

THE COLONIZATION AND LIFE-CYCLES OF *MUSCA LUSORIA*, *MUSCA XANTHOMELAS* AND *MUSCA NEVILLI*, VECTORS OF *PARAFILARIA BOVICOLA* IN SOUTH AFRICA*

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ABSTRACT

NEVILL, E. M. & SUTHERLAND, B., 1987. The colonization and life-cycles of *Musca lusoria*, *Musca xanthomelas* and *Musca nevillei*, vectors of *Parafilaria bovicola*. *Onderstepoort Journal of Veterinary Research*, 54, 607-611 (1987).

Thriving, permanent colonies of *Musca xanthomelas* and later of *Musca nevillei* were successfully established. However, because of the low reproduction potential of *Musca lusoria* a small colony only was kept for a limited period until life-cycle studies were completed.

Larvae were reared on fresh dung from cattle fed lucerne, while in general adults were fed 0.3 % citrated ox-blood, whole milk powder, sugar crystals, fresh dung and water. *M. nevillei* could be colonized only when ox-liver was substituted for ox-blood.

A comparison of the life-cycles of *M. lusoria* and *M. xanthomelas* under laboratory conditions at a constant temperature of approximately 27 °C, 60 % R.H. and 24 h illumination revealed major differences between these 2 vector species. *M. lusoria* deposits single larvae at intervals of approximately 2 days and a female can produce up to 27 in her life-time. An *M. xanthomelas* female can lay up to 4 batches of eggs, with as many as 33 eggs per batch, at intervals of approximately 5 days. A single female can produce a maximum of 94 eggs.

M. lusoria, however, showed survival advantages over *M. xanthomelas* in that its larvae reached the pupal stage at least a day sooner and its adults survived more than twice as long.

The life-cycles of *M. xanthomelas* and *M. nevillei* were similar in the laboratory, except for adult dietary requirements. The mean number of mature oocytes in the ovaries of *M. nevillei*, however, was only 15.7 compared with 26.1 in *M. xanthomelas*.

INTRODUCTION

Nevill (1975; 1985b) found that 3 species of non-biting muscid flies are involved in the biological transmission of a filarial worm, *Parafilaria bovicola*, to cattle. He subsequently determined the life-cycle in the fly (Nevill, 1981) and the route of transmission to cattle (Nevill, 1979).

The 3 fly species concerned, *Musca lusoria*, *Musca xanthomelas* and *Musca nevillei*, all belong to the subgenus *Eumusca*. They are locally referred to as 'African face flies' because their feeding habits are similar to those of a close relative, the true 'face fly' *Musca autumnalis*, found in Europe and North America. Although *M. nevillei* is a relatively common fly, it was only in 1969 that Kleynhans, in an M. Sc. study, recognized it to be a separate species from *M. xanthomelas* with which it can be confused; and only in 1987 that it was formally described (Kleynhans, 1987). Prior to 1969, therefore, *M. nevillei* was possibly referred to as *M. xanthomelas*. After 1969, because it had not yet been formally described, it was referred to as *Musca* n. sp. (Nevill, 1975), *M. xanthomelas* s.l. (Nevill, 1979) and *Musca* sp. A. (Nevill, 1985b).

The establishment of laboratory colonies of 1 or more of these vector species was essential for the artificial infection of the large numbers of cattle needed for studies on the transmission (Nevill, 1979), life-cycle (Nevill, 1981; Viljoen, 1982; Viljoen & Coetzer, 1982) and chemotherapy of *P. bovicola* (Nevill, 1985a). The availability of colonies of *M. lusoria* and *M. xanthomelas* facilitated comparisons of the life-cycles of these species. After unsuccessful attempts by the 1st author to colonize *M. nevillei*, the 2nd author was successful. This allowed a comparison of colonization methods and life-cycles for these 3 face fly vectors of *P. bovicola*. Not only could this information be of value for an understanding of the epidemiology of *P. bovicola* but it could also possibly be used to elucidate the transmission

of parasites and pathogens found in the eye and nasal secretions on which these flies prefer to feed.

MATERIALS AND METHODS

Establishment and maintenance of laboratory colonies

The fly collections were made in the northern Transvaal on the farms 'Zoutpan' (25° 24' S 28° 06' E) and 'Kaalplaas' (25° 39' S 28° 11' E). Flies were collected with hand nets when they came to feed on citrated blood placed on the backs of cattle (Nevill, 1975; 1979).

In the laboratory about 300 adult flies were kept in wire frame cages 300 × 300 × 300 mm covered with mutton cloth. These cages were kept in a constant temperature room at 27-28 °C and approximately 60 % R.H., with continuous lighting provided by a pair of 1 220 mm long, white fluorescent tubes 250 mm above the cages.

The flies were fed on ox-blood plus 0.3 % tri-sodium citrate that had been soaked up in cotton wool plus a 1:1 mixture of whole milk powder and sugar crystals in separate Petri dishes. Fresh dung, from cattle fed on lucerne alone, was provided in a 500 ml cardboard container and water in a 500 ml cotton wool-filled beaker. It was only possible to colonize *M. nevillei* after ox-liver had been provided in place of ox-blood. The blood, liver and dung were replaced daily.

The flies oviposited or larviposited on the dung, which was then removed from the cages and added to additional cattle dung on sand. On completion of their development, fly larvae migrated out of the dung and pupated on and in the sand. When they were sifted from the sand the pupae were found to consist of a mixture of dark-brown and creamy-white specimens. The latter were recognisable as the pupae of *Musca* species belonging to the subgenus *Eumusca*, since these have calcified pupal cases (Ferrari, 1975; Gilby & McKellar, 1976). This colour difference facilitated the rapid separation of the vector fly pupae from the other specimens.

Apart from small irregular differences in size and segmentation between the pupae of *M. lusoria* and those of *M. xanthomelas* and *M. nevillei*, the 1st author found a consistent difference in the appearance of the eclosion line, which stretched as a transverse median band across the anterior ends of the pupae of these species. In

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M. xanthomelas and *M. nevillei* this line is the same colour as the remainder of the pupa, whereas in *M. lusoria* it is almost black and has a moustache-like appearance (Fig. 1). This character, which can be seen with the naked eye, made it possible to instantly separate *M. lusoria* from the other 2 species and had the additional advantage of obviating injuries which usually accompany the identification of living adult flies.

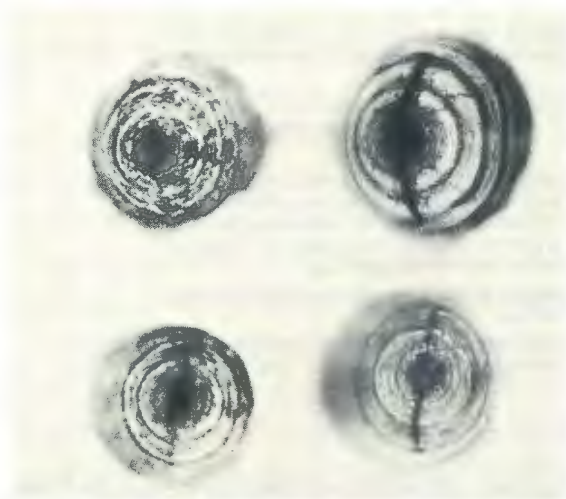


FIG. 2 The system used for culturing *Musca lusoria*, *Musca xanthomelas* and *Musca nevillei*. Larvae develop in cattle dung in the suspended wire basket and pupate in the sand on the floor of the asbestos container. The basket is lined around the sides with polythene to prevent lateral desiccation

Because *M. lusoria* deposits only 1 larva at a time it reproduces slowly and large numbers of wild-caught flies (1 000–2 000) were therefore needed over a period of 5 days to get the colony started. Occasional boosts with additional wild-caught flies were sometimes necessary even after the colony had been established.

The breeding technique was modified as experience was gained with the colonies. Larvae were reared in fresh cattle dung contained in wire baskets 150 × 150 × 150 mm with apertures of 23 × 10 mm and lined on the inside with a polythene sleeve. The linings prevented lateral desiccation and ensured maximum use of the available dung. Each basket was half-filled with fresh dung. To this was added dung containing the daily yield of eggs from the oviposition containers, the amount of



FIG. 1 A view of the anterior extremities of the calcified pupae of *Musca xanthomelas* (left) and *Musca lusoria* (right). The 2 species can be readily separated by using the colour of the transverse eclosion lines as a criterion

dung depending on the number of egg-masts which could be seen protruding from the surface. Further dung was added and packed carefully around the 'egg-dung' until the basket was filled, taking care not to smother the eggs by covering them with dung. The baskets were suspended on transverse rods which rested on the sides of sand containers (Fig. 2). To pupate, larvae emerged from the bottom or top of the basket and dropped on to the sand, which remained dry because the basket did not touch it. The pupae could easily be sifted out and the sand then re-used. The polythene liners simplified cleaning of the baskets. Pupae were placed in a cardboard cup in a clean cage into which the adults emerged to start a new generation.

Laboratory studies on the life-cycles of *M. lusoria* and *M. xanthomelas*

Studies on individual females

Newly eclosed females of both *M. lusoria* and *M. xanthomelas* were kept singly in 250 ml cardboard cups and provided with fresh blood, dung and sugar-water. Usually 2 males were included with each female, but even so mating did not always take place. In later tests, therefore, newly eclosed flies were kept in a cage until the 1st eggs or larvae were produced, when the female flies were transferred to individual cups. It was hoped that by this time they would have mated and would not need to mate again.

Using the criteria adopted by Sutherland (1978), longevity was expressed either as the mean time in days until 50% of flies died (MT_{50}) or the mean time for 100% of the flies to die (MT_{100}).

Studies on groups of flies

The following 3 approaches were followed to collect data on the life-cycles of *M. lusoria* and *M. xanthomelas*

- (i) Laboratory-reared adult flies which had eclosed within a single 24 h period were kept together in cages 300 × 240 × 200 mm covered with plastic mosquito gauze, and details of their life-cycles were recorded. When fewer than 30 flies were available, these were kept in similar, but smaller, cages measuring 250 × 150 × 150 mm.
- (ii) Cups of fresh dung on which eggs or larvae had been deposited during the preceding 3 h were removed from the cages. The approximate periods taken for development to the different larval stages and to the pupal stage were then determined by daily examination of the developing larvae.
- (iii) More detailed studies on larval developmental periods were conducted separately by making fresh dung in glass vials available to flies for 15 min. Thereafter larvae were removed at approximately 2-h intervals to determine the stage of development reached.

The number of mature oocytes in *M. xanthomelas* and *M. nevillei* as determined by dissection

At 'Zoutpan' *M. xanthomelas* was present in small numbers throughout the year while *M. nevillei*, which was usually rare, suddenly appeared in large numbers from February–April each year (Nevill, 1985b). A comparison of the total numbers of mature oocytes present in field-collected females of the 2 species and in laboratory-reared *M. xanthomelas* was made in the hope that this could help explain the field observations and the difficulties encountered in early unsuccessful attempts to colonize *M. nevillei*. For this purpose flies of both species were collected in the usual manner off cattle at 'Kaalplaas' and kept at 27 °C for 7 days to allow oocyte development to take place. They were subsequently dissected and the mature oocytes counted.

TABLE 1 Summary of results of various laboratory studies on the life-cycles of 3 face fly species (27 °C, 60 % R.H. and 24 h illumination)

Developmental period or activity	<i>M. lusoria</i>	<i>M. xanthomelas</i>	<i>M. nevillei</i>
Mating starts	Day 5	Day 4	—
Reproduction	Day 6–68	Day 5–36, 41	Day 9–?
Mean No. oocytes/♀	4	26,1	15,7
Max. No. eggs or larvae/batch	1 larva	33 eggs	—
Max. No. egg batches/♀	—	4	—
Max. No. eggs or larvae/♀	27	94	—
Period between larvae or egg batches	> 46 h	± 5 days	—
Incubation period	—	1–2 days (> 18 h)	1 day
Oviposition—			
2nd stage	1 day (> 2 h)	2 days	—
3rd stage	1–2 days (> 16 h)	2–5 days	—
prepupa	2–3 days (> 47 h)	4–5 days	4–5 days
pupation	3–4 days (> 67 h)	4–7 days	5–6 days
Pupation—adult eclosion	6–9 days	4–8 days	8 days
Oviposition—adult eclosion	10–13 days	11–16 days	14–15 days
MT ₅₀ ♀	56 days	17,6 days	18–20 days
MT ₅₀ ♂	48 days	19,0 days	—
MT ₁₀₀ ♀	74,5 days	35,1 days	—
MT ₁₀₀ ♂	77,0 days	40,3 days	—

Laboratory observations on the life-cycle of *M. nevillei*

After the colonies of *M. lusoria* and *M. xanthomelas* had been discontinued, the 2nd author succeeded in colonizing *M. nevillei*. His success appeared to be due to the replacement of fresh ox-blood with sliced ox-liver and the continued provision of whole milk powder, the use of which had been discontinued after the colony of *M. xanthomelas* had been established.

The life-cycle observations recorded for *M. nevillei* were therefore not part of a comparative study but were made during the establishment of a colony of this species.

RESULTS

A summary of the life-cycles of the 3 *Musca* spp. is given in Table 1.

M. lusoria life-cycle

After 85 days the following conclusions could be drawn from a test in which 20 female flies were taken from the main cage on the 9th day after eclosion and placed singly in cups:

- up to 27 larvae were produced by 1 female;
- the minimum interval between larval depositions was 46 h, and
- some females produced unfertilized eggs only, others unfertilized eggs and larvae and others larvae only. The totals for the 20 females were 151 eggs plus 155 larvae, i.e. a mean of 15,3 eggs plus larvae per female.

In the cages, mating was first seen 5 days after eclosion. Larvae were deposited from Day 6 to Day 68, and larviposition continued almost to the death of the female. Larvae were deposited late in the 1st stage when the 2nd stage spiracles could be seen clearly below those of the 1st stage. In 'cage' and 'cups of dung' studies the 2nd stage was reached in 1 day, the 3rd stage in 22 h–2 days, the prepupa in 2–3 days and the pupal stage in 3–4 days after larviposition. Another 6–9 days were needed before the adult fly emerged from the pupa, making a total of 10–13 days from larviposition to eclosion.

The results of the more detailed studies on the larval development of *M. lusoria* in glass vials are summarized in Fig. 3.

Larvae reached the 2nd stage in just over 2 h; the 3rd stage in 16 h; the prepupal stage in 47 h, and the pupal stage in 67 h. These minimum developmental periods for each stage are shorter than those recorded in the less accurate 'cage' and 'cups of dung' studies.

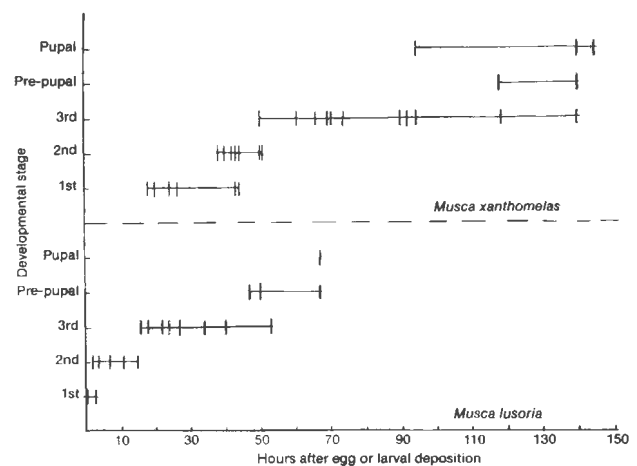


FIG. 3 Developmental periods of the immature stages of *Musca lusoria* and *Musca xanthomelas* raised in cattle dung in glass vials and inspected at approximately 2-h intervals (27 °C, 60 % R.H.)

The mean MT₅₀ for 66 *M. lusoria* females was 56,0 days and for 66 males 48,0 days. The mean MT₁₀₀ for females was 74,5 days and 77,0 days for males.

M. xanthomelas life-cycle

Some of the 72 females involved in the 'cup cage' tests produced up to 4 egg batches each, at intervals ranging from 3–21 days, the most frequent interval being 5 days. The maximum number of eggs per batch was 33 and the maximum per female 94. Oviposition began on the 5th day after eclosion and continued up to 41 days, the last large egg batch being laid on Day 24.

The results of 9 separate studies on large groups of caged flies are summarized below.

Flies mated for the 1st time 4 days after eclosion and continued to mate at intervals until 29 days after eclosion. Oviposition started on the 5th day after eclosion and active egg-laying continued for the next 7–16 days, then tapered off. The last eggs were laid on the 36th day after eclosion.

Eggs hatched after 1–2 days, larvae were in the 2nd stage after 2 days, in the 3rd stage after 2–5 days, in the prepupal stage after 4–5 days and pupated 4–7 days after oviposition.

More detailed studies on the development of eggs laid over 15 min periods in dung in glass vials generally confirmed the above developmental times but permitted

these to be determined to the nearest hour. These results, and those for *M. lusoria*, are graphically illustrated in Fig. 3. From the results of all the preceding studies it was concluded that the 1st eggs hatched after 18 h, the pupal stage lasted 4–8 days and the entire period from egg to adult fly for *M. xanthomelas* ranged from 11–16 days.

Eclosion usually occurred between approximately 04h00 and 10h00. Of the 978 flies that emerged from 1 batch of pupae 51,6 % were females.

Immediately after eclosion some flies fed on sugar but not on blood. Within 24 h, however, half the flies had blood in their abdomens and after 4 days this number had increased to 90 %.

In the 'cup cage' tests and in 7 'cage' tests involving a total of 1 269 female and 1 531 male flies, the daily mortality was recorded and used to calculate MT_{50} and MT_{100} values. The mean MT_{50} for females was 17,6 days and for males 19,0 days. The mean MT_{100} for females was 35,1 days and for males 40,3 days.

The mortality rate between oviposition and eclosion was calculated for 5 batches of 100 eggs each. Only 43,6 % of the eggs eventually gave rise to adults. To exclude the possibility that egg mortality was caused by handling, a recalculation was made using the number of eggs hatched as the initial number. This showed that 67,1 % of these eggs yielded adult flies. In a larger test involving 5 900 pupae, a 68,4 % eclosion rate was obtained.

M. nevillei life-cycle

The preoviposition period was approximately 9 days. Eggs hatched within 24 h while the larvae became fully-fed within 4–5 days. The prepupal stage lasted 24 h before creamy-white pupae were formed. Within 1 or 2 days these pupae became grey-white. The pupal period extended over approximately 8 days. The period from oviposition to adult eclosion varied from 14–15 days. The MT_{50} for adults was between 18 and 20 days.

The number of mature oocytes in *M. xanthomelas* and *M. nevillei* as determined by dissection

The results of the dissections are summarized in Table 2.

TABLE 2 The number of mature oocytes present in field-collected *Musca xanthomelas*, *Musca nevillei* and laboratory-reared *Musca xanthomelas* (27 °C, 60 % R.H. and 24 h illumination)

	Laboratory-reared	Field-collected	
	<i>M. xanthomelas</i>	<i>M. xanthomelas</i>	<i>M. nevillei</i>
No. of ♀♀ dissected	20	21	67
No. of mature oocytes/ovary			
— minimum	8	5	3
— maximum	22	18	15
No. of mature oocytes/♀			
— minimum	17	12	6
— maximum	44	36	28
— mean	27,7	26,1	15,7

The mean number of mature oocytes in the ovaries of field-collected *M. nevillei* was only 15,7 per female. By comparison field-collected *M. xanthomelas* had 1,7 times more oocytes per female (26,1), a number similar to laboratory-reared flies of the same species (27,7).

Limited counts of oocytes showed a slightly higher mean of 30,4 for *M. xanthomelas*. This was still 1,7 times more than in *M. nevillei*, which had 18,4.

DISCUSSION

Previously the only studies on the biology of *M. lusoria* and *M. xanthomelas* were field observations by Cuthbertson (1932, 1933, 1938) in Zimbabwe, plus notes on feeding habits by Patton (1936) and Zielke (1971). Cuthbertson (1932, 1933) noted that the females of both these flies have similar feeding habits, in that they feed on cattle on blood and serous exudates from lesions and screw-worm wounds, as well as the bites of blood-sucking flies such as Tabanidae, *Stomoxys*, *Lyperosia* and *Musca crassirostris*. They often jostle the blood-sucking flies away from their feeding places so that they can feed on the 'bites' of the displaced flies, an activity that was seen frequently by the 1st author during the course of the present study. In addition this author has noticed that these flies are most abundant around the eyes and muzzles of cattle (Nevill, 1975).

Cuthbertson (1932, 1933) stated that the males of both species feed on the nectar of flowers, sweet exudations of paspalum grasses infected with ergot, and on honeydew secreted by aphids and coccids. Very few males were collected near blood on cattle in the veld (Nevill, 1985b), so they may spend most of their time on vegetation, but no attempt was made to confirm this.

Fresh cattle dung and occasionally human faeces were recorded by Cuthbertson (1932) as preferred breeding material for both fly species. Cuthbertson (1933) observed that *M. lusoria* is viviparous, extruding approximately 12 late 1st stage larvae during its lifetime and breeding throughout the year. Larvae reach the 3rd stage by the 3rd day and pupate in soil beneath the dung. He found that *M. xanthomelas* lays stalked or petiolate eggs which hatch 12–18 h later, develop to mature larvae in 3–4 days, and then pupate in soil immediately adjacent to the dung in which they have developed.

In the present laboratory studies the superior reproductive potential of *M. xanthomelas* was particularly apparent, and large numbers could be reared quickly and easily, but large numbers of adult *M. lusoria* would have been required initially to produce a flourishing colony of this fly.

However, *M. lusoria* did have several factors in its favour. These included rapid development to the pupal stage (67 h compared with 4 or more days for *M. xanthomelas*) and long-lived females (MT_{50} 56,0 days) that were able to reproduce for approximately 68 days. In contrast 50 % of *M. xanthomelas* females lived for about 17,6 days and laid most of their eggs between the 5th and 21st days after eclosion. These factors would be of considerable value to *M. lusoria* under natural conditions, because frequent larval depositions and rapid development would allow its larvae to reach the 3rd stage before the eggs of *M. xanthomelas* had even hatched, and small dung pats could be vacated before they dried out. However, perhaps the greatest advantage that *M. lusoria* has over other competing flies is that it is larviparous and hence can avoid such hazards as predation, desiccation etc., which face the eggs of other flies.

The 3rd *P. bovicola* vector species, *M. nevillei*, was found on dissection to contain noticeably fewer mature oocytes than *M. xanthomelas*. Furthermore laboratory attempts to colonize this species revealed that for normal reproduction to take place the adults required ox-liver and whole powdered milk as protein sources, whereas citrated ox-blood sufficed for *M. xanthomelas*. When fed on the *M. xanthomelas* diet alone *M. nevillei* females refused to oviposit in cattle dung but laid eggs on the citrated blood pad or simply dropped their eggs anywhere in the cage.

The possible lower reproduction potential of *M. nevillei* coupled with its more demanding adult nutritional requirements may provide part of the explanation why this fly species is comparatively rare during 9 months of the year and is only common in the latter part of summer (Nevill, 1985b).

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