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THE EPIDEMIOLOGY OF *PARAFILARIA BOVICOLA* IN THE TRANSVAAL BUSHVELD OF SOUTH AFRICA*

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ABSTRACT

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A total of 20 375 flies collected off cattle on 12 farms over 36 months were identified and examined for 3rd stage *P. bovicola*. The 3 vector species accounted for 64,1 % of the flies collected and were the only fly species found to be infected. *Musca lusoria* was clearly the dominant vector fly, although large numbers of *Musca* sp. A appeared regularly between February and April each year. This phenomenon, coupled with high numbers of *M. lusoria* throughout most of the year, led to an increase in the numbers of vector flies from their lowest level in June to a peak in February–April.

Of the 13 070 vector flies examined for 3rd stage larvae only 64 (0,52 %) were positive; of these 41 were *M. lusoria* and 17 *Musca* sp. A. No positive male flies were found. Incubation of wild-caught flies for up to 13 days at 27 °C noticeably increased the larval recovery rate. Flies were found to be infected mainly from August–March. Infected *M. lusoria* were recorded from July–March and infected *Musca* sp. A from January–May. Only 6 infected *M. xanthomelas* were collected and this was during the period August–December, when most ovipositional blood spots occur on cattle.

It is concluded that *P. bovicola* transmission in the Bushveld is not correlated with peak periods of bleeding but rather with high numbers of vector flies, the various species augmenting each other so that transmission may take place almost throughout the year.

INTRODUCTION

In November 1972, at Mara Research Station in the Northern Transvaal, the vectors of *Parafilaria bovicola* were determined for the first time in South Africa (Nevill, 1975; 1980). They were found to be 3 species of muscid flies belonging to the subgenus *Eumusca*, namely *Musca lusoria*, *Musca xanthomelas* and a new *Musca* species first recognized by Kleynhans (1969). The latter is designated *Musca* sp. A in the present paper, as its description has not yet been published.

To determine the main period(s) of transmission and whether the same vector flies were involved in other parts of the Bushveld, these studies were extended to 12 widely separated farms for varying periods up to 47 months.

In these studies an attempt was made to:

1. record the relative abundance of the various muscid flies on cattle on different farms and different times of the year,
2. determine the period(s) when the various vector species were infected with 3rd stage *P. bovicola* larvae, and
3. correlate the findings of 1 and 2 with the availability of *P. bovicola* eggs as determined in a simultaneous study on the prevalence of *P. bovicola* ovipositional blood spots on cattle (Nevill, 1980; 1984).

MATERIALS AND METHODS

From July 1973 to May 1977 farms in different parts of the enzootic area of the Transvaal (=Bushveld) were visited on 1 or more occasions to collect and examine flies for 3rd stage larvae of *P. bovicola*. The method described by Nevill (1975, 1980) was followed.

Initially 12 farms were visited, but this number was soon reduced to 5, which were visited at varying intervals ranging from fortnightly for 47 months to 2-monthly for 1 year. The coordinates of these farms were given by Nevill (1975), and all the farm names and number of visits appear in Table 1. Because of its proximity to Onderstepoort (33 km), Zoutpan Research Station was visited fortnightly for a period of 47 months and more regular fly collections could be made there.

To provide an indication of fly abundance the collections were placed in the following categories:

Category 0—no flies on cattle.

Category 1—1–100 flies could be collected during a 2-hour period.

Category 2—101–200 flies could be collected during a 2-hour period.

Category 3—more than 200 flies could easily be collected within the 1st hour; collection was stopped when enough flies were available for dissection (usually 100–200).

For the purpose of comparing collections made in different months, the monthly vector and total catch means were calculated. To make all the catches directly comparable, the number of flies in collections which fell into Category 3 were doubled; this gave an approximation of what the catch might have been had collection not been stopped early. These means were used to calculate mean monthly collections for the 47-month period of the study (Fig. 1).

RESULTS

The total number of flies collected, identified and examined for 3rd stage *P. bovicola* larvae between July 1973 and June 1976 appear in Table 1.

Fly abundance on various Bushveld farms

A wide variety of muscid flies was collected, most species being recorded at localities where the greatest number of collections were made. Ten *Musca* spp. were identified with comparative certainty. The commonest *Musca* sp. collected was *Musca lusoria* (44,9 %), followed by *Musca domestica* (18,5 %), *Musca* sp. A (10,1 %), *Musca xanthomelas* (9,1 %), *Musca fasciata* (7,2 %), *Musca sorbens* (7,0 %) and *Musca crassirostris* (1,0 %).

Morellia hortensia, a fly with similar feeding habits to *M. crassirostris*, since it also has a rosette of prestomal teeth, was relatively common at 'Mooiplaats'. *Stomoxys calcitrans* was collected in small numbers only. The *Haematobia* and *Haematobosca* spp. were also scarce. These genera and the remaining 4 *Musca* spp. each accounted for less than 1 % of the collections. The 3 vector species together accounted for 64,1 % of the collection of 20 375 flies.

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TABLE 1 Summary of flies collected off cattle and examined for 3rd stage larvae of *Parafilaria bovicola* on various farms in enzootic areas of the Transvaal—July 1973 to June 1976

Farm	No. of visits	No. of flies collected																
		M. lusoria	*M. xanthomelas*	*Musca* sp. A	Vector total	% vectors of total collection	*M. domestica*	*M. fasciata*	*M. sorbens*	*M. crassirostris*	*M. lasiopthalma*	*M. conducens*	*M. freedmani*	Other* *Musca* spp.	*Morellia hortensia*	*Stomoxys calcitrans*	*Haematobia & Haematobosca* spp.	Totals
Zoutpan	83	4 763	670	1 127	6 560	76,9	1 176	449	224	44	31	3	5	6	11	20	4	8 533
Mara	13	2 303	345	651	3 299	70,5	706	359	223	48	3	9	1		21	10	1	4 680
Doornpan	6	525	413	112	1 050	36,8	966	71	635	11	3	18				30	73	2 857
Leamington	6	331	244	94	669	51,1	157	280	130	41	2			1		27	3	1 310
Mooiplaats	6	492	19	2	513	52,3	160	185	26		2			10	49	34	1	980
Kaalplaas	8	143	21	72	236	40,1	190	100	14	3	19	1			3	22		588
Varsvlei	2	88	22**		110	29,2	135		131							1		377
Syferfontein	2	172	37**		209	50,2	143	14	19	31								416
Kalkfontein	1	115	28**		143	91,1	2	9	3									157
Mooigenoeg	1	213	51**		264	87,4	16	1	19	2								302
Lodwichslust	1	6	3**		9	9,9	82											91
Nico's Kamp	1	3	5**		8	9,5	42	1		31						2		84
Totals	130	9 154	1 858	2 058	13 070	64,1	3 775	1 469	1 424	210	60	31	6	17	84	146	82	20 375
Species %		44,9	9,1	10,1	64,1		18,5	7,2	7,0	1,0	0,3	0,2	0,1	0,1	0,4	0,7	0,4	100,0
Male flies		791	239	154	1 184		462	134	221	48	17	1	1	2	5	41	67	2 183
% male flies		8,6	12,9	7,5	9,1		12,2	9,1	15,5	22,7	28,3	3,2	16,7	11,8	6,0	28,1	81,7	10,7

* Other *Musca* spp. include 1 *Musca gabonensis*, 1 *Musca lindneri*, and unidentifiable *Musca* specimens

** *Musca* sp. A was not differentiated from *M. xanthomelas* in these collections

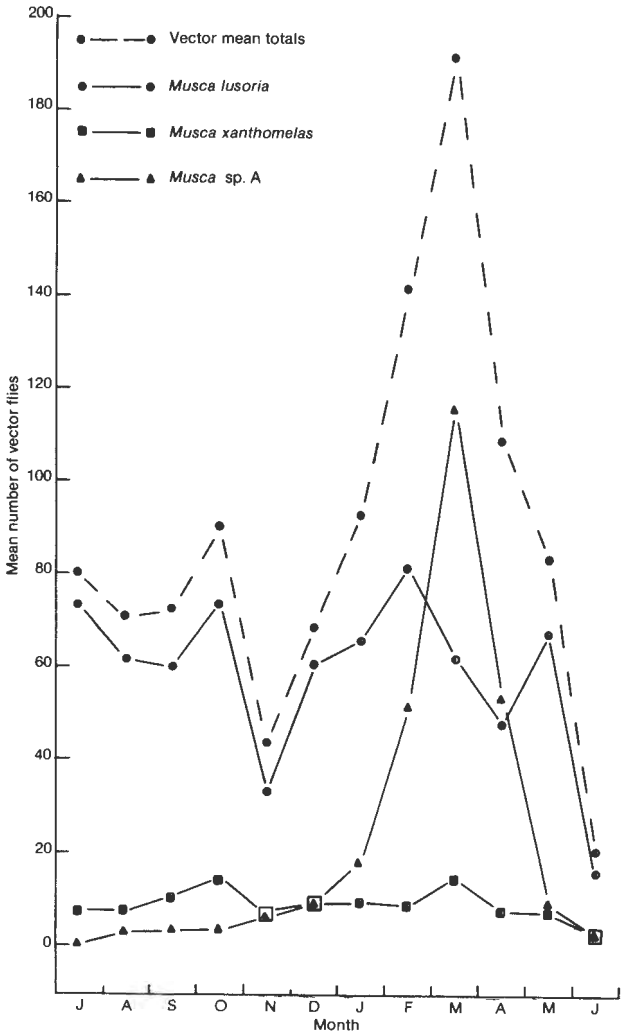

FIG. 1 Mean monthly collections of the 3 *Musca* vectors of *Parafilaria bovicola* off cattle at Zoutpan Research Station over a 47-month period, 1973–1977

There were large differences in the relative abundance of vector flies collected on the farms that were visited 6 or more times. On 'Doornpan', only 36,8 % of the flies were vector flies, with *M. domestica, M. sorbens* and *M. fasciata* accounting for 58,5 % of the flies collected. At 'Kaalplaas', with only 40,1 % vector flies, 49,3 % of the flies were *M. domestica* and *M. fasciata*. At 'Leamington' and 'Mooiplaats', vector flies were more plentiful: they accounted for just over 50 % of the flies collected, despite the fact that at 'Mooiplaats' the *M. xanthomelas* group made up only 2,1 % of the collection. On these 2 farms the 3 non-vector *Musca* spp. mentioned above made up 43,3 % and 37,9 % of the totals respectively.

At 'Mara' and 'Zoutpan', vector flies comprised 70,5 % and 76,9 % of the fly collections respectively, the other 3 *Musca* spp. mentioned in the previous paragraph being responsible for most of the remaining portion of the catches.

A mean of 9,1 % of the vector flies were males (*M. lusoria* 8,6 %, *M. xanthomelas* 12,9 % and *Musca* sp. A 7,5 %). The relatively high percentage of male *M. crassirostris* (22,7 %) and *S. calcitrans* (28,1 %) could be due to the fact that both sexes of these flies feed on blood. *Musca lasiopthalma,* however, is not an obligatory blood-feeder, so the relatively high (28,3 %) male incidence cannot be explained on this basis. Most of the *Haematobia* spp. were collected when they were attracted to man in the veld on one occasion at 'Doornpan', so the 81,7 % of males is not comparable with the other collections made off cattle in a crush. Males of the remaining fly species constituted between 3,2 % and 16,7 % of these flies' numbers.

Relative seasonal abundance of flies on various Bushveld farms

The percentage of vector flies collected monthly ranged from 33,7 % in November to 81,6 % in April, dropping below 60 % during only 3 months of the year, namely, June, September and November, when 1 or more of the species *M. domestica, M. fasciata* or *M. sorbens* increased sporadically on 1 or more farms. A detailed study of the relative abundance of each of the vector fly species at 'Zoutpan' over a 47-month period is given below.

Some of the non-vector fly species were abundant during certain seasons only. Thus during spring and early summer, *M. domestica, M. sorbens* and *M. crassirostris* were common; *M. lasiopthalma* and *M. freedmani* appeared in winter and spring, and in summer *S. calcitrans* and *Haematobia* spp. were more abundant. *M. fasciata* was present throughout the year.

Relative seasonal abundance of P. bovicola *vectors at 'Zoutpan'*

Of the 9 965 flies collected over the 47-month period, 53,9 % were *M. lusoria,* 7,3 % *M. xanthomelas* and 14,0 % *Musca* sp. A, to give an overall vector fly proportion of 75,2 %. Fig. 1 has been prepared so that the

TABLE 2 Incidence of flies infected with 3rd stage larvae of *Parafilaria bovicola* on various Bushveld farms from July 1973–June 1976

Farm	No. of visits	No. of infected flies collected				% flies infected
		M. lusoria	*M. xanthomelas*	*Musca* sp. A	Total	
Zoutpan	83	23	2	15	40	0,61
Mara	13	9	1	1	11	0,33
Doornpan	6	2	1	1	4	0,38
Leamington	6	3			3	0,45
Mooiplaats	6	4	1		5	0,97
Kaalplaas	8					
Varsvlei	2					
Syferfontein	2		1		1	0,48
Kalkfontein	1					
Mooigenoeg	1					
Lodwichslust	1					
Nico's Kamp	1					
Totals	130	41	6	17	64	
% infected		0,45	0,32	0,83	0,49	0,52*

* Mean incidence of infection in vector flies on farms on which infected flies were found

mean monthly number of each vector species collected and the overall vector mean for the 47-month period may be compared.

Although there were some differences in vector collections in the same months of different years, the mean monthly collections for nearly 4 years (Fig. 1) show that vector fly numbers were at their lowest in June, were more abundant but variable during the period July–January, reached a peak in the months of February, March and April, and fell thereafter. The most abundant vector species was *M. lusoria*, with mean collections between 60 and 82 flies for all but 3 months; the lowest number (16,0) was recovered in June. *M. xanthomelas* had a consistently low mean, ranging from 2,3 to 14,5 flies per month. The only vector species that showed a definite seasonal trend was *Musca* sp. A, which, in all the 4 years, was present in low numbers from May–January, but showed a sudden peak of abundance in the months February–April, with numbers varying between 51 and 116 flies. It was this sudden increase, combined with the consistently high numbers of *M. lusoria*, which led to these being the peak months for overall vector abundance.

Non-vector flies outnumbered vector flies in only 7 of the 47 months, these being April, July, September and October 1974, and June, October and November 1976.

The incidence of 3rd stage larvae of P. bovicola *in 3* Musca *vectors on various Bushveld farms*

A summary of the infected flies recovered on various farms appears in Table 2.

The incidence of infection was lowest in *M. xanthomelas* (0,32 %) and highest in *Musca* sp. A (0,83 %), with *M. lusoria* occupying an intermediate position (0,45 %). However, since only 64 flies out of a total of 13 070 potential vectors were found to be infected, too much emphasis should not be put on the percentages infected but rather on the absolute number of flies of each species found to be infected. Thus it would appear that *M. lusoria* plays a major role in transmission, since 41 of the 64 infected flies belonged to this species. Although comparable numbers of each of the remaining 2 vector species were examined for infective larvae, considerably more *Musca* sp. A (17) than *M. xanthomelas* (6) were found to be infected (Table 2).

Third stage larvae of *P. bovicola* were recovered from small numbers of all 3 vector flies at 'Zoutpan', 'Mara' and 'Doornpan'; from *M. lusoria* and *M. xanthomelas* at "Mooiplaats'; from *M. lusoria* at 'Leamington'; from *M. xanthomelas* at 'Syferfontein', but not from vector flies on the remaining 5 farms that were visited only once or twice, nor from flies on 'Kaalplaas'.

The incidence of infection in vector flies on the 6 farms on which infected flies were found varied from 0,33 % at 'Mara' to 0,97 % at 'Mooiplaats' with a mean of 0,52 % (Table 2).

The monthly incidence of infected vector flies on various Bushveld farms

The percentage of infected flies in any 1 month ranged from 0–3,50. The latter high recovery rate was obtained in March 1976 when 'Zoutpan' flies were incubated for 4–13 days at 27 °C before dissection for 3rd stage larvae. The usual procedure, however, was to dissect flies on the day that they were collected when the maximum percentage of infected flies recorded by this method was only 1,43.

Infected flies were found in 20 of the 36 months of the study period. The months in which no infected flies were obtained were July 1973; April–September and November 1974; April, June, September, October and December 1975; January, May and June 1976. The mean monthly cumulative number of flies of each species found infected during the 3 years of the study appear in Table 3.

The data in Table 3 and Fig. 2 show that infected flies were never recovered in June and only once in each of the months April, May, July and September. The main period during which flies were found to be infected was from August–March.

There was a difference, however, in the times at which the various vector species were found to be infected. Infected *M. lusoria* were recovered from July–March, while, except for 1 fly in October, infected *Musca* sp. A were found only from January–May. The few infected *M. xanthomelas* recorded were collected from August–December (Table 3).

DISCUSSION

Vector fly studies

The foregoing study has shown that the 3 vector fly species incriminated at Mara Research Station do in fact occur throughout the Bushveld and that they accounted for between 36,8 % and 76,9 % of all flies collected on the 5 farms that were visited 6 or more times. Although *M. lusoria* was clearly the dominant vector species on all these farms, it was strongly challenged by *M. xanthomelas* on 2 of the farms. On 1 farm, however, *M. lusoria* was almost the only vector fly present.

Taking into account local conditions or geographical location, one must expect a change in the dominant vector species. This was borne out by a fly survey in the N.W. Cape where *M. xanthomelas* consistently dominated the scene (Nevill, unpublished data, 1977).

TABLE 3 Mean monthly cumulative total number of flies infected with 3rd stage larvae of *Parafilaria bovicola* on various Bushveld farms from July 1973–June 1976

Month	No. of infected flies collected				Frequency of months when infected flies were recovered
	M. lusoria	*M. xanthomelas*	*Musca* sp. A	Totals	
July	1			1	1
August	3	1		4	2
September	6	3		9	1
October	4		1	5	2
November	3	1		4	2
December	7	1		8	2
January	5		1	6	2
February	7		4	11	3
March	5		5	10	3
April			4	4	1
May			2	2	1
June				0	0
Totals	41	6	17	64	20

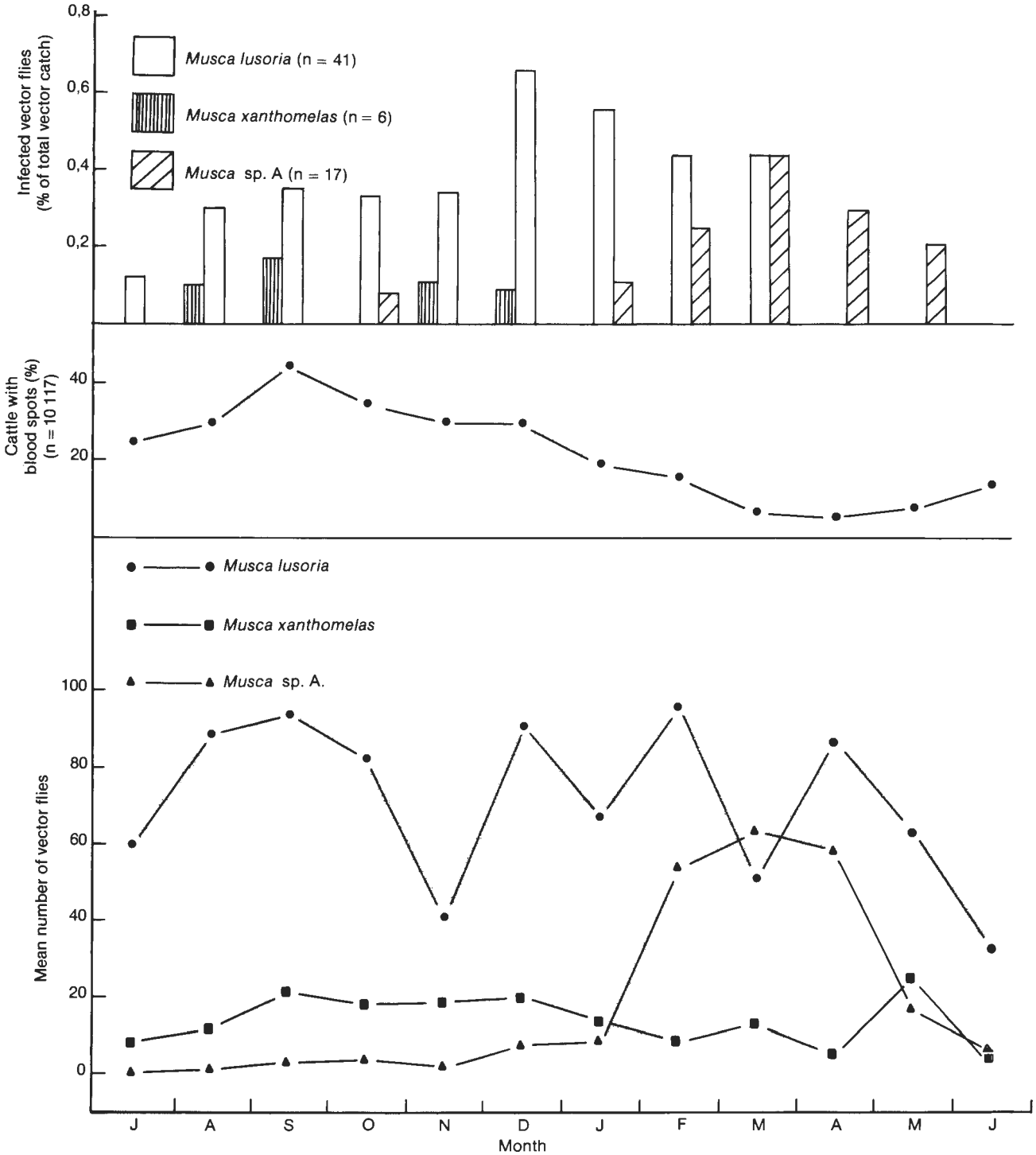

FIG. 2 Summary of nearly 4 years of field work to compare the incidence of vector flies infected with 3rd stage larvae of *Parafilaria bovicola* with the availability of infective blood spots and the abundance of the 3 vector species during any 1 month of the year. The flies were collected on Bushveld farms over 3 years while the cattle were examined at Zoutpan Research Station over 47 months, 1973–1977

A noticeable, seasonal pattern could be discerned. Again vector flies more or less dominated the collections from the 5 farms. However, it was clear that *M. lusoria* was the major vector species from winter to summer, with *M. xanthomelas* and *Musca* sp. A occurring at the same time but in much smaller numbers (Fig. 2). What was both unexpected and biologically interesting was a regular annual rapid increase in the numbers of *Musca* sp. A from February–April. At this time of the year they sometimes outnumbered *M. lusoria* (Fig. 2).

The combination of high numbers of both *M. lusoria* and *Musca* sp. A between February and April resulted in a vector peak during this period (Fig. 1), vector species constituting more than 76 % of all the flies collected at this time.

A variety of reasons probably account for the different seasonal abundance patterns of the 3 vector flies. To elucidate these would require detailed field and laboratory studies similar to those made in the United States of America on a close relative, the face fly *Musca (Eumusca) autumnalis* (Ode & Matthysse, 1967; Stoffolano & Matthysse, 1967). Such studies were beyond the scope of the present investigation, although some points made during the present study are worth noting.

M. lusoria is larviparous while the other 2 vector flies are oviparous. *M. lusoria* therefore has an immediate advantage in that the egg stage is not exposed to danger. In addition, its period of larval development is rapid, allowing it to utilize fresh dung before other dung-breeding flies, and possibly to utilize smaller quantities of dung which would normally dry out before other flies have completed their development. *M. lusoria* adults also live considerably longer than the other vector flies (Nevill, 1980).

Despite these advantages, *M. lusoria* is not always abundant and is at its lowest level in June. The writer was tempted to attribute this drop in number entirely to low atmospheric temperatures and poor rainfall at this time of the year, but he could not, in fact, do this because *M. lusoria* collections are reasonably high in July, a month in which similar climatic conditions are experienced. Some other factor(s) is therefore likely to be responsible for the July increase. This could perhaps be the termination of a hibernation period and the resumption of biological activity, which in turn could lead to greater fly activity and larger collections. Day length could well be important in this regard.

The pronounced increase in the numbers of *Musca* sp. A in the 2nd half of summer is similar to that seen by the writer for *Culicoides* biting midges at Onderstepoort (Nevill, 1971). These regularly showed peak numbers in the period January–April, and this might be considered to be the automatic result of the combined effect of rainfall, high summer temperatures and fly multiplication. *M. xanthomelas,* however, does not show this peak, thereby reaffirming the necessity for the detailed studies mentioned earlier if seasonal fluctuations of the vector flies are to be satisfactorily explained.

Flies infected with 3rd stage P. bovicola

Although a total of 20 375 flies of at least 13 species were collected and examined over a 3-year period in many different parts of the Transvaal Bushveld, only female flies of the 3 proven vector species yielded 3rd stage larvae of *P. bovicola*. Sufficient numbers of *M. domestica* (3 775), *M. fasciata* (1 469) and *M. sorbens* (1 424) were examined to exclude these as possible vectors, but because such low numbers of the other 7 or more fly species were collected, there is still a chance that further vector(s) will be found among these flies should there be sharp increases in their numbers in the future. However, since filarial worm transmission depends on the regular presence of the vector(s) at the right time, and the present survey over 3 consecutive years has only shown a limited number of fly species to be constantly present, we must conclude that in the Bushveld areas of the Transvaal *P. bovicola* transmission is effected by 1 or more of the 3 *Eumusca* species, namely, *M. lusoria, M. xanthomelas* and *Musca* sp. A.

Since the numbers of infected flies collected increased from July onwards, transmission apparently starts in winter (Fig. 2). Thereafter it is almost entirely dependent on *M. lusoria* until the 2nd half of summer (January–March), when *Musca* sp. A numbers suddenly increase and this fly plays a major role in transmission until its numbers decline during May. The presence of large populations of *M. lusoria* in early spring is possibly essential for the continued transmission of this worm, since this is the period when most *P. bovicola* eggs are available (Fig. 2). In some regions, the other vectors may be present in small numbers only, e.g., at 'Mooiplaats' where the other vectors constituted only 2,1 % of all collections as opposed to 50,2 % for *M. lusoria*. In most cases, *M. xanthomelas* appears to play a supportive role to *M. lusoria* as transmitter during the first half of the summer.

A mean of only 1 in 200 vector flies was found to harbour 3rd stage larvae. Many flies revealed 1st or 2nd stage larvae on dissection, but because these could not be identified, the flies were classed as uninfected. This implies, however, that the incidence of infected flies is probably considerably more than 0,52 % (Table 2). This supposition is supported by the 3,50 % rate of infection in 'Zoutpan' flies collected in March 1976 and dissected after 4–13 days' incubation at 27 °C, as opposed to the day of collection for all the other flies. The value of incubation has been proved by Bech-Nielsen, Bornstein, Christensson, Wallgren, Zakrisson & Chirico (1982) in Sweden, who incubated all wild-caught *Musca autumnalis* for 12 days before dissecting them. Their overall infection rate was 3,5 % with a peak rate of 29,8 % in June.

Epidemiology

At the start of these studies the writer suspected that most transmission would take place when most infective material (blood spots) is available. However, although a peak of blood spots was recorded regularly in spring (September), infected flies were recovered every month of the year except June. The highest incidence was from December–March (Fig. 2), so it is possible that many cattle were infected during this period. Since the apparent prepatent period in a high percentage of cattle ranged from approximately 191–279 days (Nevill, 1984), it is likely that cattle infected between December and March bled for the first time from July–January and contributed to the creation of the peak of bleeding seen in spring and early summer (Fig. 2).

Apart from the presence of infected flies during the spring and early summer period, further proof that transmission took place at this time was provided by the short apparent prepatent period of *P. bovicola* in many calves born at 'Zoutpan' between October and December, an indication that they were infected at or soon after birth. These calves bled for the first time from May–September, the period when the incidence of cattle with blood spots increases rapidly to a peak (Fig. 2).

Although the preceding remarks may seem to provide sufficient explanation for the marked seasonal periodicity of blood spot appearance, the writer believes that this is only part of the explanation and that the remainder has to do with the requirements of the female worm, which possibly requires ideal conditions before ovipositing (Nevill, 1984).

The clear differences in the seasonal abundance of the 3 vector species helps to explain why transmission is not solely related to the peak bleeding period. As can be seen in Fig. 2, *M. lusoria* is abundant throughout most of the year and infected *M. lusoria* were recovered from July–March. Although this species is an effective vector in summer it is especially important for the transmission of *P. bovicola* in the early spring period, when populations of the 2 other vector species are low and thus able to play only a minor role in transmission. In fact during July–December of the 3-year study period, a total of 24 infected *M. lusoria* were found as opposed to only 6 *M. xanthomelas* and 1 *Musca* sp. A.

M. xanthomelas numbers remained low throughout the year and it was only in spring and early summer, when many cattle bled and much infective material was available, that infected flies of this species were found. The 3rd vector species, *Musca* sp. A, exists in extremely low numbers for 8–9 months of the year, with the result that during the period June–January only 2 infected flies were recovered over the 3-year study period. Between February and April, however, its numbers increase suddenly so that, although few cattle with blood spots are

present then, the sheer numbers of this vector species (and possibly its ability to seek out and feed on the few available blood spots) ensure that it is an important vector of *P. bovicola* during the second half of summer (Fig. 2).

Because of the abundance of 1 or more of the vector species during almost every month of the year (with the possible exception of June), transmission in the Bushveld is assured and infected cattle introduced into an uninfected area of the Bushveld will almost certainly act as foci for new infections. Once an infection is established, the level and optimum periods of transmission will eventually be determined by seasonal factors affecting the abundance of the fly vectors and possibly also the developing worms in the vectors and/or the host animals.

On the Highveld, *P. bovicola* has yet to become established despite frequent movements of infected cattle into this region (Carmichael & Koster, 1978). Although only limited seasonal abundance surveys of vectors on the Highveld have been undertaken (Nevill, 1980), there is evidence to suggest that, because of a shortage of vector flies during early summer when most blood spots are present on cattle, transmission could not get under way. Even in late summer (when few blood spots are available), vector numbers were much lower than in the Bushveld. This is a situation similar to that seen in the Bushveld with *Musca* sp. A from June–January, when its numbers were too low for effective transmission to occur even though infective blood spots were plentiful (Fig. 2).

In the laboratory, all the studies on the development of *P. bovicola* in the vector flies were conducted at 27 °C (Nevill, 1981). At this constant temperature, development to the infective 3rd stage larva took 11 days. At lower temperatures this developmental time will almost certainly be extended and on the Highveld where temperatures are generally lower than in the Bushveld, this could lead to the rate of *P. bovicola* transmission being reduced.

The developmental stages in cattle are unlikely to be affected by atmospheric temperatures, since cattle must maintain their body temperature. However, in order to oviposit the female worm makes a hole to the outside and protrudes her head and vulva. During this process she can possibly be directly affected by low atmospheric temperatures, which may result in egg-laying being delayed or reduced on the colder Highveld. Although there is no direct evidence to support the above theory, it appears that in cattle kept in heated stables in winter in Sweden, blood spots start more than 2 months before cattle are let out to pasture (Bech-Nielsen *et al.*, 1982), whereas typical bleeding was not recorded from infected cattle kept in unheated stables at Onderstepoort (Nevill, 1979).

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