Effects of Temperature on the Rate of Increase of *Stomoxys calcitrans* and *Stomoxys niger niger* (Diptera: Muscidae) from La Réunion Island

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J. Med. Entomol. 42(6): 959–965 (2005)

ABSTRACT Adult survival and reproduction were compared between two *Stomoxys* species that co-occur in La Réunion, the cosmopolitan *Stomoxys calcitrans* (L.), and the tropical *Stomoxys niger niger* Macquart. In a first experiment, mean longevity and fecundity were determined at five constant temperatures from 15 to 35°C, after development at the same temperatures. Adult longevity was greatest at 20°C in *S. calcitrans* and at 15°C in *S. niger*. Adult *S. niger* survived longer than adult *S. calcitrans*, especially at 15°C. At 35°C, all flies died within 3 d. Reproduction occurred only within the 20–30°C range, and *S. niger* laid more eggs than *S. calcitrans*. In both species, lifetime fecundity tended to decrease when temperature increased, because of the shortening of the oviposition period. In a second experiment, adults were maintained at 15°C after development at 25°C. The higher temperature during development significantly increased adult longevity in *S. calcitrans* but not in *S. niger*. Reproduction occurred at 15°C, with notable fecundity in *S. calcitrans* (22 eggs per female) but not in *S. niger* (<1 egg per female). Using previous results on immature survival and developmental time in the two species, several life history parameters were compared at each temperature. Generation time decreased with increasing temperature and was highly similar in both species. Concurrently, the intrinsic rate of increase (r) increased with temperature from 15 to 30°C. At 15°C, r was higher in *S. calcitrans*, but within the 20–30°C range, r was higher in *S. niger*. The results suggest 1) *S. niger* has evolved a strategy of survival without any reproduction during the tropical winter, in contrast with *S. calcitrans* that breeds more continuously; and 2) *S. niger* may outnumber *S. calcitrans* in warm areas, at least when development occurs in media of poor quality.

KEY WORDS Stomoxyines, temperature, reproduction, rate of increase, La Réunion island

STOMOXYINES ARE BLOOD-SUCKING INSECTS (Diptera: Muscidae) associated with cattle and wildlife throughout the world (Zumpt 1973). Two species occur in La Réunion island, the cosmopolitan *Stomoxys calcitrans* (L.) and the tropical *Stomoxys niger niger* Macquart. Both have become pests in dairy barns. Very large numbers of *Stomoxys* are observed during the wet and warm season (November–April), with daily catches of up to 5,000 flies per Vavoua trap (unpublished data). They are responsible for painful bites and blood predation and are potential mechanical vectors of pathogens, although the role of stable flies in the transmission of anaplasmosis and bovine leukosis is questionable (Potgieter et al. 1981, Buxton et al. 1985, Weber et al. 1988)

Preliminary observations along an altitude gradient in La Réunion and the work of Kunz and Monty (1976) in Mauritius suggested that temperature plays an important role in determining the relative abundance of the two *Stomoxys* species. The effects of temperature on *S. calcitrans* have been studied extensively in North America and South Africa (Berry and Kunz 1977, 1978; Kunz et al. 1977; Sutherland 1979; Lysyk 1998), but such data are not available for *S. niger*. A systematic comparison was therefore undertaken between the responses to temperature of the two species in La Réunion. Gilles et al. (2005) studied immature survival and developmental rate at five constant temperatures. They showed that 1) immature survival was higher in *S. calcitrans* than in *S. niger* at all temperatures; 2) at 35°C, immature survival was very low in both species; 3) at 15°C, the egg was the least cold-resistant stage in *S. niger;* but 4) surprisingly, *S. niger* developed slightly faster than *S. calcitrans* at low temperatures, suggesting that the tropical species was better adapted for larval development under cold conditions. In the current study, adult longevity and reproduction were investigated in the same temperature range. The rate of increase of the two species was

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0022-2585/05/0959–0965$04.00/0

calculated at each temperature, which will serve to explain field data on their distribution and abundance.

In a first experiment, the rate of increase was measured after complete life cycles at each temperature, in contrast with most studies, in which temperature effects at the adult stage were investigated using flies that had developed under standard laboratory conditions (Lysyk 1998). Temperature during development, however, is likely to influence the life history traits in adults (Berry and Kunz 1977, 1978), despite the contradictory results of Sutherland (1979). This point was reexamined in the second experiment, by comparing the traits of adults maintained at low temperature (15°C) after they had developed at either 15 or 25°C. Note that changes in temperature during an insect's life may be ecologically relevant, because different life stages rarely encounter similar temperatures under natural conditions. Thus, lower temperatures at the adult stage than during development can simulate the environment of adult flies not only at the beginning of the cold season but also at the end of the cold season if larvae develop in warmer microhabitats than the ambient temperature.

Materials and Methods

Study Area. La Réunion, the largest volcanic island of the Mascarene archipelago (2,507 km^2), lies 800 km east of Madagascar (21° 20′ S, 55° 15′ E). The island rises to 3,069 m and is under the influence of a humid tropical climate. Mean annual temperatures are 23–26°C at sea level. Annual rainfall ranges from 700 to 1,200 mm on the west coast to 3,000–5,000 mm on the east coast. La Réunion has >36,000 head of cattle, found mainly in moderately elevated areas.

Biological Material. Insects were from recent stock colonies of *S. calcitrans* and *S. niger;* the oldest were third generation in the laboratory. Colonies were established during the summer activity peak, from flies trapped at a dairy farm in the southeast of the island (910-m elevation). The same rearing methods were used for both species. Flies were maintained at 25°C and 70% RH under a photoperiod of 12:12 (L:D) h. Cages (30 by 30 by 30 cm) containing ≈1000 adults were placed over an oviposition substrate composed of ground leaves of elephant grass, *Pennisetum purpureum* Schumacher. The same substrate was used as larval development medium. The flies were fed daily with bovine blood collected twice a week from a slaughterhouse and citrated at 6 g $liter^{-1}$. For this, sponges dampened with blood and warmed at 38°C in a water bath were laid on the top of each cage for 45 min. The oviposition substrate was changed daily.

To obtain adults that developed at given temperatures (15, 20, 25, 30, and 35°C), freshly laid eggs were collected with a brush and put into dishes (10 cm in diameter by 10 cm in height) containing elephant grass. The dishes were covered with mosquito tulle to prevent larvae from exiting and placed in climatic chambers (MLR-350, Sanyo, Tokyo, Japan) at the five constant temperatures, with a relative humidity of ≈70% and a photoperiod of 12:12 (L:D) h. Larvae were kept in the same medium after hatching. Pupae were transferred to plastic boxes containing a slightly moistened sponge and were kept under the same temperature, humidity, and photoperiod conditions until adult emergence.

Experiment 1. In the first experiment, adult flies were kept at the same temperature as during development (15, 20, 25, 30, and 35°C) so that the life history parameters corresponded to entire life cycles at each temperature. Newly emerged adults of *S. calcitrans* (219 females, 233 males) and *S. niger* (194 females, 199 males) were placed in cages for several days. In both species, at least four cages were used at each temperature, except for one cage at 35°C because few adult flies emerged. Relative humidity, monitored using a thermo-hygrograph, averaged 80%, and photoperiod was left at 12:12 (L:D) h. The adults were fed daily with citrated bovine blood provided for 45 min. The females were induced to oviposit on a black cloth placed below their cage and kept moist by a wet sponge. Dead females, dead males, and eggs were collected every morning, until the last fly died. This protocol gave, at each temperature, the number of females and males alive at the beginning of each day, and the number of eggs laid per surviving female per day (M_x). The following parameters were determined: 1) mean adult longevity in each sex and its standard error; 2) the duration of the preoviposition period (overall estimate for all cages); and 3) mean lifetime fecundity, i.e., the total number of eggs collected, divided by the number of females at the beginning of the experiment. All results are given as grand means, after pooling results from individual cages.

To calculate net reproductive rate, generation time, and the intrinsic rate of increase, the immature developmental time and immature survival that were determined at each temperature by Gilles et al. (2005) were used. The proportion of females surviving from the egg stage to age x (l_x) was calculated as the product of immature survival and female survival from emergence to age x. Age-specific fecundities were divided by two ($m_x = M_x/2$), assuming 1:1 sex ratios (Ramsamy 1979, Lysyk 1998). Net reproductive rate (R_0) was calculated as $\Sigma_{x=0}\, l_x m_x$, cohort generation time (T_c) was calculated as $\Sigma_{x=0}\, x l_x m_x / R_0$, and the intrinsic rate of increase (r) was calculated using the Euler-Lotka equation $1 = \Sigma_{x=0}\, e^{-rx} l_x m_x$ (Hedrick 1984, David et al. 1995).

Experiment 2. In the second experiment, adult flies that had developed at the optimal temperature (25°C in both species) were transferred to a lower temperature (15°C) within 6 h of emergence. The aim was to assess the life history parameters when only the adult stage was subjected to cold. All life history parameters were determined as in experiment 1, except that the females were kept individually with two males in small cages. Thirty individual females of each species were used in this experiment.

Statistical Analyses. In experiment 1, individual times of death were pooled across cages, by species, sex, and temperature, and differences in mean longevity at the five temperatures were tested using one-

Table 1. Mean longevity (in days) of adult *S. calcitrans* and *S. niger* reared at five constant temperatures (experiment 1)

Temp(°C)	*S. calcitrans*				*S. niger*			
	Female		Male		Female		Male	
	n	Mean ± SE	*n*	Mean ± SE	*n*	Mean ± SE	*n*	Mean ± SE
15	27	11.48 ± 1.43a	46	10.26 ± 0.83a	61	40.79 ± 4.40a	47	40.62 ± 4.90a
20	67	23.73 ± 2.04b	55	25.69 ± 2.21b	47	32.96 ± 3.29a	55	27.45 ± 2.96a
25	62	10.19 ± 1.26a	61	6.93 ± 0.87c	43	14.28 ± 1.26b	42	13.80 ± 1.70b
30	51	5.80 ± 0.84c	59	4.27 ± 0.56d	41	10.88 ± 0.99b	51	7.20 ± 0.70b
35	12	1.75 ± 0.22d	12	1.58 ± 0.19e	2	1.00 ± 0.00c	4	1.00 ± 0.00c

Means followed by different letters within a column are significantly different at the 5% level.

way analyses of variance (ANOVAs). Multiple comparisons among pairs of means were made using the Tukey–Kramer method. All comparisons of means between the two species and between experiments 1 and 2 were made using Student's *t*-tests. As there were no individual data for fecundity in experiment 1, variances among cages were calculated as indicated in Sokal and Rohlf (1995), chapter 8, and used as estimates of the variance of fecundity at each temperature.

Before ANOVAs and *t*-tests, the equality of sample variances was tested using the F_{max} test (Sokal and Rohlf 1995), and when they were found to be unequal, the data were $\log_{10}$-transformed to make the variances uniform.

Results

Adult Longevity. Mean adult longevity when all stages were maintained at the same temperature (experiment 1) is given in Table 1. In male and female *S. calcitrans*, mean longevity was significantly greater at 20°C than at 15°C and then decreased when temperature increased from 20 to 35°C. In male and female *S. niger*, mean longevity was greatest at 15°C and decreased gradually at higher temperatures. The maximum life span showed similar changes with temperature: for both sexes, the maximum life span was longer at 20°C in *S. calcitrans*, but at 15°C in *S. niger* (see Fig. 1 for females). At 35°C, no fly survived longer than 3 d, and the life cycle could not be completed in either species; accordingly, the data obtained at 35°C were subsequently ignored.

At a given temperature, mean adult longevity was generally greater in *S. niger* than in *S. calcitrans* (Table 1). The tropical species' advantage was significant ($P < 0.001$) at 15, 25, and 30°C for both sexes. The survival curves for adult *S. calcitrans* (see Fig. 1 for females) showed higher mortality rates at younger ages. In *S. niger*, deaths occurred more uniformly during the adult life, especially at 25 and 30°C.

When adults were reared at 15°C after development at 25°C (experiment 2), adult longevity increased significantly in *S. calcitrans:* female longevity was 36.7 d (versus 11.5 d in experiment 1; $t = 5.16$, df = 55, $P < 0.001$) and male longevity was 30.8 d (versus 10.3 d in experiment 1; $t = 7.23$, df = 104, $P < 0.001$). In contrast, adult longevity did not increase for *S. niger* in experiment 2: female longevity remained unchanged (38.1 d versus 40.8 d in experiment 1; nonsignificant difference) and male longevity even decreased (22.9 d versus 40.6 d in experiment 1; $t = 3.43$, df = 105, $P < 0.001$).

Reproduction. In experiment 1, no reproduction occurred at 15 and 35°C, in both *S. calcitrans* and *S. niger*. Within the 20–30°C range, the preoviposition period was longer at 20°C in both species (16 d in *S. calcitrans* and 10 d in *S. niger*). The shortest times before oviposition were at 25°C in *S. calcitrans* (8 d) and at 30°C in *S. niger* (7 d). The duration of oviposition decreased markedly when temperature increased from 20 to 30°C (Fig. 1). *S. calcitrans* females laid eggs for 44 d at 20°C, 32 d at 25°C, and 14 d at 30°C. The corresponding figures for *S. niger* females were 63 d at 20°C, 21 d at 25°C, and 19 d at 30°C.

In both species, the mean lifetime fecundity tended to decrease when temperature increased from 20 to 30°C, although within-species differences were not significant because of large variations among cages. The mean number of eggs laid per female varied from 63 at 20°C to 19 at 30°C in *S. calcitrans* and from 138 at 20°C to 53 at 30°C in *S. niger*. This pattern reflected the decrease in the duration of oviposition between 20 and 30°C, which was not compensated by the concurrent increase in M_x values in both species (Fig. 1). *S. niger* laid more eggs than *S. calcitrans* and the difference was significant at 30°C ($t = 3.84$, df = 90, $P < 0.001$).

In experiment 2, reproduction occurred at 15°C, albeit at a very low level in *S. niger* (Fig. 2). In both species, oviposition began much later than at higher temperatures in experiment 1, with preoviposition periods reaching 28 d in *S. calcitrans* and 36 d in *S. niger*. Oviposition was short in spite of the prolonged survival of adult females. The mean lifetime fecundity was 22 eggs per female in *S. calcitrans* and was extremely low (0.3 eggs per female) in *S. niger*. The between-species difference in fecundity was significant ($t = 3.43$, df = 58, $P < 0.01$).

Life History Parameters. The variations of the main life history parameters in relation to temperature are shown in Fig. 3 (experiments 1 and 2 combined). In both species, the net reproductive rate (R_0) strongly increased with temperature from 15 to 20°C and then declined from 20 to 30°C. It was zero at 35°C. *S. niger* showed higher R_0 values than *S. calcitrans* within the 20–30°C range, but the reverse was found at 15°C.

Generation time decreased with increasing temperatures, ranging from ≥105 d at 15°C to ≤26 d at 30°C.

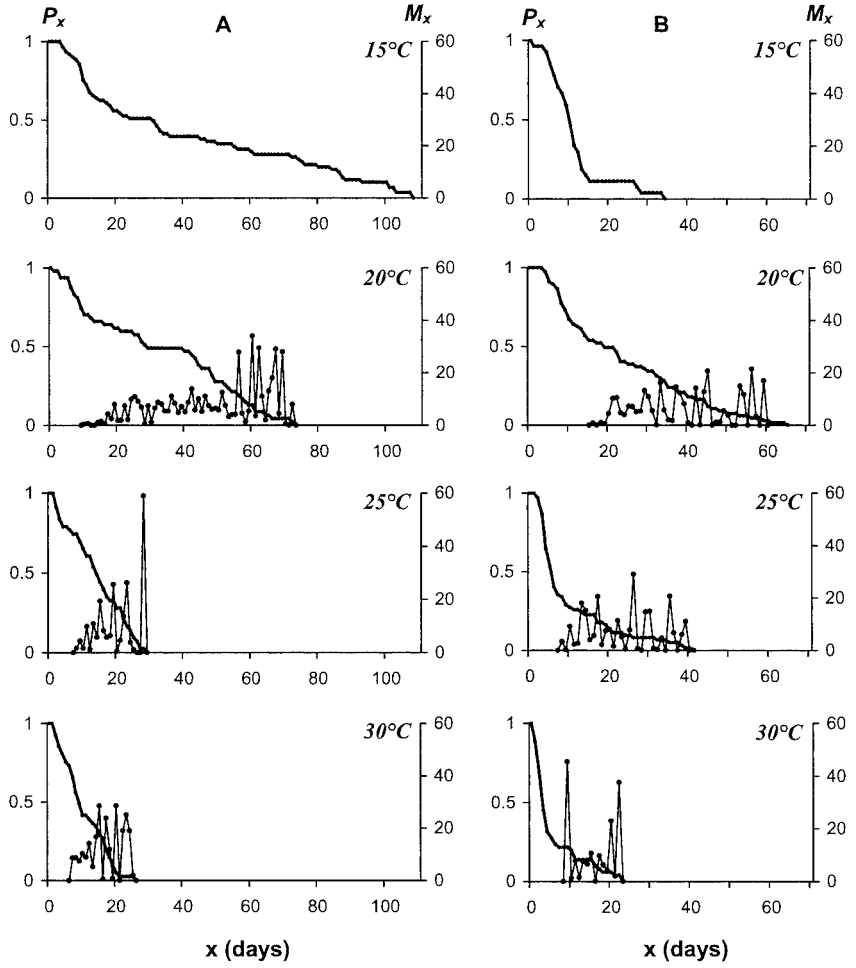

Fig. 1. Proportion of adult females surviving from emergence (P_x) and number of eggs laid per surviving female per day (M_x) at four constant temperatures (experiment 1) (A, *S. niger*; B, *S. calcitrans*).

The values were similar in both species at all temperatures.

The intrinsic rate of increase (r) varied inversely with the generation time, increasing with temperature from 15 to 30°C in both species. However, there were some differences between species, reflecting the differences in R_0: within the 20–30°C range, r was higher in *S. niger*, but at 15°C it was higher in *S. calcitrans*. At the colder temperature, the rate of increase of *S. niger* was <0 ($r = -0.026$).

Discussion

Puzzling results have been obtained for *S. calcitrans* in this study, because of high mortality rates early in the adult life. This mortality resulted in much lower fecundity and R_0 values than in other studies (Lysyk 1998). In most cages, more than half of the females died before the oviposition period. Berry and Kunz (1977) recorded similar levels of mortality in some experiments, which they ascribed to temperature stress. That explanation does not hold in the current study. In fact, the rearing conditions of adult *S. calcitrans* (temperature, relative humidity, photoperiod, and sex ratio in the samples) had already been used in other studies without inducing early mortality. The food given to the flies (blood only once a day, no sugar) might have affected survival, but only marginally (Jones et al. 1992). Alternative explanations may be 1) a high incidence of pathogens and microscopic parasites; 2) strong selection for survival under artificial conditions, which might vanish after a few generations (Ramsamy 1979); and 3) larval food of poor quality—elephant grass without any supplement—affecting the adult stage (DuToit 1975). In many insect species, adults draw nutrients from larval reserves and current feeding (Boggs 1997), and this is particularly true for species whose diet changes with the life stage.

Irrespective of the early adult mortality, *S. calcitrans* females that survived until the oviposition period showed moderate fecundity. They laid more eggs than in Sutherland's (1979) study in South Africa, but less than in many other studies (Parr 1962, Labrecque et

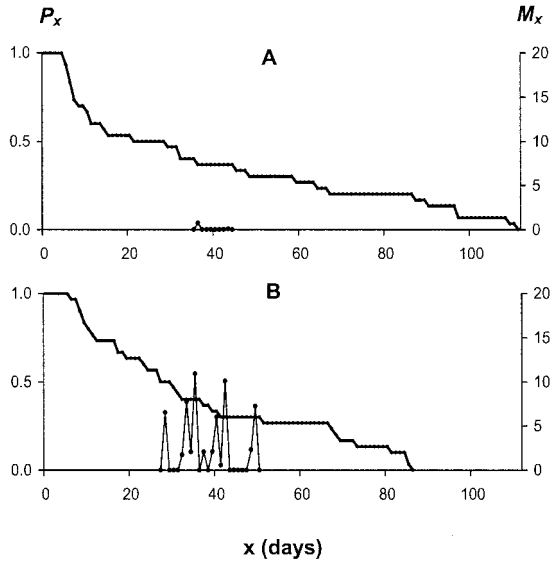

Fig. 2. Proportion of adult females surviving from emergence (P_x) and number of eggs laid per surviving female per day (M_x) at 15°C (experiment 2) (A, *S. niger*; B, *S. calcitrans*). For M_x, the vertical scale is not the same as in Fig. 1.

al. 1975, Berry and Kunz 1978, Lysyk 1998). The very low fecundity reported by Sutherland (1979) may be due to the very short daylength that he used. In the current study, the relatively low fecundity may have the same cause as adult female mortality, i.e., occurrence of pathogens, nonadaptation to artificial conditions, and/or poor-quality food. In the literature, the highest levels of fecundity were recorded when flies were fed blood ad libitum, after the larvae were reared in very rich media, including wheat flour, meat, and bone meal, or yeast (Berry and Kunz 1978, Lysyk 1998).

The first results on the longevity and reproduction of adult *S. niger* have been more satisfactory: adult mortality rates during the preoviposition period were lower than in *S. calcitrans*, and mean lifetime fecundity was markedly higher than in *S. calcitrans* at favorable temperatures. The rearing conditions, although they resulted in lower immature survival in *S. niger* than in *S. calcitrans* (Gilles et al. 2005), have proved to be more favorable to *S. niger* during the whole life cycle.

The effects of temperature on the population growth potential of *S. calcitrans* in La Réunion can be investigated only if the high mortality rates do not alter the normal pattern of variation. Comparisons with previous studies suggest this condition is met. A number of parameters determined in La Réunion, namely, developmental time, immature survival, length of the preoviposition period, and generation time, were in reasonably good agreement with values reported elsewhere at similar temperatures (Parr 1962, Kunz et al. 1977, Berry and Kunz 1978, Sutherland 1979, Lysyk 1998). Only R_0 in the 20–30°C range was highly affected by adult mortality. As a result, the rates of increase were lower than those in Lysyk (1998) but

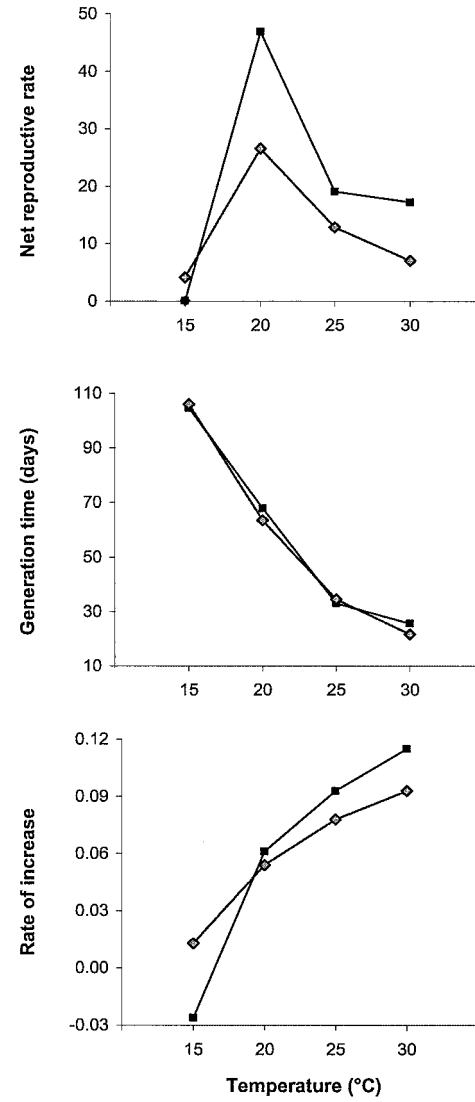

Fig. 3. Relations between temperature and net reproductive rate, generation time, and intrinsic rate of increase in *S. niger* (■) and *S. calcitrans* (◇). Data shown at 20, 25, and 30°C are from experiment 1, and data shown at 15°C are from experiment 2.

showed a similar trend of variation with temperature. Typically, *S. calcitrans* has a low rate of increase at 15°C, which increases with temperature up to 30°C, and falls dramatically at 35°C. Whether populations can survive at the extremes (15 and 35°C) is open to debate. Limited egg laying has been reported for these temperatures (Berry and Kunz 1978, Sutherland 1979, Lysyk 1998), but after the flies had developed at more optimal temperatures, as in experiment 2. In the current study, no reproduction occurred when temperature remained at 15 and 35°C throughout the life cycle.

The effects of temperature on the rate of increase of *S. niger* are very similar to those observed in *S.*

calcitrans. *S. niger* has a very low *r* value at 15°C, which increases with temperature up to 30°C, and falls dramatically at 35°C. A few females laid eggs at 15°C after development at 25°C, but fecundity was extremely low. No reproduction occurred when temperature remained at 15 and 35°C throughout the life cycle, as in *S. calcitrans*.

Temperature is probably not the only important factor in the population dynamics of Stomoxyines. Other abiotic and biotic factors act individually or interact with temperature (DuToit 1975, Berry and Kunz 1977, Jones et al. 1992). Ideally, comparisons between the two *Stomoxys* species should be made under several rearing conditions corresponding to their respective requirements. In this study, comparisons were made under conditions unfavorable to *S. calcitrans*, which may have unduly lowered *r* values in this species. The results, however, clearly show that *S. calcitrans* has an advantage over *S. niger* at low temperatures. At 15°C, *S. calcitrans* has shown some capacity to complete its life cycle and to increase in number—at least after developing at optimal temperature. This notion is consistent with what is known of its overwintering strategy in the temperate zone, which involves continuous breeding in sufficiently warm shelters (Sømme 1961, Greene et al. 1989, Thomas et al. 1990). In contrast, *S. niger* was incapable of reaching $r = 0$ at 15°C. This species seems to have evolved a strategy of survival without any reproduction during the tropical winter. Its eggs are susceptible to cold; at 15°C, they show a significantly higher mortality than those of *S. calcitrans* (Gilles et al. 2005). However, larvae and pupae develop easily at low temperatures, and adults can survive for several months at 15°C—significantly longer than adults of *S. calcitrans*.

At higher temperatures, greater *r* values were observed in *S. niger* than in *S. calcitrans*. This result, though consistent with the high incidence of the tropical species in Mauritius (Kunz and Monty 1976) and the warm coastal area of La Réunion, may depend on rearing conditions. The use of larval media of poor quality (elephant grass) may be of particular importance. In natural situations, that condition prevails at some distance from dairy farms, where *S. niger* reproduces (Kunz and Monty 1976). However, media richer in cattle manure are probably more favorable to *S. calcitrans* (Parr 1962, Kunz and Monty 1976, Hogsette et al. 1987, Lysyk 1993), and it might be useful to make further comparisons between the two species using these media.

Acknowledgments

We are grateful to E. Tillard, M. Cléro, and K. Le Roux (CIRAD, La Réunion) and to the "Groupement Régional de Défense Sanitaire du Bétail de La Réunion" for assistance. We thank two anonymous reviewers for helpful comments on the manuscript. This research was funded by the CIRAD-3P, the Conseil Régional of La Réunion island and the CNRS (UMR 5175).

References Cited

Berry, I. L., and S. E. Kunz. 1977. Mortality of adult stable flies. Environ. Entomol. 6: 569–574.

Berry, I. L., and S. E. Kunz. 1978. Oviposition of stable flies in response to temperature and humidity. Environ. Entomol. 7: 213–216.

Boggs, C. L. 1997. Reproductive allocation from reserves and income in butterfly species with differing adult diets. Ecology 78: 181–191.

Buxton, B. A., N. C. Hinkle, and R. D. Schultz. 1985. Role of insects in the transmission of bovine leukosis virus: potential for transmission by stable flies, horn flies, and tabanids. Am. J. Vet. Res. 46: 123–126.

David, J.-F., M.-L. Celerier, and C. Henry. 1995. Note on the use of the basic equation of demography. Oikos 73: 285–288.

DuToit, G.D.G. 1975. Reproductive capacity and longevity of stable flies maintained on different kinds of blood. J. S. Afr. Vet. Assoc. 46: 345–347.

Gilles, J., J.-F. David, and G. Duvallet. 2005. Temperature effects on development and survival of two stable flies, *Stomoxys calcitrans* and *Stomoxys niger niger* (Diptera: Muscidae), in La Réunion island. J. Med. Entomol. 42: 260–265.

Greene, G. L., J. A. Hogsette, and R. S. Patterson. 1989. Parasites that attack stable fly and house fly (Diptera: Muscidae) puparia during the winter on dairies in northwestern Florida. J. Econ. Entomol. 82: 412–415.

Hedrick, P. W. 1984. Population biology. Jones & Bartlett, Boston, MA.

Hogsette, J., J. P. Ruff, and C. J. Jones. 1987. Stable fly biology and control in the northwest Florida. J. Agric. Entomol. 4: 1–11.

Jones, C. J., D. E. Milne, R. S. Patterson, E. T. Schreiber, and J. A. Milio. 1992. Nectar feeding by *Stomoxys calcitrans* (Diptera: Muscidae): effects on reproduction and survival. Environ. Entomol. 21: 141–147.

Kunz, S. E., I. L. Berry, and K. W. Foerster. 1977. The development of the immature forms of *Stomoxys calcitrans*. Ann. Entomol. Soc. Am. 70: 169–172.

Kunz, S. E., and J. Monty. 1976. Biology and ecology of *Stomoxys nigra* Macquart and *Stomoxys calcitrans* (L.) (Diptera, Muscidae) in Mauritius. Bull. Entomol. Res. 66: 745–755.

Labrecque, G. C., D. E. Weidhaas, and T. L. Whitfield. 1975. Graphic models as intermediate steps to computerized simulations of stable fly populations. Mosq. News 35: 316–321.

Lysyk, T. J. 1993. Adult resting and larval development sites of stable flies and house flies (Diptera: Muscidae) on dairies in Alberta. J. Econ. Entomol. 86: 1746–1753.

Lysyk, T. J. 1998. Relationships between temperature and life-history parameters of *Stomoxys calcitrans* (Diptera: Muscidae). J. Med. Entomol. 35: 107–119.

Parr, H.C.M. 1962. Studies on *Stomoxys calcitrans* (L.) in Uganda, East Africa. II.—Notes on life-history and behaviour. Bull. Entomol. Res. 52: 437–443.

Potgieter, F. T., B. Sutherland, and H. C. Biggs. 1981. Attempts to transmit *Anaplasma marginale* with *Hippobosca rufipes* and *Stomoxys calcitrans*. Onderstepoort. J. Vet. Res. 48: 119–122.

Ramsamy, M. P. 1979. Studies on the large-scale rearing of the stable fly, *Stomoxys nigra* Macquart (Diptera: Muscidae). Bull. Entomol. Res. 69: 477–489.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry, 3rd ed., Freeman, New York.

Sømme, L. 1961. On the overwintering of house flies (*Musca domestica* L.) and stable flies (*Stomoxys calcitrans* (L.)) in Norway. Nor. Entomol. Tidsskr. 11: 191–223.

Sutherland, B. 1979. Some effects of temperature on the adults, eggs and pupae of *Stomoxys calcitrans* (L.) (Diptera: Muscidae). Onderstepoort. J. Vet. Res. 46: 223–227.

Thomas, G. D., I. L. Berry, S. R. Skoda, and D. R. Berkebile. 1990. Seasonal ovipositional status of field populations of female stable flies (Diptera, Muscidae) in cattle feedlots as measured by two sampling methods. Environ. Entomol. 19: 1597–1604.

Weber, A. F., R. D. Moon, D. K. Sorensen, D. W. Bates, J. C. Meiske, C. A. Brown, N. L. Rohland, E. C. Hooker, and W. O. Strand. 1988. Evaluation of the stable fly (*Stomoxys calcitrans*) as a vector of enzootic bovine leukosis. Am. J. Vet. Res. 49: 1543–1549.

Zumpt, F. 1973. The Stomoxyine biting flies of the world. Taxonomy, biology, economic importance and control measures. Gustav Fischer Verlag, Stuttgart, Germany.

Received 7 January 2005; accepted 28 May 2005.