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PARASITES OF DOMESTIC AND WILD ANIMALS IN SOUTH AFRICA. I. *OESTRUS OVIS* IN SHEEP*

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ABSTRACT

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Separate groups of 3 oestrid-free lambs were exposed to infestation on irrigated pasture for periods of approximately 33 days each over 30 months, and on dry-land pasture for approximately 42 days over a period of 18 months. With some exceptions, the lambs slaughtered from October–June were found to be infested with *Oestrus ovis* while, with one exception, those slaughtered from July–September were free.

A minimum of 4 sheeps' heads, obtained weekly over 24 months from the Pretoria Municipal Abattoir, was examined for infestation. Of a total of 542 heads examined, 73,4% were infested, having a mean burden of 15,2 larvae.

Mean larval burdens were slightly greater in hornless than in horned sheep, in Dorper-type than in Merino-type sheep, and in lambs than in sheep with 2 or more permanent incisors. The largest larval burdens were recovered from sheep slaughtered during May and June and the smallest during September and October. The greatest number of 1st instar larvae were recovered during May and June and the smallest during September, but those recovered during the latter month were the largest.

With one exception, mature larvae which pupated after 21 March or before 16 August failed to hatch as viable flies. Those which pupated after 16 August hatched as flies after a pupal stage of approximately 50 days and the first flies to hatch were invariably recovered during the first 2 weeks of October. The pupal stage decreased to approximately 25 days during December and January and increased again to approximately 50 days for flies hatching during May. No flies hatched between 18 May and 1 October.

The following life cycle for *Oestrus ovis* is suggested: sheep are repeatedly infested from October–June; thereafter infestation survives in the sheeps' heads until August, mainly as 1st instar larvae, then as pupae and larvae until fresh infestation takes place during October.

Résumé

LES PARASITES DES ANIMAUX DOMESTIQUES ET SAUVAGES EN AFRIQUE DU SUD. I. OESTRUS OVIS *CHEZ LE MOUTON*

Au cours d'une période de 30 *mois,* 3 *groupes d'agneaux indemnes d'*Oestrus ovis *ont éte infesté avec ce parasite sur pâturage irrigué en périodes de* 33 *jours environ et au cours de* 18 *mois en périodes de* 42 *jours sur pâturage non-irrigué. A quelque exceptions près, les agneaux abattus d'octobre à juin étaient infestés avec* O. ovis, *tandis que, sauf un seul agneau, ceux qui ont été abattus de juillet à septembre étaient indemnes de ce parasite.*

Au cours de 24 *mois au moins* 4 *têtes d'agneau recueillies par semaine de l'abattoir municipal de Pretoria ont été soumises à un examen pour la présence du parasite. Sur* 542 *têtes examinées,* 73,4% *étaient infestées avec une moyenne de* 15,2 *larves par tête.*

L'infestation moyenne chez les moutons dépourvus de cornes était plus faible que chez les moutons cornus, chez la race de type Dorper que chez la race de type Merinos et chez les agneaux que chez les moutons ayant 2 *incisives permanentes ou plus. Les infestations les plus marquées se sont manifestées chez les moutons abattus aux mois de mai et juin, tandis que ceux abattus aux mois de septembre et octobre étaient légèrement infestés. Le plus grand nombre de larves du premier stade a été recueilli aux mois de mai et juin et le plus petit nombre au mois de septembre, alors que ces dernières étaient les plus larges.*

Avec une seule exception les larves adultes sortantes du stade pupal après le 21 *mars ou avant le* 16 *août ne se sont pas développées en mouches viables. L'éclosion de mouches des larves sortant du stade pupal après le* 16 *août avait lieu à la suite d'un stade pupal de* 50 *jours environ, alors que les premières mouches à éclore étaient constamment recueillies pendant les* 2 *premières semaines d'octobre. Le stade pupal était abrégé à* 25 *jours à peu près aux mois de décembre et janvier, tandis que celui des mouches écloses au mois de mai s'est allongé à* 50 *jours environ. Aucune mouche n'a éclos du* 18 *mai au premier octobre.*

L'auteur propose le cycle suivant du développement de O. ovis: *L'infestation répétée du mouton a lieu du mois d'octobre au mois de juin; ensuite l'infestation persiste dans la tête du mouton jusqu'au mois d'aout, d'abord comme larves du premier stade et ensuite comme pupes et larves jusqu'à la nouvelle infestation au mois d'octobre.*

INTRODUCTION

The sheep nasal bot fly *Oestrus ovis* was originally a Palaearctic species but is now found in all sheep-farming areas of the world (Zumpt, 1965). Its spread has been promoted by the importation of large numbers of infested sheep, while its survival in new habitats has been assured by the wide range of its temperature requirements and the relatively minor role placed by moisture (Rogers & Knapp, 1973), plus its ability to overwinter in the sino-nasal area of the host animal (Cobbett & Mitchell, 1941).

Because of the fly's ubiquity and the high incidence of infestation, the life cycle and bionomics of *O. ovis* have been the subject of many scientific publications (Bedford, 1925; Mitchell & Cobbett, 1933; Fallis, 1940; Cobbett & Mitchell, 1941; Meleney, Cobbett & Peterson, 1962; Knapp & Rogers, 1968; Abul-Hab, 1970; Kettle, 1973; Rogers & Knapp, 1973).

Bedford (1925) states that in South Africa the flies are active from the beginning of September until May. Du Toit & Fiedler (1956) suggest a pattern of infestation with peak burdens from October–January whereas June and July are comparatively free. In a few sheep, slaughtered during a 14-month period from October 1970–December 1971, the highest levels of infestion were encountered from February–June 1971 (Horak & Snijders, 1974).

In South Africa infestation with the larvae of *O. ovis* retards the live mass gains of Merino lambs (Horak & Snijders, 1974) and infestation is very

* This survey was conducted while the author was employed at the MSD Research Centre, Hennops River

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prevalent in certain areas (Horak, Louw & Raymond, 1971). The present study was conducted to determine the prevalence of infestation, its seasonal incidence and possible methods of control.

The results of the 3 surveys in sheep maintained on irrigated or dry-land pasture and in sheep slaughtered at the Pretoria Municipal Abattoir will be discussed as an entity in this report.

SURVEY 1. THE SEASONAL INCIDENCE OF *O. OVIS* IN SHEEP ON IRRIGATED PASTURES IN A SUMMER RAINFALL REGION

Materials and Methods

Pastures

The pastures at the MSD Research Centre at Hennops River (25° 50′ S; 27° 58′ E, Alt. ±1 280 m) in the district of Pretoria consist of approximately 3 ha of grass/clover leys established in 1967. Of these approximately 1,8 ha were grazed during the survey.

Infestation and management

During the survey period *O. ovis* infestation was maintained on the pasture by a group of sheep varying in number from 8–68. These sheep grazed within the confines of a movable pen and were moved to fresh pasture whenever the vegetation within the pen had been depleted. Irrigation was supplied by means of a sprinkler system, approximately 37 mm of water being applied on each occasion.

Tracer lambs

At 4-weekly-intervals a group of 3 lambs, born and raised under relatively worm-free conditions, was treated with thiabendazole and rafoxanide to eliminate nematode and *O. ovis* infestations and housed indoors for the next 4 weeks to prevent re-infestation. From March 1971–August 1973 a fresh group of lambs was placed with the other sheep in the movable pen on the pastures at approximately 28-day-intervals and removed after approximately 33 days, thus allowing an overlap of 5 days between successive groups.

After removal from the pastures the lambs were starved under worm- and oestrid-free conditions for 48 h prior to slaughter.

Larval recovery

At slaughter the head was severed from the carcass and the skin removed from the dorsal surface to below the orbital fossae. A sagittal section through the head was cut with a handsaw. All larvae present on the mucosa of the nasal septum, nasal passages and conchae were removed with fine-tipped forceps, counted, and provisionally identified as to stage of development, before being placed in 70% alcohol. Thereafter, the septum and conchae were removed for closer examination, the sinuses were opened and the larvae recovered and stored as above. Whenever mature 3rd instar larvae were present, these were placed in approximately 4 cm of vermiculite in a glass jar with a nylon gauze top and allowed to pupate on the laboratory verandah.

The tracheae and bronchial trees of all the lambs slaughtered before June 1973 were opened and thoroughly washed, and the washings sieved and examined for *O. ovis*.

When all the larvae from a particular batch of lambs had been collected, they were examined under a stereoscopic microscope and the stages of development identified.

General

Daily minimum and maximum atmospheric temperatures on the pastures and laboratory verandah were recorded as well as rainfall and irrigation on the pastures.

Results

The mean burdens of *O. ovis* larvae recovered from the 3 lambs slaughtered on each occasion and the mean minimum and maximum temperatures on the pastures are presented in Fig. 1.

With the exception of the 3 lambs exposed at the start of the survey, one or more of the lambs in each group introduced between September and May during the 2½ years of the survey became infested

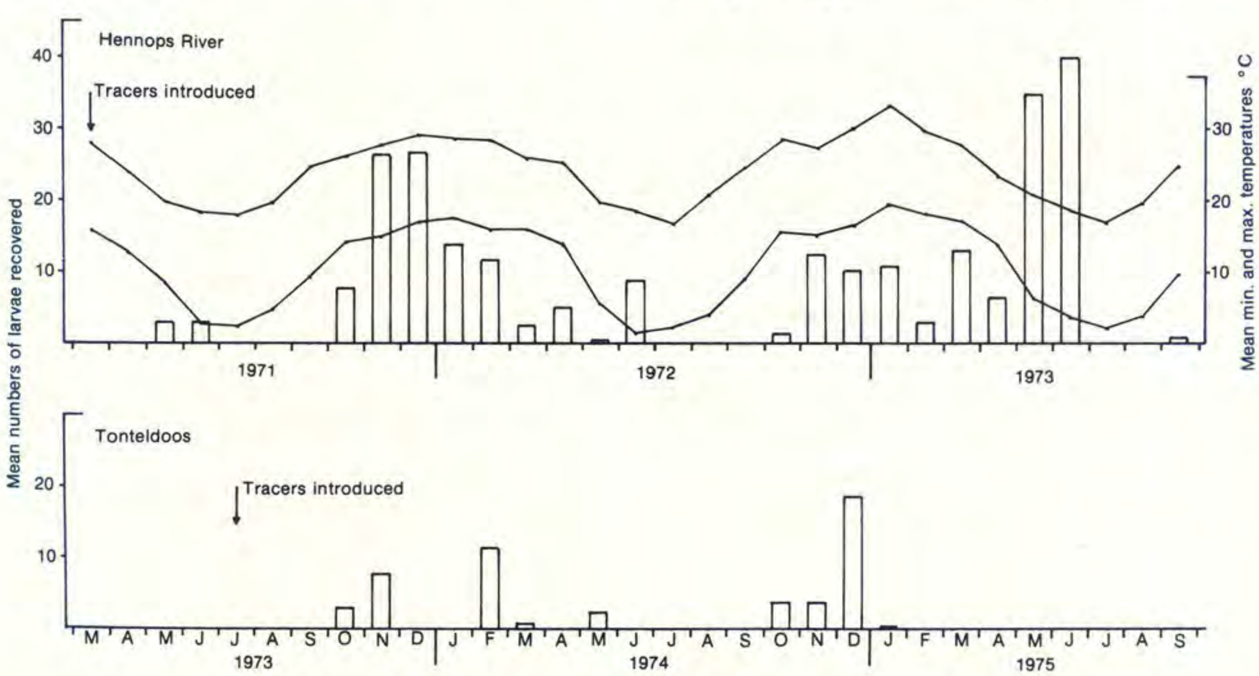

FIG. 1 The mean numbers of *O. ovis* larvae recovered from the tracer lambs at Hennops River and Tonteldoos

with *O. ovis*. In 1973 one of the lambs introduced during August was also infested but none of the other lambs introduced during June, July or August were affected. Every lamb introduced during September, October and December 1971 became infested; also those introduced during May, on 29 September, in December 1972 and from February–May 1973. Peak larval burdens were recovered from the lambs slaughtered during November and December 1971, and during May and June 1973.

Third instar larvae were recovered from lambs slaughtered during May, November and December 1971, January–March and during November 1972, and January, April and June 1973. Thus, during the period of survey, larvae developed to the third instar in 35 days during the months October–June.

No larvae were recovered from the lungs of the sheep.

The findings for the mature larvae that were allowed to pupate on the laboratory verandah are included in Fig. 5 and will be discussed later.

Except in June 1971, when no rain fell and approximately 75 mm of water were applied as irrigation, the monthly precipitation of rainfall and irrigation always exceeded 100 mm. Monthly mean atmospheric temperatures below 16 °C were recorded from May–August in each year.

SURVEY 2. THE SEASONAL INCIDENCE OF *O. OVIS* IN SHEEP ON DRYLAND PASTURES IN A SUMMER RAINFALL REGION

Materials and Methods

Pastures

The survey was conducted on a farm in the Tonteldoos area (25° 19′ S; 29° 59′ E, Alt. 1 676 m) of the Transvaal Highveld.

From 18 May–8 August 1973 the sheep grazed a pasture containing mixed natural grasses, maize and oats. From then until 19 September 1973 they were kept in a small camp planted with kikuyu grass and fed lucerne hay and maize meal as supplements. Thereafter they grazed an *Eragrostis curvula* pasture until 17 October and were then placed on natural grazing until 29 May 1974, when they were moved to a rested camp of *Eragrostis* pasture. On 9 July they were returned to the kikuyu pasture and fed supplements until 3 October, when they were placed in a paddock of natural grazing until the conclusion of the survey.

Infestation

During the survey period, *O. ovis* infestation was maintained on the pastures by a group of approximately 90 lambs which were treated with rafoxanide and thiabendazole on 18 May 1973 and not again. They grazed with a flock varying in number between 400 and 950 lambs. Of these, one group of 90 lambs was treated with rafoxanide for *O. ovis* infestation at 28-day-intervals and the remainder were treated with rafoxanide during November 1973, February, April, June and November 1974.

Tracer lambs

At 28-day-intervals a group of 3 lambs, born and raised under relatively worm-free conditions, was treated with thiabendazole and rafoxanide and housed indoors for the next 4 weeks to prevent infestation.

From June 1973 until December 1974 a group of these lambs was placed with the flock of lambs at Tonteldoos at approximately 28-day-intervals and removed after approximately 42 days, allowing an overlap of 14 days between successive groups.

After removal from the pastures the lambs were housed under worm and oestrid-free conditions and starved for 24–48 h before slaughter.

Larval recovery

The methods described in Survey 1 were used.

Climate

No climatic data were collected. Winter and summer temperatures are lower than at Hennops River and mean annual rainfall is approximately 850 mm, generally falling between September and May.

Results

As a number of the tracer lambs died as a result of mal-adaptation to the conditions at pasture, only 1 or 2 were available for necropsy on certain occasions.

The mean recoveries of *O. ovis* larvae from the lambs slaughtered at each occasion are graphically illustrated in Fig. 1.

All the lambs slaughtered during November 1973 and December 1974 were infested with *O. ovis*, peak larval burdens being recovered during these months and in February 1974.

The lambs slaughtered during August, September and December 1973 and January, April, June–September 1974 were free of infestation, but after the winter months infestation was encountered in the lambs slaughtered during October in both years.

No larvae were recovered from the lungs of any of the lambs.

SURVEY 3. THE INCIDENCE OF *O. OVIS* INFESTATION IN SHEEP SLAUGHTERED AT THE PRETORIA MUNICIPAL ABATTOIR

Materials and Methods

Except on 2 occasions, the heads of at least 5 sheep were collected at the Pretoria Municipal Abattoir at least once a week from November 1971–October 1973. In addition the heads of 4 sheep that had been grazing the pastures at Hennops River were included during February 1972.

From 10 February 1972–13 February 1973 the districts of origin of the sheep were noted. The breed of sheep (as accurately as could be ascertained from the head alone), whether they were horned or not and their dentition were recorded throughout the survey period.

All the heads were examined for *O. ovis* larvae.

The numbers and stages of development of the larvae and sites within the head from which they were recovered were recorded, as were dead larvae. From May 1972–October 1973 the total lengths of 1st and 2nd instar larvae were measured.

From May 1972 a record was kept of the number of visibly larger-than-average 1st instar larvae seen and the sites within the head from which they were collected.

As in the case of the mature 3rd instar larvae recovered from all these sheep those from lambs slaughtered in Surveys 1 and 2 were placed in glass jars containing vermiculite and allowed to pupate on the laboratory verandah.

The lengths of the pupal periods during the various months of the year were recorded from July 1971 until February 1974, as were the numbers of larvae allowed to pupate and the numbers of flies hatching from these pupae from 11 February 1972 onwards.

Results

Of the 259 sheep heads examined between February 1972 and February 1973, 145 came from the Cape Province, 100 from the Orange Free State and 14 from the Transvaal.

The mean monthly incidence of infestation and larval burdens are illustrated in Fig. 2.

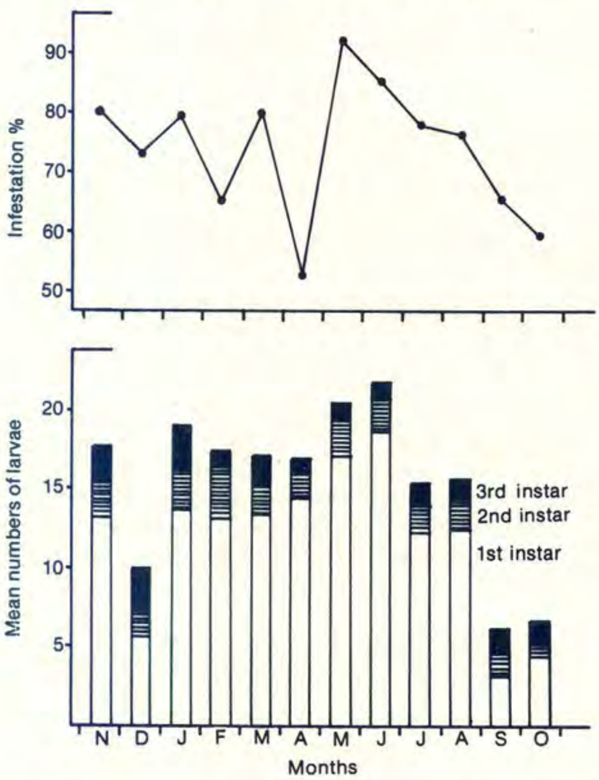

FIG. 2 The mean monthly incidence of infestation and *O. ovis* burdens of sheep slaughtered at the Pretoria Municipal Abattoir

Except in February, April, September and October, the mean incidence of infestation always exceeded 70%.

The larval burdens, averaging 17,7 in November, decreased in December, then, rising rapidly, reached a peak of 21,7 larvae in June, but declined again to less than 7 larvae in September and October. The overall mean incidence of infestation in the 542 heads examined was 73,4% and the mean burden was 15,2 larvae.

Except in February and April, when the mean larval burdens were high although the incidence of infestation was low, a fairly close correlation existed between burden and incidence for the remaining months of the year.

The greatest number of 1st instar larvae was recovered during May and June and the smallest during September. The largest number of 2nd instar larvae was recovered during February and 3rd instar larvae reached peak numbers from November–January.

The greatest number of larvae recovered from any one head was 105, from a sheep slaughtered during April 1973. Fifty-four infested sheep also harboured dead larvae and a further 21 harboured dead larvae only. In addition 16 heads contained no larvae but exhibited lesions of sinusitis typical of infestation.

Table 1 is a summary of the mean burdens of larvae recovered from horned and hornless sheep slaughtered throughout the survey, and indicates the effects of age and breed on the incidence of infestation.

The incidence of infestation and the total larval burdens in hornless sheep were slightly higher than those in horned sheep. The mean numbers of 2nd and 3rd instar larvae, however, were slightly greater in horned than in hornless sheep.

The incidence of infestation and the mean number of 2nd and 3rd instar larvae were slightly greater in older Merino-type sheep than in Merino-type lambs, but the total larval burdens of these lambs exceeded those of the older sheep. The incidence of infestation in Dorper-type lambs and older sheep was virtually the same. The lambs, however, harboured greater total burdens but fewer 2nd and 3rd instar larvae than the older Dorper-type sheep.

When Merino-type sheep were compared with Dorper-type sheep the incidence of infestation and the larval burdens of the latter were slightly greater than those of the former breed.

The largest number of 2nd and 3rd instar larvae recovered from a single animal was 31, from a sheep slaughtered during December 1971.

TABLE 1 *Survey* 3. The mean numbers of *O. ovis* larvae recovered in relation to the presence or absence of horns, breed and age of the sheep

Group	No. of sheep examined	Mean No. of larvae recovered			Percentage infested
		1st Instar	2nd & 3rd Instar	Total	
Horned sheep	204	10,0	3,9	13,9	71,1
Hornless sheep	338	12,7	3,3	16,0	74,6
Merino lambs	164	12,5	3,1	15,6	70,1
Merinos 2 tooth and older	174	9,3	3,6	12,9	73,0
Dorper lambs	162	13,4	3,6	17,0	75,9
Dorpers 2 tooth and older	37	9,5	4,4	13,9	75,7
All Merinos	338	10,8	3,4	14,2	71,6
All Dorpers	199	12,7	3,8	16,5	75,9

Five Dormer sheep were examined and are not included in the findings on breed

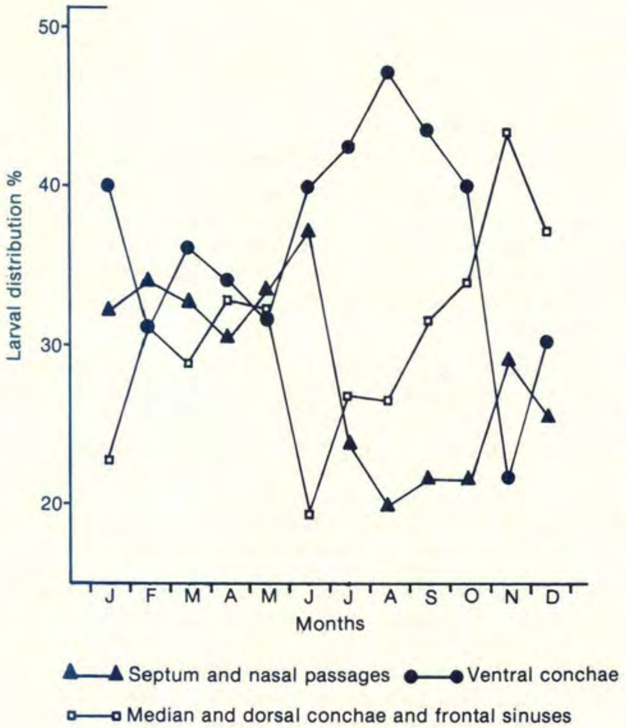

FIG. 3 The distribution of 1st instar *O. ovis* larvae at various sites in the heads of sheep. A few larvae, recovered from the pharyngeal area and maxillary, palatine and lachrymal sinuses, are not included on the graph

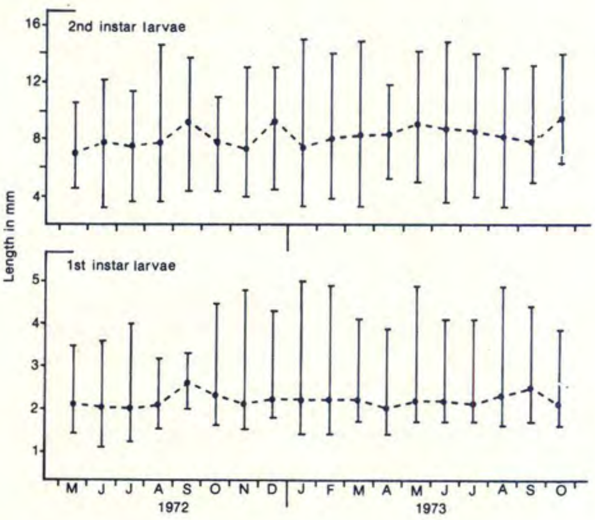

FIG. 4 The mean and ranges in length of 1st and 2nd instar *O. ovis* larvae

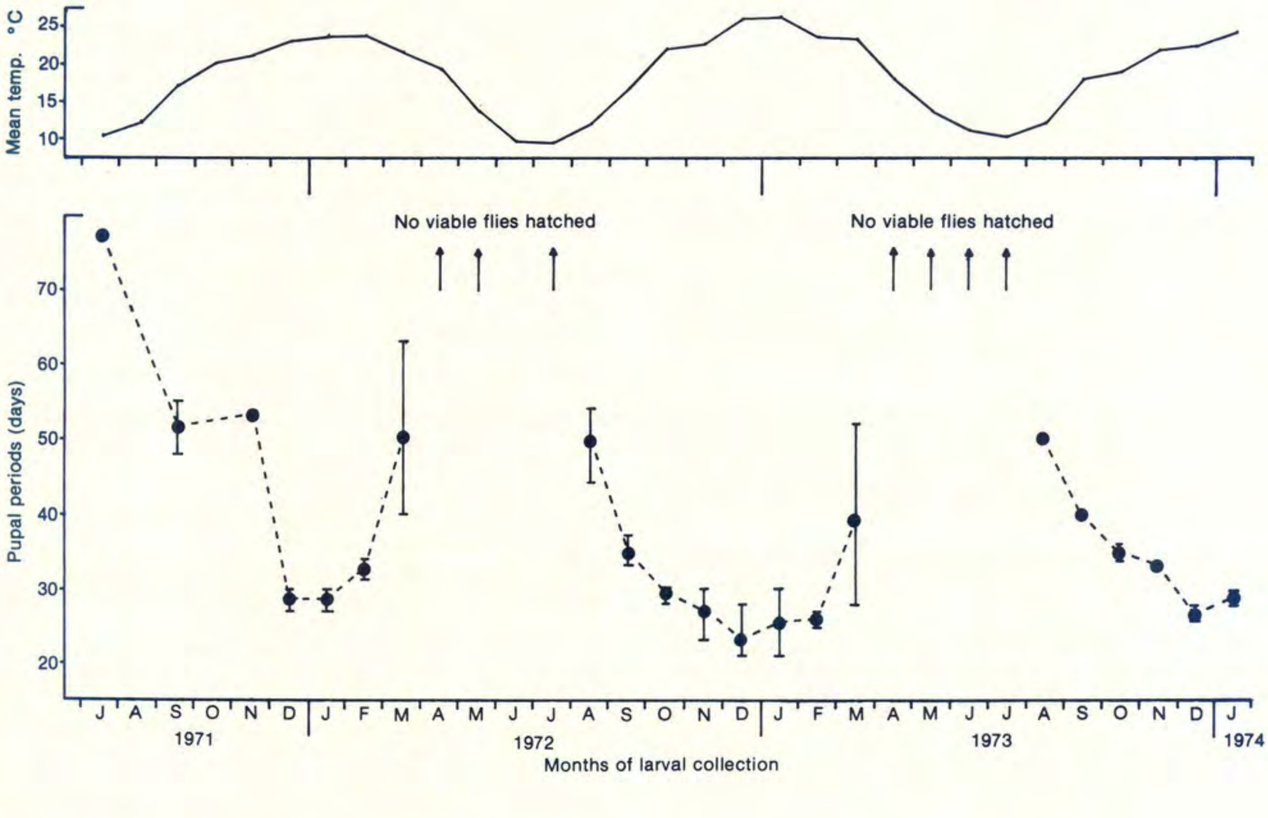

FIG. 5 The mean and ranges in length of the pupal periods of *O. ovis* recovered from sheep

The mean monthly percentage distributions of 1st instar larvae at various sites in the head are graphically illustrated in Fig. 3.

The numbers of larvae reached a peak on the nasal septum and passages from November–April, on the ventral turbinate bones from April–August and on the median and dorsal turbinate bones and in the frontal sinuses during September and October.

A total of 239 visibly larger-than-average 1st instar larvae was recorded during the examination of the heads. Of these, 105 (43,9%) were recovered from the median and dorsal turbinate bones, 47 (19,7%) from the septum and nasal passages and 33 (13,8%) from the maxillary, palatine and lachrymal sinuses and pharyngeal area.

The mean and ranges in length of 1st and 2nd instar larvae recovered from May 1972–October 1973 are illustrated in Fig. 4.

First instar larvae reached their greatest mean length in September and October 1972, and August and September 1973. The smallest larva recovered at this stage of development was 1,1 mm and the largest 5,0 mm in length. The 1st ecdysis usually occurred when the larvae had reached a mean length of 4,3 (range 3,3–5,0) mm.

The mean length of 2nd instar larvae exceeded 9,0 mm in September and December 1972, and during May and October 1973. The smallest larva at this stage of development was 3,2 mm and the largest 15,0 mm long. The 2nd ecdysis usually took place when the larvae had reached a mean length of 12,7 (range 11,0–15,0) mm.

The length in days of the pupal periods of the larvae which were allowed to pupate and hatch on the laboratory verandah is graphically represented in Fig. 5. This figure also shows the mean monthly atmospheric temperatures on the verandah.

In general terms the length of the pupal period decreased from approximately 50 days for flies hatching in spring to approximately 25 days for those hatching in mid-summer. It then increased to 50 days again for those hatching in autumn.

The longest pupal periods were 96 and 103 days for 2 larvae collected in June 1973, but neither of the flies that hatched could expand their wings. The longest pupal period preceding the hatching of a normal fly was 77 days. The shortest pupal period was 21 days for larvae collected in December 1972 and January 1973.

The first normal flies to hatch during the spring of each year emerged on 5 October 1971, 6 October 1972 and 11 October 1973. The last flies to hatch during the autumn of each year were recovered on 23 May 1972 and 11 May 1973.

The monthly mean temperatures on the laboratory verandah fell below 16,0 °C from May–August in each year of the survey.

With one exception, namely, the larva collected during July 1971, no viable flies hatched from larvae collected between 22 March and 15 August in any year.

Excluding all the latter larvae, 84 (67,2%) of the 125 larvae collected from 11 February 1972 onwards emerged as flies.

Most flies from a batch of larvae collected on the same day hatched within 2–3 days of one another. This period could, however, be as long as 7 days.

Discussion

The results obtained in these 3 surveys of *O. ovis* in sheep will be considered together as the findings are interrelated.

The life cycle of O. ovis *at Hennops River*

The life cycle of *O. ovis* would probably be the same in all those regions of southern Africa where the climate is similar to that prevailing at Hennops River, viz., the eastern Cape, the Natal midlands, the Orange Free State and the eastern and southern Transvaal.

Flies hatch during the first 2 weeks of October from pupae formed from larvae deposited during August. These flies, if kept in confinement, have an average lifespan of 1½ days during summer and 8 days during autumn (Cobbett & Mitchell, 1941) and 16 days at room temperature (Fallis, 1940). In nature, however, flies have been found to survive for 37 days (Ternovoi & Mikhailenko, 1973).

The females infest sheep by depositing 1st instar larvae in or around the nostrils (Bedford, 1925; Capelle, 1966). When these larvae grow to approximately 4,3 and 12,7 mm in length, they undergo the 1st and 2nd ecdyses, respectively. Some of them can develop to mature 3rd instar larvae in 25–35 days (Cobbett & Mitchell, 1941; Survey 1) and they will leave the sheeps' heads, pupate and hatch into flies 19–66 days later (Bedford, 1925; Fallis, 1940; Cobbett & Mitchell, 1941). This life cycle may be repeated several times during the summer. The last flies appearing before winter hatch during May; these would infest sheep with larvae that would have to overwinter in their hosts' heads until August as pupae are unlikely to survive on the grazing. The absence of new infestations during the winter months is borne out by the ever-diminishing numbers of 1st instar larvae recovered during these months (Fig. 2), as well as by the increase in their mean lengths during August–October (Fig. 4). The new generation of flies after the winter would then hatch during the first 2 weeks of October.

Using the figures recorded by Cobbett & Mitchell (1941) plus those obtained during these surveys, and assuming a time lapse of 4 days in spring and autumn and 3 days in summer between the flies hatching and the deposition of new infestations, a life cycle as summarized in Table 2 is proposed.

TABLE 2 A proposed life cycle for *O. ovis* in sheep at Hennops River

Date	Item
Early October	Flies hatch (after a pupal period of 51 days) and infest sheep
Mid-November	Mature larvae leave sheep and pupate
Mid-December	Flies hatch (after a pupal period of 28 days) and infest sheep
Mid-January..	Mature larvae leave sheep and pupate
Mid - February	Flies hatch (after a pupal period of 23 days) and infest sheep
Mid-March....	Mature larvae leave sheep and pupate
Mid-May.....	Flies hatch (after a pupal period of 50 days) and infest sheep
Mid-August...	Only mature larvae which leave sheep after this date will give rise to flies
Early October	Flies hatch (after a pupal period of 51 days) and infest sheep

Under optimum conditions, as many as 4 generations of flies may hatch per year at Hennops River. Cobbett & Mitchell (1941), however, demonstrated that, although some larvae used for a single artificial infestation could mature within 25 days, others from the same infestation could take as long as 11 months to reach the 3rd instar. Thus some of the larvae deposited in spring could give rise to several generations of flies and others to only a single generation during a year.

Rogers & Knapp (1973) have shown that, although relative humidity apparently does not influence the percentage of adults emerging from pupae, temperature does. While 27 °C was optimum, a constant temperature either below 16 °C or above 32 °C was fatal. Their findings are supported by the present surveys since only those larvae collected when the monthly mean temperature exceeded 16 °C for all or part of the pupal period gave rise to flies (Fig. 5). The pupae kept in dry vermiculite on the laboratory verandah hatched in early spring at virtually the same time that the first larvae were being deposited in the nostrils of sheep on the pastures at Hennops River. These pastures were supplied with abundant moisture all the year round, thus confirming that moisture or the absence thereof did not affect the emergence of the flies.

If temperatures are higher than at Hennops River, flies would probably hatch throughout the year, whereas in cooler regions the fly season would be shorter. Cobbett & Mitchell (1941) found that in west Texas, where the winters are moderate, bot flies were active during all months of the year except January and February whereas in north eastern New Mexico, where the winters are cold, such activity was observed only during the warm days of summer and early fall.

Rogers & Knapp (1973) showed that larvae harboured by lambs kept at a relatively high temperature matured more rapidly than larvae in lambs kept at a lower temperature. This could also reduce generation time in warm climates.

A comparison of the surveys at Hennops River and Tonteldoos

The difference in the incidence of infestation in the tracer lambs on the 2 properties was probably largely due to husbandry practices. At Hennops River the tracer lambs grazed a relatively confined area with a flock of sheep that were mostly untreated for *O. ovis* infestation. As a result, fly populations could increase considerably on these pastures. The number of sheep in the movable pen never exceeded 74 and the 3 tracer lambs were thus not extenuated in a large flock of sheep.

At Tonteldoos the tracer lambs ran with a flock of 400–950 lambs. Of these approximately 90 were never treated for *O. ovis* infestation, 90 were treated at 28-day-intervals and the remainder were treated on 5 occasions during the survey period. It was thus unlikely that fly numbers would increase markedly and the chances of one or more of the tracer lambs becoming infested in a flock of such proportions during their 6 week period of exposure must be considered slender. Nevertheless the fact that the first infestations recorded after the winter during both years of this survey were in the sheep slaughtered during October confirms the findings at Hennops River.

Seasonal incidence

Peak burdens of 1st instar larvae were recovered from the sheep slaughtered at the Pretoria abattoir during May and June. Similar observations were made by Kettle (1973) in surveys at 7 meat works in New Zealand, where he found peak burdens of 1st instar larvae in the sheep slaughtered during May and June, and, in a separate survey conducted at Petone, during May. In the Northern Hemisphere, in the south eastern United States, Meleney *et al.* (1962) recovered peak 1st instar larval burdens from sheep slaughtered from 16 October–15 December. In Kentucky, Knapp & Rogers (1968) and Rogers & Knapp (1973) recorded peak 1st instar larval burdens during October and November, and Fallis (1940) in Canada recovered the greatest number of larvae (presumably 1st instar, judging by his measurements) during November, from an undisclosed number of sheep.

These findings suggest either considerable fly activity during the autumn months in both hemispheres or the accumulation of larvae in the sheeps' heads during these months. At Hennops River considerable fly activity did take place during May 1972 and from February–May 1973 as all the sheep introduced during these months were infested and individual burdens were high. These large larval burdens ensure that some of the larvae will overwinter in the sheep and give rise to flies during the following spring.

The progressive decrease in the number of larvae recovered from the sheep slaughtered at the abattoir during the winter and early spring can be ascribed to 3 factors. Firstly, no new infestation was taking place; secondly, a fairly large percentage of the larvae did not survive (Cobbett & Mitchell, 1941; Meleney *et al.*, 1962; Rogers & Knapp, 1973) and, thirdly, some of the larvae continued to develop to the mature 3rd instar and leave the sheeps' heads during the winter months (Knapp & Rogers, 1968).

Thus, by early spring, only a few larvae were left (Fig. 2) and these matured rapidly, as can be seen by the greater mean lengths of the 1st instar larvae (Fig. 4), and the high proportion of 3rd instar larvae present (Fig. 2). These findings are similar to those of Meleney *et al.* (1962), Knapp & Rogers (1968) and Rogers & Knapp (1973) in the Northern Hemisphere.

Viable pupae accumulate on the grazing from mid-August onwards. Large numbers of flies hatch in the spring and give rise to the increased number of larvae recovered from the sheep slaughtered during November. These larvae probably mature rapidly, as do the few remaining overwintering larvae, and leave the sheeps' heads, thus resulting in lower larval burdens in December before the second generation of flies has hatched and started to infest sheep. Thereafter mean larval burdens increase again and reach a peak in autumn. Except in February and April, the percentage of sheep infested with *O. ovis* closely parallels the mean larval burdens (Fig. 2).

These findings warrant further discussion. The percentage of sheep infested during February and April was low compared with the infestation rates before and after these 2 months, yet the mean burdens of 17,4 and 16,9 larvae compare favourably with those of 17,1 larvae for March and 20,3 larvae for May (Fig. 2). Thus the individual sheep infested in

February and April were carrying particularly large numbers of larvae to arrive at these relatively high mean burdens.

A possible reason for the low percentage infestation during these months is that some of the sheep may have been treated with systemic larvicides during February, March and April if the large larval burdens were causing clinical symptoms. This surmise is supported by the findings of Horak & Snijders (1974), who recorded the highest incidence of purulent or haemorrhagic nasal discharge during February and March in a flock of sheep kept on the Transvaal Highveld. Had the incidence of infestation during February and April not been so low, the mean larval burdens in the sheep slaughtered during these months could possibly have been the highest in the survey.

Larvicides probably accounted for the fact that the overall mean incidence of infestation during the survey was no higher than 73,4%. The fact that 21 sheep harboured dead larvae only, and a further 16 exhibited purulent sinusitis but no larvae, suggests recent therapeutic intervention. If the latter 2 groups are included amongst the infested sheep in the survey, the overall incidence of infestation in sheep slaughtered at the Pretoria abattoir would be 80,3%.

Rogers & Knapp (1973) found that 45,5% of 3rd instar larvae removed from sheeps' heads originating from northern Kentucky and bordering states were dead. In the Pretoria Municipal Abattoir survey, 850 living and 109 dead 3rd instar larvae were recovered from the 542 sheeps' heads examined, a mortality of only 11,4%. The findings of Rogers & Knapp (1973) suggest that the longer the larvae spend in the sheep's head, the higher their mortality rate. During July in Kentucky, when the generation time was relatively brief, all 26 of the 3rd instar larvae recovered were living, while from October–March, when the generation time was extended by winter, nearly 82% of 3rd instar larvae recovered were dead. The results of the South African surveys suggest that generation time was relatively brief throughout the year, thus accounting for the small number of dead 3rd instar larvae recovered. The greatest numbers of these larvae were recovered in February 1972 when 23 were recorded, followed by May 1972 (12) and October 1973 (10 larvae), but no seasonal pattern could be established.

Moulting sites

Nearly half (43,9%) of the visibly larger-than-average 1st instar larvae were recovered from the median and dorsal turbinate bones and frontal sinuses, suggesting that these are the most favoured sites for moulting to the 2nd instar. This confirms the observations of Cobbett & Mitchell (1941), who state that "these minute grubs usually migrate to the posterior nasal structures, the ethmoid turbinates, before changing to the 2nd instar". Further confirmation comes from the findings that during the late winter and early spring, when no new infestation was taking place and the 1st instar larvae already present were growing progressively larger (Fig. 4), there was a tendency for these larger larvae to be recovered from the median and dorsal turbinate bones and the frontal sinuses (Fig. 3).

Second and 3rd instar larvae were generally recovered from the frontal sinuses and this fact plus the recovery of many cast skins of the 2nd moult in this site suggest that the 2nd moult took place there.

Overwintering

Overwintering of pupae from autumn until spring did not occur on the verandah at Hennops River. Rogers & Knapp (1973) suggest that the pupal period may last longer than 90 days at a constant temperature of 16 °C, but when these pupae were brought to room temperature suddenly none emerged. They also found that pupae, maintained in a pupation box in their natural environment in Kentucky from March–September, had a longer pupal stage than those held at a constant temperature. Some adults pupating during the spring took 70 days to emerge and fewer pupae produced adults in this environment than in any other where emergence occurred.

The results of the present study indicate that in the moderate climatic conditions prevailing in the areas from which the sheep originated, overwintering as completely dormant 1st instar larvae within the nasal passages of the host probably does not take place. Development through the various larval stages is prolonged and a smaller proportion of the larvae reach the 3rd instar during April, May and June than during other months (Fig. 2). Thus overwintering takes place by a combination of factors: reduced rate of larval development in autumn and early winter, with some larvae remaining in the host until the spring, and an extended pupal period for those that pupate in late winter and early spring.

These results and those published elsewhere all indicate that *O. ovis* has adapted to the climate prevailing wherever sheep are kept. Where the winters are cold, as in Canada, north eastern New Mexico and New Zealand, when overwintering, the larvae remain dormant in the 1st instar (Fallis, 1940; Cobbett & Mitchell 1941; Kettle, 1973). In warmer climates, such as in Texas, Kentucky and in the survey area in South Africa, development of the larval stages continues throughout winter (Cobbett & Mitchell, 1941; Rogers & Knapp, 1973), but probably only those larvae that pupate in the late winter and thereafter will give rise to adults.

Retarded development or dormancy in the 1st instar during the winter months is presumably not related to the lower temperature of the air inhaled by the sheep. In a study on the effect of low atmospheric temperature on the temperature of the sinuses and nasal passages, Rogers, Knapp, Cook & Crowe (1968) concluded that, at depths of 50 mm or more, atmospheric temperatures as low as —12 °C may not affect the nasal temperature sufficiently to produce quiescence in *O. ovis* larvae. The effect may be one of photo-period or temperature on the developing fly in the puparium or on the newly hatched fly in autumn, causing it to produce larvae capable of retarded development or dormancy. This would correspond to the observations made on *Lucilia caesar* by Ring (1967).

Control

Virtually complete control can be obtained by drenching with rafoxanide at 28-day-intervals from October–June as this remedy apparently prevents the acquisition of infestation between drenches (Snijders, Horak & Louw, 1973). The labour involved in such a programme would not, however, be justified by a sufficiently high increase in productivity (Horak & Snijders, 1974).

A more practical programme would be drenching—

(i) in March, to prevent the late summer–autumn build-up of infestation,

(ii) in June or July, to eliminate the over-wintering infestation; and

(iii) in November, to control the newly acquired spring infestations.

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