Genetic Structure and Gene Flow Along an Altitudinal Gradient Among Two Stomoxyine Species (Diptera: Muscidae) on La Réunion Island

JÉRÉMIE GILLES,1,2,3 ISABELLE LITRICO,4 EMMANUEL TILLARD,2 AND GERARD DUVALLET5


ABSTRACT Seasonal variations of insect population sizes are often dramatic, particularly in temperate regions and at altitudes where the climatic conditions are unfavorable to insect development during the winter. Decline of population size (or bottlenecks) and founder events may reduce the genetic variability and may create genetic differentiation between populations by drift and founder effects, but this reduction of genetic diversity is strongly influenced by gene flow between populations. In this study, we determined the population genetic structure for two stomoxyine species (Diptera: Muscidae), Stomoxys calcitrans (L.) and Stomoxys niger niger Macquart, which co-occur in dairy barns along an altitudinal gradient on La Réunion island. Using microsatellite markers, we quantified the genetic variation within and among populations for different altitudes. This study displays that, contrary to expectations, genetic diversity is not correlated with altitude and that genetic differentiation is not larger among high-altitude populations than among low-altitude populations. These results attest to the small drift and founder effects in high-altitude populations despite drastic decreases in population size during the winter. Furthermore, at the island scale, the populations of S. calcitrans were slightly differentiated, but those of S. niger niger were not. Together, the results revealed large levels of gene flow on La Réunion Island despite the dramatic geographic barriers, and they emphasize the importance of considering agricultural practices to restrict the dispersal of stomoxyines.

KEY WORDS genetic structure, microsatellite markers, altitudinal gradient, stable flies, La Réunion Island

Colonization and extinction cycles (Barrett and Husband 1989, Whitlock and McCauley 1990, Husband and Barrett 1996) and variations in population density (Brown 1994, Lynch et al. 1995) strongly influence genetic variability in space and time. Many theoretical studies (Slatkin 1977, 1993; Wade and McCauley 1988; Whitlock and McCauley 1990; Austerlitz et al. 1997, 2000; Le Corre and Kremer 1998) have shown the genetic impact of population founder after extinction or reduction of population size (bottleneck). Under drift and founder effects, genetic diversity may decrease and the differentiation between populations may be high. When populations are founded, genetic diversity and differentiation are influenced by the composition of founders (Wade and McCauley 1988, Whitlock and McCauley 1990, McCauley 1991). If populations are founded by a few individuals, diversity may be low and differentiation high. But it is rare for populations to be completely isolated, and the gene flow homogenize allelic frequencies (Reichow and Smith 2001) when we consider neutral markers. So, when bottlenecks or extinctions reoccur, a drift–migration equilibrium may be reached, each influenced by the ecology of the species and by human activities (Colson 2002).

For insects, seasonal variations of population size are often dramatic (Gilles 2005, Goulson et al. 2005, Henning et al. 2005), in particular, during the winter in temperate regions or at higher altitudes where climatic conditions are unfavorable to insect development. The seasonal decline of insect population size and founder events may reduce the genetic variability and may create genetic differentiation in space and time.

On La Réunion Island, two Stomoxys species (Diptera: Muscidae), the cosmopolitan Stomoxys calcitrans (L.) and the tropical Stomoxys niger niger Macquart, are

1 Institut für Vergleichende Tropenmedizin und Parasitologie-Leopoldstraße 5, D-80802 München, Germany.
2 CIRAD-EMVT, Programme Productions Animales, Pole de Protection des Plantes, 7 chemin de l’IRAT, 97410 St Pierre de La Réunion, France.
3 Corresponding author. Current address: Institut für Vergleichende Tropenmedizin und Parasitologie-Department of Comparative Tropical Medicine and Parasitology, Leopoldstraße 5, D-80802 München, Germany (e-mail: jeremie.gilles@tropa.vetmed.uni-muenchen.de).
4 INRA, Unité de Génétique et d’Amélioration des Plantes Fourragères, 86600 Luignan, France.
5 Département Ecologie des Arthropodes–UMR 5175 CEFE, Université Paul-Valéry, Route de Mende, 34190 Montpellier cedex 5, France.
found in dairy barns. These blood-sucking insects associated with cattle (Zumpt 1973) have become pests and cause important economic losses. Their bites are painful and they are potential mechanical vectors of pathogens (Gilles et al. 2007). Gilles (2005) observed 1) spatial variation along an altitudinal gradient and 2) seasonal variation in the abundance of these two species in the south of La Réunion island. These variations were related to climatic factors, mainly temperature (positive relationship) and relative humidity (negative relationship). In unfavorable season (winter), Stomoxys populations decrease; the higher the altitude, the higher the decrease. When environmental conditions (e.g., temperature and humidity) become favorable, at the beginning of summer, Stomoxys populations increase.

Our aim is to better understand the impact of population size fluctuations on the genetic structure of two species of Stomoxys, S. calcitrans and S. niger niger on La Réunion Island and to determine their colonization dynamics. We addressed the following questions: 1) Is the diversity of high-altitude populations, which show greater size reduction, lower than that of low-altitude populations? 2) Is the differentiation among high-altitude populations higher than among low-altitude populations? and 3) How are Stomoxys populations differentiated at island scale? Answers to each of these questions may help with the development of control strategies on La Réunion Island.

### Materials and Methods

**Study Sites and Sample Collection.** La Réunion is a volcanic island (2,507 km²) ~800 km east of Madagascar (21° 20’ S, 55° 15’ E). The climate is humid tropical, with heavy rains in summer. At the end of summer (April 2003), 379 S. calcitrans adults were allocated into 13 populations and 404 S. niger niger adults were allocated into 14 populations (Table 1; Fig. 1) after capture in Vavoua traps (Laveissière and Grébaut 1990) in dairy barns.

Seven populations (population 1–7; Fig. 1) were located along an altitudinal gradient (100–1,600-m elevation), and the abundance of the two species was recorded weekly during a 90-wk period with Vavoua traps. Trapped flies were identified in the laboratory according to Zumpt (1973).

**DNA Extraction and Microsatellite Protocol.** The individuals were crushed with tungsten microbars, and their DNA was extracted following the DNeasy tissue kit (QIAGEN, Hilden, Germany) protocol. The S. calcitrans were genotyped with nine microsatellite loci: S. calcitrans (ScA7, ScD10, ScD7, ScA6, ScA3, ScA11, and ScF7) identified by Gilles et al. (2004) on this species and two (ScF1 and ScN1) identified on S. niger niger (Gilles et al. 2005). The S. niger niger were genotyped using six microsatellite loci: four loci (ScE5, ScE2, ScB10, and ScF1) identified by Gilles et al. (2005) on this species and two (ScA7 and ScD10) identified on S. calcitrans (Gilles et al. 2004). The other loci identified for S. calcitrans and S. niger niger (Gilles et al. 2004, 2005) were excluded from the analysis.

### Table 1. Values (mean ± SE) of Ne, Hs, He, and Fst in populations of S. calcitrans and S. niger niger.

<table>
<thead>
<tr>
<th>Population</th>
<th>Region</th>
<th>Coordinates</th>
<th>Altitude (m)</th>
<th>n</th>
<th>Ne</th>
<th>Hs</th>
<th>He</th>
<th>Fst</th>
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<tr>
<td>1</td>
<td>BPA</td>
<td>21° 24’ S, 53° 54’ E</td>
<td>100</td>
<td>30</td>
<td>0.6297 (0.1657)</td>
<td>0.5914 (0.2139)</td>
<td>0.6575 (0.1859)</td>
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<tr>
<td>2</td>
<td>BIP</td>
<td>21° 24’ S, 53° 54’ E</td>
<td>900</td>
<td>39</td>
<td>0.6297 (0.1657)</td>
<td>0.5914 (0.2139)</td>
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<tr>
<td>3</td>
<td>GICD</td>
<td>21° 21’ S, 53° 54’ E</td>
<td>1,200</td>
<td>30</td>
<td>0.6297 (0.1657)</td>
<td>0.5914 (0.2139)</td>
<td>0.6575 (0.1859)</td>
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<td>0.6575 (0.1859)</td>
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<tr>
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<td>30</td>
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<tr>
<td>9</td>
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<td>0.5914 (0.2139)</td>
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<td>0.6575 (0.1859)</td>
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<tr>
<td>13</td>
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<tr>
<td>15</td>
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<td>30</td>
<td>0.6297 (0.1657)</td>
<td>0.5914 (0.2139)</td>
<td>0.6575 (0.1859)</td>
<td>0.00</td>
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</tbody>
</table>

* P ≤ 0.05; ** P ≤ 0.01; *** P ≤ 0.001.
because of the probable occurrence of null alleles. Primer sequences, amplification conditions, and allele scoring were as reported previously (Gilles et al. 2004, 2005). Polymerase chain reaction (PCR) products were analyzed on an ABI 3100 automated sequencer (Applied Biosystems, Foster City, CA), and subsequent analysis was carried out using GeneScan Analysis 3.7 (Applied Biosystems). Fourteen individuals were replicated to check repeatability.

Genetic Diversity within Populations. For each species, we calculated the mean number of alleles per locus \( (N_a) \), Nei’s unbiased expected heterozygosity \( (H_E) \) (Nei 1978), observed heterozygosity \( (H_o) \), and Wright’s inbreeding coefficient \( (F_{IS}) \) according to Weir and Cockerham (1984) by using Genetix version 4.04 (Belkhir et al. 2001). The test for departure from Hardy–Weinberg equilibrium was conducted using 1,000 permutations in each population by Genetix version 4.04 (Belkhir et al. 2001). The test for departure from Hardy–Weinberg equilibrium was conducted using 1,000 permutations in each population by Genetix version 4.04 (Belkhir et al. 2001). For the seven populations located along the altitudinal gradient (1–7), Spearman rank correlation coefficients (SAS Institute 2001) were calculated to test for a relationship between \( H_E \) and population size at the sampling time (March–April 2003).

Genetic Differentiation among Populations. To consider the differentiation between populations, the \( F_{ST} \) were calculated according to the Weir and Cockerham (1984) procedure and tested using 1,000 permutations of individuals among populations or regions (Genetix version 4.04; Belkhir et al. 2001) (Fig. 1; Table 2). Regions were defined according to distance between populations and to geographical barriers (e.g., mountains and valleys), which may be important obstacles to fly migrations. To test the isolation by distance, correlations between genetic distances (measured as \( F_{ST} \)) and spatial distances between pairs of populations were calculated and tested following the Mantel permutation procedure (Genetix version

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![Fig. 1. (a) Location of La Réunion Island. (b) Sampled breeders (fly populations) for genotyping individuals of *S. calcitrans* and *S. niger niger*. The five regions (r1, r2, r3, r4, and r5) used in grouped genetic analyses are delimited by plain font black lines.](image)

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<table>
<thead>
<tr>
<th>Region</th>
<th>( n ) of <em>S. calcitrans</em></th>
<th>( n ) of <em>S. niger niger</em></th>
<th>Pop/region</th>
<th>Pop altitude (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>R1</td>
<td>210</td>
<td>208</td>
<td>1</td>
<td>100</td>
</tr>
<tr>
<td></td>
<td></td>
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<td></td>
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<td></td>
<td>7</td>
<td>1,600</td>
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<tr>
<td>R2</td>
<td>60</td>
<td>60</td>
<td>8</td>
<td>80</td>
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<tr>
<td>R3</td>
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<td>900</td>
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<td></td>
<td></td>
<td></td>
<td>14</td>
<td>1,100</td>
</tr>
</tbody>
</table>

(only for *S. niger niger*)
In addition, the genetic differentiation was tested by grouping 1) populations per region (Fig. 1; Table 2) and 2) populations (1–7) per altitude (Table 3).

Results

Genetic Diversity within Populations. The mean number of alleles per locus was 5.88 and 5.30 for *S. calcitrans* and *S. niger niger*, respectively. The mean number of alleles per locus and per population varied from 5.22 to 6.55 for *S. calcitrans* and from 4.50 to 6.00 for *S. niger niger* (Table 1). For Nei’s $H_E$ values ranged from 0.60 to 0.65 for *S. calcitrans* and from 0.56 to 0.70 for *S. niger niger* (Table 1). For Ho, values ranged from 0.50 to 0.65 for *S. calcitrans* and from 0.54 to 0.68 for *S. niger niger* (Table 1). For both species, no correlation was observed between Nei’s $H_E$ values and altitude ($P > 0.5$) and between Nei’s $H_E$ values and the population size ($P > 0.5$). However, for *S. calcitrans*, the mean number of alleles per locus was significantly correlated with the size of population in the sampled period ($R_s = 0.54; P < 0.05$), but there was no correlation ($P > 0.1$) for *S. niger niger*. Regarding $F_{IS}$, the global value for *S. calcitrans* was 0.078 ($P < 0.001$), and the $F_{IS}$ values per population were relatively low: from 0 to 0.12 (Table 1) except for the population 7 ($F_{IS} = 0.20; P < 0.001$). In the same way, the global $F_{IS}$ value for *S. niger niger* was 0.094 ($P < 0.001$), and the $F_{IS}$ per population ranged from 0 to 0.20 (Table 1). $F_{IS}$ values varied between loci (Fig. 2), probably because the null alleles are present for some loci. Thus, this variation between loci does not support the notion that inbreeding explains the $F_{IS}$ values in our study.

Genetic Differentiation among Populations. On the island scale, the $F_{ST}$ value for *S. calcitrans* was 0.02 ($P < 0.001$), whereas that for *S. niger niger* was not significantly different ($P > 0.1$). Several pairwise differences among populations occurred, however, as population 13 of *S. niger niger* differed from all others (Table 4). Furthermore, for both species, when we grouped populations by region (Fig. 1; Table 2) or by altitude for the seven populations located along the transect (Table 3), the differences were low but significant: $F_{ST} = 0.01, P < 0.001$ and $F_{ST} = 0.033, P < 0.001$ for *S. calcitrans* and $F_{ST} = 0, P > 0.1$ and $F_{ST} = 0, P > 0.5$ for *S. niger niger*. But when we grouped populations by region or altitude, genetic differences...
were not correlated with geographic distances (Man- tel permutation procedure not significant). For pop- ulations on the altitudinal transect (1–7), high-altitude populations (>1,200 m) were not more differentiated than low-altitude populations (S. calcitrans: F_{ST} = 0.02, P < 0.001 versus F_{ST} = 0.02, P < 0.001 and S. niger niger: F_{ST} = 0, P > 0.1 versus F_{ST} = 0, P > 0.1).

Discussion

Key results are, first, that genetic diversity was not correlated with the altitude of populations and that genetic differentiation was not greater for high-alti- tude populations than low-altitude populations. De- spite the large reduction of size during the winter in high-altitude populations, our results attest to low drift and founder effects. Second, unlike S. calcitrans whose populations are slightly differentiated, we observed no genetic differentiation between the populations of S. niger niger at the island scale and no distance isolation for both species. The latter result indicates that gene flow is important at the small and large scales.

Variable Degrees of Genetic Differentiation be- tween Species and Populations. At the island scale, genetic differentiation among populations varied ac- cording to species. Indeed, there was no genetic differ- entiation for S. niger niger, but populations of S. calcitrans were slightly differentiated. Why do these close species differ? The high flight capacity of these flies may explain the important gene flow at the island scale, but passive transport might play an important part in the gene flow on La Réunion Island. Cultural practices and manure or sugarcane (Saccharum L.) transports between different parts of the island may allow large gene flow despite dramatic geographic barriers. Some eggs, larvae, and pupae of Stomoxys are found in sugarcane leaves and in manures, these sub- strates constituting the laying site (personal observa- tion; Kunz and Monty 1976, Barré 1981). The transport of these substrates seems to strongly contribute to the passive transport of the Stomoxys spp. Moreover, whereas manures are laying sites for S. calcitrans, sug- arcane leaves constitute the preferential laying sites for S. niger niger (Kunz and Monty 1976, Barré 1981), and sugarcane leaves are widely transported in the island, particularly during the harvest. Thus, the lack of genetic structure of S. niger niger populations could be the result of massive transport of sugarcane resi- dues at the island scale.

At a lower scale, regarding differentiation along the altitudinal gradient, S. calcitrans and S. niger niger populations showed no isolation by distance, but some populations, populations 3 and 13, with different farm- ing methods are more differentiated than the others (apart from the geographic location). The differenti- ation of these two populations may result from drift effect in relation to small numbers. This assumption is supported by diversity values among S. calcitrans in these two populations and S. niger niger in population 13, because the mean number of alleles per locus and heterozygosity values were low. Harper et al. (2003) showed that among Lepidoptera the genetic diversity is all the higher as the population size is high. The diversity and differentiation of these populations may depend on intrinsic (or local) factors of the breeders, factors that may influence the population size. Gilles (2005) suggested that the quantity of larval resources could limit the density of stable fly species. These larval resources are directly associated with agricul- tural practices.

No Drift Effect at High Altitude Despite the Re- duction of Population Size. Although many studies (Wright 1931, Whitlock and McCauley 1990, Brown 1994, Husband and Barrett 1996, Brooks et al. 1997) showed population size fluctuations govern genetic diversity, our results display no impact of recurrent reduction of population size on the diversity. Indeed, the genetic diversity and differentiation values were not correlated with the altitude of populations, al- though high-altitude populations have extreme reduc- tions of size compared with low-altitude populations. These results concur with two possible scenarios of population dynamics for S. calcitrans and S. niger niger. 1) Variations in relative abundance of the two stomoxys species during winter did not result from a real decline of the population size. This situation has been reported for other species. For example, in Aus- tralia, Chapman et al. (1999) showed that the popu-
lutions of *Aedes vigilax* (Skuse) almost disappear when environmental conditions are unfavorable, but stocks of immature forms (eggs) persist several months and allow the population to keep its initial size and then to limit the drift effect. 2) The population bottleneck may really exist but, at the end of winter, new populations may be created from a lot of individuals from other populations at lower altitudes (source populations). If there are many migrants, the probability for postbottleneck populations to reach the genetic diversity of source populations may be high, and the population differentiation will be small. But, if there are few migrants, the genetic diversity may stay low and the population differentiation high (Slatkin 1977). In addition, Slatkin (1995) showed that a few migrant individuals of second generation could be enough to prevent drift effects. So, although these two scenarios of population colonization are possible and are not incompatible, it is unlikely that the functioning of high-altitude populations is independent on La Réunion Island. Indeed, regarding the degree of differentiation, the populations of *S. calcitrans* differed slightly on the island scale and those of *S. niger niger* did not differ. In addition, genetic differentiation was independent of geographic distance. These results point out large gene flow between populations, yet this is not surprising given the high flight capacity of stable flies. Some studies (Bailey et al. 1979, Hogsette et al. 1987) showed that *S. calcitrans* is able to fly far (several hundred kilometers), and Chevillon et al. (1995) showed no isolation by distance at the scale of Sardinia among *Culex pipiens* L. with individuals migrating long distances and thus limiting the genetic differentiation.

In our study, it is difficult to determine the part of migrant individuals and the part of immature stages wintering in manure or in vegetal substrates in decomposition, yet we think immature stocks were probably very large (personal observations). Thus, it would be of interest 1) to perform a capture-mark-release protocol to know effective migrations of the two *Stomoxys* species and 2) to determine the genetic structure at different periods of the year.

In conclusion, we emphasize the importance of considering all stages of the life cycle of insects to understand the impact of periodic variations of the population size on the genetic structure. And particular focus should be placed on immature stages of these two stomoxyine species, which are able to develop and then spend the winter “protected” in specific substrates. Genetic analyses should be carried out at different periods of the year to establish the population dynamics of stomoxyine species, in particular the role of migrants and immature stocks in the colonization by high-altitude populations on La Réunion Island. In addition, agricultural practices seem to be an important factor to take into account to understand population dynamics of *S. calcitrans* and *S. niger niger* in farms of the Réunion Island. This calls for better knowledge of the breeding site.

Otherwise, as we observed only small or null genetic differentiation between populations at the island scale, our results may have implications in the control of the two *Stomoxys* species. Indeed, large gene flow between different parts of the island may in part be explained by the transport of larval substrates such as manure or sugarcane leaves and not only by the dispersal of adults. These findings should allow us to orientate fly control programs.

Acknowledgments

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