Life Fertility Tables of *Piophila casei* L. (Diptera: Piophilidae) Reared at Five Different Temperatures

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ABSTRACT *Piophila casei* L. or cheese skipper is a well-known fly with a controversial role: it is considered harmful in the food industries but important in nature as a detritivore and useful for studies in forensic entomology. The temperature response of *P. casei* was studied at five constant temperatures: 15, 19, 25, 28, and 32°C. The lowest mortality percentage of eggs was recorded at 15°C and the highest at 32°C. Conversely, less mortality was observed for maggots at higher temperatures. The developmental time from first instar to adult decreased with temperature reaching the lowest value at 32°C (13.7 d). Adult longevity was strongly affected by temperature, decreasing from 20.5 d at 15°C to 6.6 d at 32°C. Mean total fecundity per female was higher at 25°C and lower at 15 and 19°C, whereas the best performance in mean daily total fecundity per female was recorded at 32°C. Male longevity followed a similar trend to the one observed for females. The net reproductive rate (R_0) was greatest at 25°C, whereas the highest r_m was recorded at 32°C. At this latter temperature, the highest mean generation time (T) and doubling time (D) were also observed. The finite rate of increase (λ) was augmented slightly with higher temperatures.

KEY WORDS *Piophila casei*, developmental time, life history, life table

THE CHEESE SKIPPER FLY, *Piophila casei* Linneus (Diptera: Piophilidae), is a species belonging to a small genus that has been reported throughout the world and is considered a cosmopolitan species (McAlpine 1977). *P. casei* is an insect that generates interest in different fields; its biology has stimulated the interest of several entomologists since the beginning of the last century (Alessandrini 1907, Simmons 1927, Smart 1935), probably because of the dispersal of the fly into various habitats and to the controversial role it plays: it is considered important in nature as a detritivore and harmful in some food industries. Typically, its larvae prefer to develop in exposed carrion, including human corpses in advanced stages of decay (McAlpine 1977, Smith 1986, van der Louw and van der Linde 1993). Nevertheless, *P. casei* frequently assumes a high local economic importance because of the serious damage that it can cause in stored products with abundant sources of protein. Direct damage is caused by the larvae that develop inside cheese, milk derivatives, ham, meat, and cured fish (Simmons 1927, Leclercq 1946, Zuska and Lestovka 1965, Domenichini 1976, Hegazi et al. 1978, Busvine 1980, Haines and Rees 1989), whereas indirect damage is possible in food manufacturing industries where the fly can vector pathogens (Greenberg 1971, Domenichini 1991). For the food industry, the presence of the fly is undesirable. Unfortunately, chemical control of the fly in food manufacturing areas is difficult because of the chemical residuals and the propensity of *P. casei* to develop resistance to insecticides (Rossi and Presciuttini 1996). Curiously, larvae of *P. casei* are fundamental in the production of some valuable cheeses in Italy (Ottogalli 2001) and Croatia (Miokovic et al. 1997).

This species is also of medical and veterinary interest because of the various myasies (enteric, nasal, and urinal) that it can cause (Zumpt 1965, Perez Inigo 1971, el Serougi el 1991, Saleh and el Sibae 1993, Passos et al. 2004). Moreover, *P. casei* is an important fly species in forensic entomology because is informative for the estimation of postmortem interval (Smith 1986, Early and Goff 1986, Liu and Greenberg 1989, Schoenly et al. 1996, De Jong and Chadwick 1999).

To date, there are only a few partial studies on the biology of the cheese skipper (Smart 1935, Hegazi et al. 1978, Costa et al. 1986, Belcari and Antonelli 1992), and none of these provide useful data on the effect of temperature on demographic parameters (e.g., development, longevity, fecundity, and life tables). Construction and analysis of life fertility tables is a standard ecological method used to describe and estimate the insect population dynamics for any given time. They can be used to generate useful models of insect populations in various environmental conditions (Gilbert et al. 1976, Southwood 1978, Southwood and Henderson 2000). In this study, flies were reared in controlled environments at five different constant temperatures. Results are recorded and summarized

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as life table statistics to provide useful information for the control of *P. casei* in food industry in which temperatures could be regulated and for its practical use in forensic entomology, for which limited published information on its biology are available (Anderson 1999).

Materials and Methods

Rearing Conditions. A colony of *P. casei* was established in the laboratory in 2001 from wild specimens collected in some ripening rooms of dairies located in Ragusa, Italy. Colonies were reared for ≈1 yr before the experiments began in cages (length 40 cm by width 50 cm by height 50 cm) maintained in climatic chambers at a constant temperature of 27 ± 1°C, 70 ± 5% RH, and a L8:D16 photoperiod. This photoperiod was chosen because it is the standard regime maintained in dairies. The flies were fed with an artificial diet consisting of agar (20 g), powdered milk (80 g), dry yeast (50 g), nipagine (1 g), ethyl alcohol (10 ml), and water (1,000 ml) (Sacchi et al. 1971). Fresh diet was provided every 2 d and was used as an oviposition substrate and moisture source.

Development and Survivorship of Immature Stages. The effects of temperature on developmental time, survival, and fecundity of *P. casei* were evaluated in growth chambers at constant temperatures of 15, 19, 25, 28, and 35 ± 1°C, 70 ± 5% RH, and a L8: D16 photoperiod. These temperatures were selected because they are similar to the range recorded in dairies in the periods of higher infestation level (in autumn and summer).

To obtain synchronized eggs, adult females (≈200 for each temperature) were incubated at 28°C for 5 h. The eggs of the flies (<2 h old) were collected with a palette knife from stock colonies, put in groups of 10 into plastic petri dishes (9 cm in diameter by 2 cm high), and incubated at the five temperatures. The total number of eggs incubated at each temperature were 630, 850, 1,120, 1,682, and 1,810 at 15, 19, 25, 28, and 32°C, respectively. Each petri dish containing 10 eggs was considered one replicate. To record developmental time and percentage of egg eclosion, progress in embryonic development was monitored twice a day with a stereoscopic microscope until hatching.

To determine juvenile developmental time, survival, and sex ratio of the larval stages at the five temperatures, all the newly hatched larvae (with the exception of those maintained at 15°C, for which only 401 larvae were selected) were collected and transferred in groups of 10 into bigger plastic petri dishes (12 cm in diameter by 2.5 cm high). Development and mortality of larvae were recorded daily (twice a day in trials at 28 and 32°C) until they reached the pupal stage. The age of the larvae was determined on the basis of the different degrees of sclerotization of the cephalopharyngeal apparatus. Food was replaced daily during the whole period of larval and pupae development to maintain a constant level of humidity.

Natural mortality of the immature stages of *P. casei* in all treatments was expressed as relative mortality rate (day^{-1}) using the following formula (Rabbinge 1976):

$$RMR = \ln N_t - \ln N_{t+\Delta t}/\Delta t$$

where $\ln N_t$ and $\ln N_{t+\Delta t}$ are the natural logarithm of the number of larvae at the beginning and at the end of the stage, respectively, and Δt is the developmental time.

Longevity and Reproduction. To evaluate the number of eggs laid and adult longevity of the cheese skipper at the five temperatures, 40 male:female pairs of newly emerged adults (<1 h old) were randomly chosen from those followed during larval development. Pairs were confined in separate Plexiglas containers (12 cm in diameter by 3 cm high), provided with vent holes on the lid and covered with a fine mesh nylon screen to allow ventilation. Food was replaced daily, and temperature was checked daily by placing a thermometer inside containers without larvae. Preoviposition (the age, in days, before the first deposition of eggs), oviposition period (days), number of eggs laid, and survival of adults were recorded daily until all adults had died.

Statistical Analysis and Fertility Tables. The effects of treatments on eggs, larval developmental times, and adult life history (i.e., longevity, preoviposition, and oviposition period) were determined using a one-way analysis of variance (ANOVA), and *t*-tests ($P = 0.05$) were used for post hoc comparisons (StatSoft 1996).

Life and fertility tables were constructed on the basis of life history of immature stages and adults observed during the experiment. From previous laboratory results, we assumed a sex ratio of 1:1 in all treatments. For each temperature, daily age-specific survivorship (l_x) and age-specific fecundity (m_x) were used to calculate intrinsic rate of natural increase (r_m), expressed as the number of females produced per female per day, using the following formula (Birch 1948):

$$\sum_{x=1}^{\omega} e^{-r_m x} l_x m_x = 1$$

where ω is the oldest age class, l_x and m_x are the proportion of surviving females at the age x and the number of female progeny produced per female in the age interval x, respectively. With a stable age distribution and under given climatic and food conditions, the intrinsic rate of natural increase is a useful comparative statistic of population growth potential (Southwood 1978). Values of r_m were compared using confidence intervals, and the estimated SE of r_m was calculated by the Jacknife method (Hulting et al. 1990). Further data were also calculated for each temperature: gross reproductive rate ($GRR = \Sigma M_x$ or the total number of eggs produced per female during the lifetime), net reproductive rate ($R_0 = \Sigma l_x m_x$ or the number of female offspring produced per female), finite capacity for increase ($\lambda = e^{rm}$ or the number of times the population will multiply itself per unit of

Table 1. Mean developmental time (days ± SE) of the immature stages of *P. casei* at five constant temperatures

Instars	15°C	*n*	19°C	*n*	25°C	*n*	28°C	*n*	32°C	*n*
Egg	7.4 ± 0.1a	630	3.9 ± 0.1b	733	1.4 ± 0.02c	874	1.5 ± 0.01c	949	1.0 ± 0.01d	950
L1	8.8 ± 0.1a	401	6.3 ± 0.1b	462	3.8 ± 0.03c	874	3.3 ± 0.02d	890	2.5 ± 0.02e	950
L2	6.5 ± 0.1a	300	6.2 ± 0.1a	281	4.1 ± 0.03b	596	3.8 ± 0.01b	623	3.1 ± 0.01c	767
L3	17.0 ± 0.3a	114	13.9 ± 0.3b	239	6.5 ± 0.1c	452	4.7 ± 0.1d	449	4.0 ± 0.02e	419
Pupae	17.4 ± 0.3a	114	14.3 ± 0.2b	174	6.9 ± 0.1c	421	6.4 ± 0.1c	405	4.1 ± 0.1d	400
L1–pupae	50.0 ± 0.4	114	39.8 ± 0.4	174	21.9 ± 0.2	182	18.2 ± 0.7	400	13.7 ± 0.1	400

Means within a row followed by the same letter are not significant different (*t*-test, $P > 0.05$).

time), mean generation time ($T = \ln R_0/r_m$, measured in days), and doubling time ($D = \ln 2/r_m$ or the number of days required for the population to double its numbers) (Birch, 1948, Andrewartha and Birch 1954, Southwood 1978). Capacity for increase ($r_c = \ln R_0/T_c$) and cohort generation time ($T_c = \Sigma x l_x m_x/\Sigma l_x m_x$) (Laughlin 1965) were also calculated.

Results

Development and Survivorship of Immature Stages. The effects of five constant temperatures on *P. casei* development are summarized in Table 1. Temperature significantly affected embryonic development ($F = 5818,3$; df = 4,4131; $P < 0.05$); at 15°C, embryonic development was completed in 7.4 d, which was the longest time required. About one half that time was necessary at 19°C (3.9 d), and very short intervals were recorded at 25, 28, and 32°C (1.4, 1.5, and 1 d, respectively). No significant difference ($P > 0.05$, *t*-test) was noted between 25 and 28°C, whereas the differences at the other temperatures were significant. Developmental time of the larval stages was strongly influenced by temperature. Significant differences were recorded in almost all the treatments (Table 1). More than twice the number of days was needed at 15 and 19°C compared with the other temperatures. At 32°C, all the three larval stages were completed in <10 d. Duration of pupal stage reflected the trend observed during the previous instars ($F = 2113$; df = 4,1065; $P < 0.05$); at 15°C, the number of days was significantly higher (17.4 d) than at the other temperatures, whereas it was similar at 25 and 28°C (6.9 and 6.4 d, respectively) and very low at 32°C (4.1 d). High mortality occurred among eggs maintained at the higher temperatures (Table 2). An interesting finding was that, at 15 and 19°C, a low mortality rate was recorded, whereas the proportion of eggs that did not complete the embryonic development increased progressively with temperatures. Regarding mortality of the other larval stages, the results indicate that the first instar was more affected at 15 and 19°C (0.052 and 0.073, respectively), whereas at 25, 28, and 32°C, mortality was very low (0, 0.020, and 0, respectively). The mortality recorded with pupae was very low at all temperatures, and it is interesting to note that, at 15°C, all pupae reached adulthood. Data on total mortality indicate that at 32°C mortality was the highest, in consequence of the great number of eggs that did not complete embryonic development. However, at 15 and 19°C, eggs survived better, but greater mortality occurred in the following instars, with exception of the pupal stage at 15°C.

Table 2. Relative mortality rate (per day) for the immature stages of *P. casei* at five constant temperatures

Instars	15°C	19°C	25°C	28°C	32°C
Egg	0.0014	0.0387	0.1775	0.3865	0.6349
L1	0.0516	0.0733	0	0.0195	0
L2	0.0443	0.0802	0.0934	0.0939	0.0690
L3	0.2932	0.0352	0.0425	0.0697	0.0756
Pupae	0	0.0262	0.0103	0.0161	0.0113
Total	0.0475	0.0492	0.0343	0.0468	0.0631

Longevity and Reproduction. Temperature also affected adult longevity ($F = 30.7$; df = 4,195; $P < 0.05$ for females; $F = 42.5$; df = 4,195; $P < 0.05$, for males; Table 3). No difference ($P > 0.05$) in longevity was evident between females kept at 15 and 19°C (20.5 and 17.5 d, respectively), whereas both were significantly longer ($P < 0.05$) compared with 25, 28, and 32°C (13.3, 8.5, and 6.6 d, respectively). Among these latter temperatures, the differences were significant in all the cases ($P < 0.05$). Males, on average, lived slightly shorter times than females, but similar trends in longevity were observed at all tested temperatures (Table 3). Adult survival decreased gradually with time at each temperature tested (Fig. 1). At 36°C, a steeper decline in adult survivorship was observed, whereas it was slowest at 15 and 19°C. Mating occurred without noteworthy courtship behavior, and the sexually receptive period of females varied with temperature. This interval was longer at 15 and 19°C than at 28 and 32°C. Females of the cheese skipper are monogamous and are refractory to further copulations after mating. If females were disturbed during copulation, they again became receptive within a short period of time. Females deposited their eggs essentially in batches of a variable number of eggs (from 3 to 100). Sometimes, at the beginning of the oviposition period, eggs were laid singly. Temperature had a significant effect on the duration of the preoviposition and oviposition period and on cumulative number at eggs laid (Table 3). Compared with other temperatures, preoviposition time was significantly longer at 15 and 19°C (5.9 and 4.8 d, respectively; $P < 0.05$), and despite greater survival, the average number of eggs laid (99.3 and 97.2 eggs per female, respectively) and the oviposition rate (3.8 and 5.8, respectively) were significantly smaller. However, under these conditions, a more regular distribution of eggs was laid during the oviposition pe-

Table 3. Adult longevity, preoviposition period, fecundity, and oviposition rate of *P. casei* at five different temperatures

	15°C	19°C	25°C	28°C	32°C
Male longevity (d)	17.7 ± 0.5a	17.6 ± 1.5a	9.3 ± 0.9b	8.1 ± 0.6b	6.5 ± 0.5c
Female longevity (d)	20.5 ± 1.6a	17.5 ± 1.3a	13.3 ± 0.9b	8.5 ± 0.7c	6.6 ± 0.4d
Preoviposition period (d)	5.9 ± 0.3a	4.8 ± 0.3b	3.4 ± 0.1c	2.3 ± 0.1d	1.3 ± 0.1e
Fecundity (no. eggs)	99.3 ± 20.2a	97.2 ± 9.7a	136.6 ± 18.5ab	110.1 ± 10.2a	125.1 ± 8.5ab
Oviposition rate (no. eggs/d)	3.8 ± 0.6a	5.8 ± 0.6a	9.6 ± 1.3b	12.2 ± 0.9b	17.9 ± 0.9c

Means within a row followed by the same letter are not significant different (*t*-test, $P > 0.05$).

riod. At 25°C, the distribution was similar to the previous, but the average number of eggs laid (136.6 eggs per female) was higher during the entire lifespan. It reached the peak after ≈6 d and decreased slowly in ≈12 d. At 28 and 32°C, females of the cheese skipper produced an average of 110.1 and 125.1 eggs, respectively, and the preoviposition period was significantly shorter (2.3 and 1.3 d, respectively). Oviposition rate resulted the highest at 32°C (17.9 eggs/d), and no significant differences were recorded between at 25 and 28°C ($P > 0.05$). At these latter conditions, the number of eggs laid increased rapidly 1 d after the beginning of oviposition, with higher production during the second to third day (22.5 and 37.1 eggs per

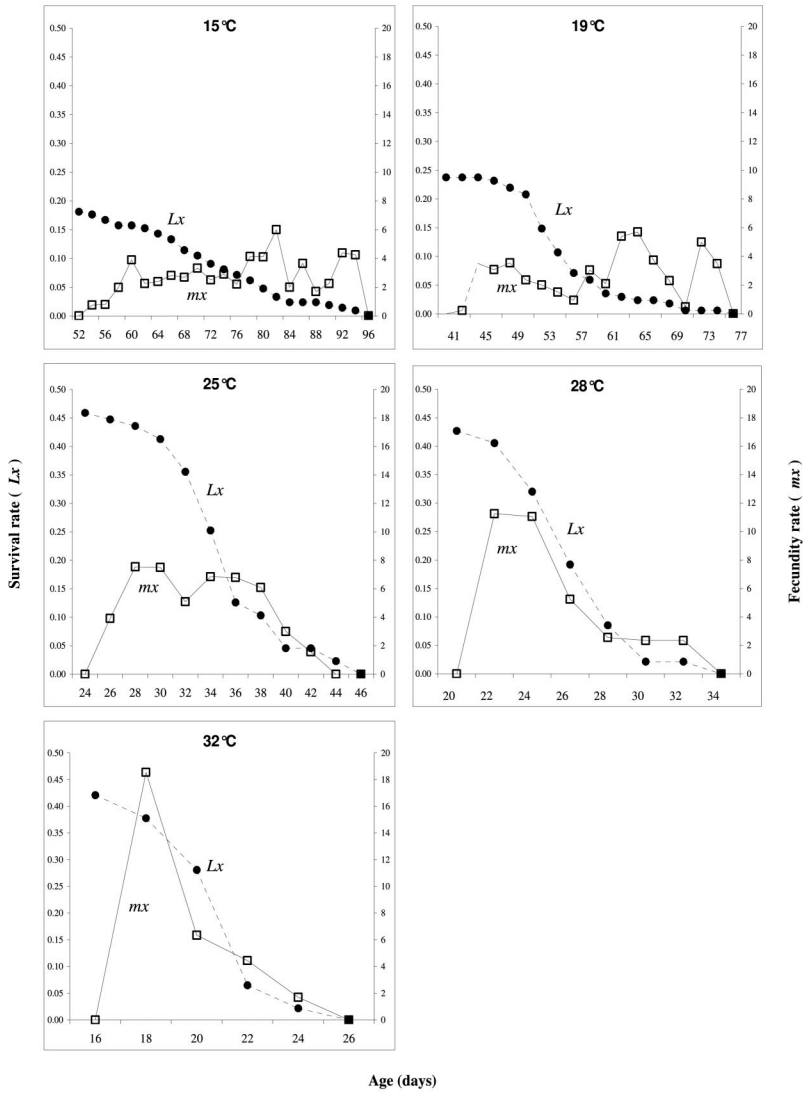

Fig. 1. Survival rate (l_x) and age-specific fecundity rate (m_x) of *P. casei* at five constant temperatures.

Table 4. Demographic statistics of *P. casei* at five constant temperatures

	15°C	19°C	25°C	28°C	32°C
R_o	4.50	4.13	13.38	9.43	9.12
r_m (±SE)	0.0222 (±0.021)	0.0278 (±0.0071)	0.0862 (±0.0037)	0.0955 (±0.0016)	0.1216 (±0.001)
r_c	0.0229	0.0268	0.0848	0.0950	0.1212
T	67.74	51.12	30.11	23.49	18.18
T_c	68.66	51.69	30.60	23.60	18.24
l	1.02	1.03	1.09	1.10	1.13
D	31.23	24.98	8.05	7.26	5.70
S_{mx}	121.94	97.02	96.77	69.60	61.10

R_o, net reproductive rate; r_m, intrinsic rate of natural increase; T, mean generation time; T_c, cohort generation time; l, finite capacity for increase; D, doubling time; S_{mx}, gross reproductive time.

female), and production progressively decreased from ≈10 to 4 d at 28 and 32°C, respectively.

Fertility Tables. Differences in the flies' temperature responses are further evidenced by their intrinsic rates of natural increase (r_m; Table 4). Based on the calculated r_m values, the highest reproductive potential of *P. casei* was recorded at 32°C (0.1216), and good performances were observed also at 25 and 28°C (0.0862 and 0.0955, respectively). Data on r_m values at 15 and 19°C indicate a slow but considerable capacity to increase (0.0222 and 0.0278, respectively), reflecting a certain difficulty of this fly to develop at low temperatures. The other parameters calculated show similar decreases with temperature. It is notable that the highest net reproductive rate (R_0) was recorded at 25°C, reflecting essentially the better equilibrium between longevity and fecundity of females at this temperature. The lowest values were estimated at 15 and 19°C (4.50 and 4.13, respectively). Consistent with the pattern of longevity gross reproductive time, ΣM_x was highest at 15°C (121.9) and lowest at 32°C (61.1). The mean generation time (T), doubling time (D), and finite rate of increase (λ) were lowest at 32°C (18.2, 5.7, and 1.13, respectively). Conversely, at 15°C, the fly showed the worst performance. The slight augment of λ with increasing temperatures indicates, however, that, under most conditions, the populations are rather stable.

Discussion

Temperature is a key factor for the development, survival, and reproduction of poikilothermic organisms (Andrewartha and Birch, 1954, Sharpe and DeMichele 1977). This study is a complete report of the life cycle of *P. casei* at different temperatures. A partial study on the effects of temperature on larvae of *P. casei* was conducted by Belcari and Antonelli (1992), who recorded the development between 9 and 45°C. They reported 10–36°C as a useful range for embryonic development. The authors observed that the eggs developed in 1.2, 1, and 0.9 d at 25, 28, and 33°C, respectively, whereas this took a noticeably shorter time at 13 and 18°C (4.7 and 2.9 d, respectively). Our data agree also with Hegazi et al. (1978) (1.02 d at 28°C) and differ from those reported by Costa et al. (1986), who recorded 2 d at 27°C.

Data recorded by Belcari and Antonelli (1992) on developmental time of larvae appear partially different from our results, but comparisons are difficult to make because of the different temperatures used in their research, although the diet used was the same as us. They reported that larvae required 31.1 and 14.7 d at 13 and 18°C, respectively. More similar are the data at 28 and 33°C (13.2 and 8.7 d, respectively). Similar findings were reported by Sacchi et al. (1971) at 27–30°C. Hegazi et al. (1978) stated a decisive role of the quantity of proteins in the diet of the larvae in their developmental time. The authors, using fermented milk with different contents of proteins as the diet, assessed that, at 27°C, larvae completed the development in 8.4 and 14.3 d when fed on food containing 5.6 and 3.06% of proteins. Costa et al. (1986), rearing the larvae at 27°C with cured dried meat, found only 6 d required to complete the three larval stages. The decisive role of protein on development of detritivore flies is shown in several studies (Daniels et al. 1991, Tachibana and Hideharu 2001). The larvae fed on meat had markedly reduced developmental time with respect to other diets based on milk and yeast.

Although slightly higher, the percentage of mortality on pupae recorded by Belcari and Antonelli (1992) was similar to the results obtained in this study. On the contrary, the times recorded by Busvine (1980) and Smart (1935) at 25°C (8.3 d) were noticeably higher. Hegazi et al. (1978) at 27°C found 6.4 and 7.3 d, depending on the food offered.

The great plasticity of the species has been shown by other research, which reported that larvae can survive temperatures of 9–10°C for up to 6 months (Busvine 1980) and can survive for 30 d at 5°C (Sacchi et al. 1971). Other studies have shown that larvae could resist −4°C for >10 d (Hegazi et al. 1978) and −15°C for 2–3 d (Sacchi et al. 1971). In this study at 15°C, eggs were the stage more resistant. This finding does not agree with the findings of Belcari and Antonelli (1992), who recorded a lower survival of eggs at 13 and 18° and greater survival at 28 and 33°C. The same authors, in accordance with our results, reported a strong percentage of mortality observed on larvae at 13 and 18°C (87.5 and 50.4%, respectively), whereas the percentage of larvae that completed juvenile stages was higher at 28 and 33°C (19.7 and 12.9, respectively). Belcari and Antonelli (1992) asserted that the optimal thermic conditions for the development of preimaginal instars of *P. casei* is ~33–36°C, because under these conditions, the mortality remained below 10%. Our results show good performance of the fly at

temperature between 15 and 28°C, whereas the highest mortality rate occurred at 32°C. This pattern could reflect the holarctic origin of Piophilidae (McAlpine 1977).

Few data are available on longevity and survivorship of adults of *P. casei.* Hegazi et al. (1978) reported a very short lifespan at 27°C compared with our results. Depending on the protein contained in the food offered, females lived on average only 5.4 and 4.6 d and males lived 4.3 and 3.5 d. In this study, reduced longevity of both females and males at 32°C emphasizes the adverse effects of high temperatures on longevity and also on fecundity, considering that the best performance was observed at 25°C. At 15°C, even though females lived longer, they were less fecund. The fecundity curves indicate that the ovipositional peak was reached at the beginning of the reproductive cycle, confirming the hypothesis of Sharpe and DeMichele (1977), who associated this behavior with the increase in metabolic rate.

The biological data obtained in this study indicate that this species is well adapted to a wide range of thermic regimens, and this characteristic, together with its good reproductive potential at various conditions, can lead to a strong capacity to colonize different environments. When storage conditions are favorable to rapid development of flies, detection at an early stage can prevent serious levels of damage. Data obtained through laboratory conditions could be useful for predicting the biotic potential under specific field conditions. Moreover, further research on the role of quality of food on the developmental rate and fecundity of *P. casei* is needed.

The findings of this study could provide useful data for forensic entomology. For example, if a population reaches a stable age–stage distribution and the mortality factors are only the physiological ones, a *P. casei* population at 32°C can multiply 9.118 times in an average of 18.178 d, with an exponential rate of 0.236/d. In a case reported by Benecke (1998), the presence of *P. casei* in a decayed human body was informative to date the death. Nishida (1984) studied the growth rate of *Chrysomya megacephala* (F.) (Diptera: Calliphoridae) at different temperatures and found that the data can be used successfully to estimate the postmortem interval.

Because of the importance of *P. casei* as a food storage pest and in medical and forensic entomology, more attention should be addressed to the ecology of the fly.

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References Cited

Alessandrini, G. 1907. Sulla resistenza vitale delle larve di *Piophila casei* (L.). Boll. Soc. Zool. It. 8: 374–380.

Anderson, G. S. 1999. Wildlife forensic entomology: determining time of death in two killed black bears cubs. J. Forensic Sci. 44: 856–859.

Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago, IL.

Belcari, A., and R. Antonelli. 1992. Limiti termici ed optimum di sviluppo degli stadi preimmaginali di *Piophila casei* (L.), (Diptera Piophilidae), 107–117 pp. *In* Atti 5° Simposio sulla difesa antiparassitaria nelle industrie alimentari e la protezione degli alimenti, Piacenza, Italy. 23–25 September.

Benecke, M. 1998. Six forensic entomology cases: description and commentary. J. Forensic Sci. 43: 797–805.

Birch, L. 1948. The intrinsic rate of natural increase of an insect population. J. Anim. Ecol. 17: 15–26.

Busvine, J. R. 1980. Houseflies and blowflies. Insect and hygiene. The biology and control of insect pests of medical and domestic importance. Chapman & Hall, London.

Costa, P.R.P., R. Gurvitz, G. Muller, and P. B. Ribeiro. 1986. Ciclo vital de *Piophila casei* L. (Diptera: Piophilidae). Arch. Bras. Med. Vet. Zoo. 38: 191–196.

Daniels, S., K. Simkiss, and R. H. Smith. 1991. A simple larval diet for populations studies on the bowfly *Lucilia sericata* (Diptera: Calliphoridae). Med. Vet. Entomol. 5: 283–292.

De Jong, G. D., and J. W. Chadwick. 1999. Decomposition and arthropod succession on exposed rabbit carrion during summer at high altitude in Colorado, USA. J. Med. Entomol. 36: 833–845.

Domenichini, G. 1978. La contaminazione biotica nei formaggi pecorini in stagionatura. Scienza e tecnica lattierocasearia. 29: 182–193. *In* Giornata di studio su nuovi aspetti della produzione del formaggio fiore sardo. Sassari, Italy.

Domenichini, G. 1991. Ricerche entomatiche e microbiologiche. Agrobiotecnologie nei processi di valorizzazione dei prodotti e sottoprodotti agricoli. Consiglio Nazionale Ricerche, R.A.I.S.A., Volterra, Italy.

Early, M., and M. L. Goff. 1986. Arthropod succession patterns in exposed carrion on the island of O'ahu, Hawaiian Islands, USA. J. Med. Entomol. 23: 520–531.

el Serougi, A. O. 1991. A case of urinary myasis due to *Piophila casei.* J. Egypt. Soc. Parasit. 21: 595–596.

Gilbert, N., A. P. Gutierrez, B. D. Frazer, and R. E. Jones. 1976. Ecological relationship. Freeman Press, San Francisco, CA.

Greenberg, B. 1971. Flies and disease. Princeton University Press, Princeton, NJ.

Haines, C. P., and D. P. Rees. 1989. A field guide to the types of insects and mites infesting cured fish. FAO Fisheries, Rome, Italy.

Hegazi, E. M., F. H. el Gayar, I. A. Rawah, and S. A. Ali. 1978. Factors affecting the bionomics of *Piophila casei* (L.). Z. Angew. Entomol. 85: 327–335.

Hulting, F. L., D. B. Orr, and J. J. Obrycki. 1990. A computer program for calculation and statistical comparison of intrinsic rates of increase and associated life table parameters. Fla. Entomol. 73: 601–612.

Laughlin, R. 1965. Capacity for increase: a useful population statistic. J. Anim. Ecol. 34: 77–91.

Leclercq, M. 1946. Observation ècologiques sur les mouches de nos habitations. Rev. Franç. Entomol. 13: 76–79.

Liu, D., and B. Greenberg. 1989. Immature stages of some flies of forensic importance. Ann. Entomol. Soc Am. 82: 80–93.

McAlpine, J. F. 1977. A revised classification of the Piophilidae, including "Neottiophilidae" and "Thyreophoridae"

(Diptera: Schizophora). Mem. Entomol. Soc. Can. 103: 1–66.

Miokovic, B., J. Zivkovic, and L. Kozacinski. 1997. Autochthonous Croatian "rotten" cheese. Veterinarski Arkiv. 67: 25–32.

Nishida, K. 1984. Experimental studies on the estimation of postmortem intervals by means of fly larvae infesting human cadavers. Jap. J. Legal Med. 38: 24–41.

Ottogalli, G. 2001. Atlante dei formaggi. Hoeply, Milano, Italy.

Passos, M.R.L., N. A. Barreto, R. Q. Varella, G.H.S. Rodrigues, and D. A. Lewis. 2004. Penile myasis: a case report. Sex. Transmit. Infect. 80: 183–184.

Perez Inigo, C. 1971. Dipterous and Coleopterous pseudoparasites of the human intestine. Graellsia. 2. 7: 161–176.

Rabbinge, R. 1976. Biological control of fruit-tree red spider mite. Pudec, Wageningen, The Netherlands.

Rossi, E., and S. Presciuttini. 1996. Development of insecticide resistance in *Piophila casei* (Diptera: Piophilidae) strains selected with low doses of deltamethrin. J. Econ. Entomol. 89: 15–20.

Sacchi, L., A. Gigolo, and G. Cestari. 1971. Un metodo di allevamento di *Piophila casei* L. Riv. Parassit. 32: 289–301.

Saleh, M. S., and M. M. el Sibae. 1993. Urino-genital myasis due to *P. casei.* J. Egypt. Soc. Parasit. 23: 737–739.

Schoenly, K., M. L. Goff, J. D. Wells, and W. D. Lord. 1996. Quantifying statistical uncertainly in succession-based entomological estimates of the postmortem interval in death scene investigations: a simulation study. Am. Entomol. 42: 106–112.

Sharpe, P.J.H., and D. W. DeMichele. 1977. Reaction kinetics of poikilotherm development. J. Theor. Biol. 64: 649–670.

Simmons, P. 1927. The cheese skipper as a pest in cured meats. U.S. Department of Agriculture. Bull. 1453, Washington.

Southwood, T.R.E. 1978. Ecological methods. Chapman & Hall, London, UK.

Southwood, T.R.E., and P. A. Henderson. 2000. Ecological methods. 3rd ed. Blackwell Scientific, Malden, MA.

Smart, J. 1935. The effects of temperature and humidity on the cheese skipper, *P. casei.* J. Exp. Biol. 12: 384–389.

Smith, K.G.V. 1986. A manual of forensic entomology. Cornell University Press, Ithaca, NY.

StatSoft. 1996. STATISTICA for Windows. StatSoft, Tulsa, OK.

Tachibana, S., and N. Hideharu. 2001. An artificial diet for blow fly larvae, *Lucilia sericata* (Meigen) (Diptera: Calliphoridae). Appl. Entomol. Zool. 36: 521–523.

van der Louw, S. and T. C. van der Linde. 1993. Insects frequenting decomposing corpses in Central South Africa. Afr. Entomol. 1: 265–269.

Zumpt, F. 1965. Myasis in man and animals in the Old World. Butterworths, London, UK.

Zuska, J., and P. Lestovka. 1965. A review of the Czechoslovak species of the Piophilidae with special references to their importance to food industry (Diptera, Acaliptrata). Acta Entomol. Bohemoslov. 62: 141–157.

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