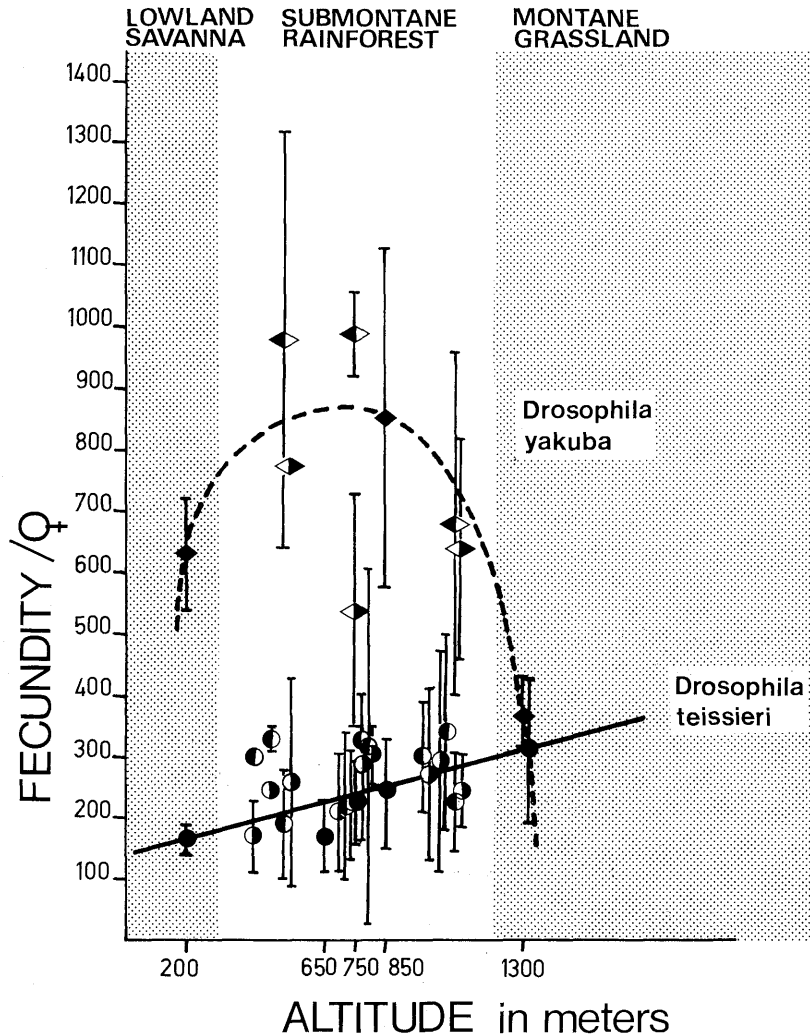


Fig. 1. Alternative fecundity gradients in *Drosophila teissieri* (circles) and *D. yakuba* (lozenges) in various habitats and altitudes in the Ivory Coast. Populations from the Lamto lowland savannas are compared to populations from various altitudes (ranging from 650 to 1300 meters) on Mt Nimba. The distinction is made between populations living in the submontane forest and those living in the montane *Loudetia* grassland. Sympatric crosses are represented in black; allopatric crosses half black and half white, the black half being towards the place of origin of the female. For a given cross there are two points corresponding to both directions of cross. The standard error corresponds in general to four females. The figure should be read with a ruler, the fecundity value of allopatric pairs being plotted at an intermediate altitude with regard to those where the paired individuals originate (e.g. In *D. yakuba* the cross Lamto 200 m  $\times$  Nimba 1300 m is plotted at 750 m).

tions are not significantly different ( $p=.05$ ). In contrast, in *D. yakuba*, although the standard error is also large, the fecundity values of the sympatric pairs fully discriminate ( $p=.05$ ) except Lamto and Nimba 850 m.

It remains that in both species there is a strong between-population variation that is independent of distance. But this variation results in alternative clines, smooth in *D. teissieri* or stepped in *D. yakuba*, with a trend toward decreased fecundity with altitude in the latter and toward increased fecundity in the former. This increase in fecundity with altitude in *D. teissieri* is a rare phenomenon that is noteworthy. This may be correlated with the discovery of *D. teissieri* only at 3000 meters on Mt Elgon in Kenya while the geographical range of *D. yakuba* there, extends from the bottom of the mountain to that altitude (Lachaise *et al.*, 1987). This can be connected with the greater tolerance of the former species to the physiological stresses (desiccation, cold temperature stresses, high temperature stresses at 95 or 0% RH) than the latter (Stanley *et al.*, 1980). It is also worth noting that Tantawy and El Helw (1970) comparing Scottish and Egyptian populations of *D. melanogaster* also observed enhanced fecundity when at 15°C in the Scottish populations but when at 28°C in the Egyptian populations, that is in conditions similar to those found in the wild.

If fecundity in *D. teissieri* is positively correlated with elevations, in contrast, it seems to be independent of the habitat (i.e. submontane forest versus lowland savannas and montane grassland) which is known to severely affect its population size. Hence, it can be concluded that, in *D. teissieri*, altitude alone rather than habitat directly acts on fecundity. This conclusion is supported further by ecological considerations on *D. teissieri*. The individuals collected in Lamto lowlands originate in fact in semi-deciduous gallery forests which include the savannas, and those baited in the montane grassland of Mt Nimba may have moved from the top of forested ravines nearby. The forest species *D. teissieri* does not live in the true open space of the montane grassland. Hence, the altitudinal cline of fecundity in *D. teissieri* may, to some extent, be entirely included within forested habitats. This accounts for the apparent lack of influence of the habitat on fecundity. In contrast, the open-space species, *D. yakuba*, lives also with reduced populations in the submontane forest of Mt Nimba and the convergent tendency observed in fecundity between lowland savanna and montane grassland suggests some influence of the habitat on its fecundity. Nevertheless, it remains true that when considering the sole two open habitats (i.e. Lamto lowland savannas and Nimba montane grasslands) fecundity significantly decreases with altitude.

In view of the comparison of sympatric and allopatric crosses there is good evidence that the differences observed have a genetic basis. The allopatric pairs (the female originating from a given altitude and the male from another) give, in the majority of crosses, a fecundity value that is intermediate between those of either relevant sympatric pairs. In *D. teissieri* fecundity varies irrespective of

the direction of cross. In contrast, in *D. yakuba* a significant departure may be observed in the two reciprocal crosses. This is particularly visible in the cross Lamto 200 m with Nimba 1300 m where the fecundities observed in the two directions of cross fully discriminate that is when the female and the male originate from extreme environments (i.e. altitude, mean temperature, daily regime of temperature). In the cross of Lamto 200 m ♂ × Nimba 1300 m ♀ the number of offsprings produced is intermediate between those produced by either relevant sympatric cross (i.e. Lamto ♀ × Lamto ♂ and Nimba 1300 m ♀ × Nimba 1300 m ♂). In contrast, a striking phenomenon of positive heterosis is observed in the reciprocal cross of Lamto 200 m ♀ × Nimba 1300 m ♂, that is when the parental female has a higher fitness. Considering that fecundity is mostly affected by mother, this may be due to a maternal effect. It is also of interest to connect this result with the assumption that heterosis is higher in extreme environments (see Parsons, 1971 and David *et al.*, 1984, for reviews).

In a general way the climatic opposition between dry and wet seasons becomes more marked with altitude. Mean temperatures decrease with altitude. The daily range of temperature remains high at higher elevation and that of relative humidity increases with altitude: they can vary from 12 to 27°C and from 15 to 100% respectively at a higher elevation. Thus, fecundity appears quite higher in *D. teissieri* at higher elevations where the climatic characteristics are more dramatic. Such a relation was shown to exist between more especially the daily temperature regime and the genetic structure of experimental populations (Beardmore, 1961; Beardmore and Levine, 1963). Populations kept in a variable environment, that is a daily temperature regime of 17–27°C, were genetically more variable and had a higher viability than populations kept in constant thermal conditions. Similarly, Parsons (1987) argued that phenotypic and genotypic variability tend to be high under conditions of severe physical and biological stress, especially for quantitative traits important in determining survival. Most recently, Jones *et al.* (1987) have presented evidence of a wider thermal niche for high-altitude populations of *D. melanogaster* than for lowland populations.

In spite of moderate altitude, and due to the abruptness of its slopes, Mt Nimba provides particularly dramatic conditions of tropical environment changing with altitude. Although the populations of both *Drosophila teissieri* and *D. yakuba* are geographically very close to one another on Mt Nimba they strongly differ in their respective fecundity under laboratory conditions, with the exception of the highest altitude populations. A marked intraspecific difference is observed with the populations living in the Lamto lowlands. There is no convergence in *D. teissieri* and *D. yakuba* with regard to the impact of environmental factors acting on fecundity. Fecundity decreases with altitude (considering open habitats only) in *D. yakuba* while it increases in *D. teissieri*. Fecundity seems to be, to some extent, habitat-dependent in *D. yakuba* while apparently not so in *D. teissieri*. Hence, the major conclusions to emerge is that in these tropical species of

*Drosophila*: —fecundity does not vary randomly; —this variation is not purely physiological but has a genetic basis: —geographic distance alone (e.g. Lamto-Nimba vs. Nimba 650–Nimba 850 m) cannot account for the results observed. These two closely related species, *D. teissieri* and *D. yakuba*, have either been exposed to different selective regimes (e.g., altitude vs. habitat) or have responded differently to the same selective regime (e.g., altitude+habitat).

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