Erratic behaviour as a protective device against predation has been described for a number of invertebrate species (Humphries & Driver, 1969). Humphries (1971) also described erratic movements and cataleptic posture in the escape behaviour of *C.garei* and *C.fringillae* (Walker).

The data describing the activity of *C.garei* shows this species to be activated by light, a feature which may play an important role in dispersal from the open nest of pheasant. This species emigrates from the nest (Marshall, 1981) and it has been shown for *Ceratophyllus g.gallinae* (Schrank) that, depending on physiological age, there is a positive or negative phototactic response to light (Humphries, 1968).

These preliminary investigations indicate that the apparatus has potential applications for testing the effects of environmental cues, insecticides and sonic repellants on the activity profiles of fleas.

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The louse *Trinoton anserinum* (Amblycera: Phthiraptera), an intermediate host of *Sarconema eurycerca* (Filarioidea: Nematoda), a heartworm of swans

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Abstract. The role of the louse *Trinoton anserinum* (F) as an intermediate host of *Sarconema eurycerca* (Wehr) was investigated in swans. 8.3% of healthy swans carried one to twelve lice per bird, dispersed contagiously. Injured and lead-poisoned swans were more heavily infected.

The mouthparts appear designed to penetrate the hosts' skin; the mandibles are robust and asymmetric, and the maxillae have a serrated intercutting surface. 22% fed exclusively on blood and 33% on both blood and feather. All life-cycle stages fed upon blood and the barbs and barbules from down feathers; hooklets from contour feathers were only found in adults. 9% of lice were infected with developing nematode larvae in the head, thorax or abdomen.

Lice labelled with Technetium 99 m moved towards the scapulas and the wings. Lice were found to be highly active and were mobile.

Key words. *Trinoton anserinum*, intermediate host, *Sarconema eurycerca*, filarial heartworm, host, swans.

Introduction

Seegar *et al.* (1976) and Seegar (1977) implicated the phthirapteran louse, *T.anserinum* (Fig. 1), as an intermediate host of the heartworm *S.eurycerca* in the whistling swan *Cygnus c.columbianus* (Ord) in U.S.A., and in the mute swan *Cygnus olor* (Gmelin) in Britain but failed to establish ongoing development of larvae in the louse. This paper examines the interactions between *T.anserinum*, *S.eurycerca* and the swan (principally *C.olor*) with specific reference to the role of the insect as an intermediate host.

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Four general morphological and behavioural attributes of intermediate hosts are considered. (1) The degree of association between insect and host which ensures an opportunity to contact the filarial parasite. (2) A capability to acquire microfilariae by feeding on the blood of the definitive host. (3) A suitable environment within which developmental stages of the larval parasite (L_1–L_3) can develop and from which the infective L_3 larva is able to leave and invade another host. (4) A degree of mobility to ensure the transmission of the parasite from host to host.

Materials and Methods

1. *The degree of association between insect and host.* Swans were captured by baiting, by

canoe round-ups or in swan pipes. Five mute swans (*C.olor*) were held in captivity at a field station and lead-poisoned individuals were studied at swan rescue centres.

Swans were deloused by hand-searching which our experience has shown to be the most reliable method. Population structures were determined biometrically by arranging individuals into ascending size-class categories; that all nymphal stages had been found was confirmed by applying a Dyar's plot (Teissier, 1936).

2. *Acquisition of microfilariae by the louse.* Mouthparts, alimentary canal, crop contents and feeding mechanism of the louse were examined microscopically. For a study of the alimentary canal freshly killed lice were dissected in physiological saline.

Feeding was observed, by video, in newly moulted pale lice secured by the dorsal surface to the stage of a dissecting microscope to which a TV camera was attached. Swan blood (20°C) was placed in contact with the mouthparts and ingestion recorded. Fresh infected blood and centrifuged plasma containing live microfilariae of *S.eurycerca* were offered in the same way.

3. *Development of S.eurycerca within the insect.* Laboratory rearing of *T.anserinum* was attempted by placing culture containers into environmental cabinets maintained at 22°C, 65% r.h.; 30°C, 80% r.h.; 32°C, 80% r.h.; and 35°C, 80% r.h. Lice were fed on warmed (20°C) fresh swan blood once a day.

4. *Louse mobility.* The isotope, Technetium 99 m (0.1 ml in saline, 5 mCi (185 kBq)), was mixed with a small volume of Araldite glue. A drop (*c.* 5 μl) of the mixture was placed on the prothorax of the louse and allowed to set. Twenty lice marked in this way were released onto the captive swan and individually monitored with a hand-held scintillation counter between noon and midnight. The number of movements in 30 min intervals during 12 h periods were recorded.

An electronic analogue thermometer (Comark 1625) was used to produce a map of skin temperatures, readings being taken at the base of the feathers. Wing temperatures were measured whilst the wings were folded and all readings were from regions above the waterline.

Fig. 1(a). Ventral view of *Trinoton anserinum* female (bar = 100 μm).

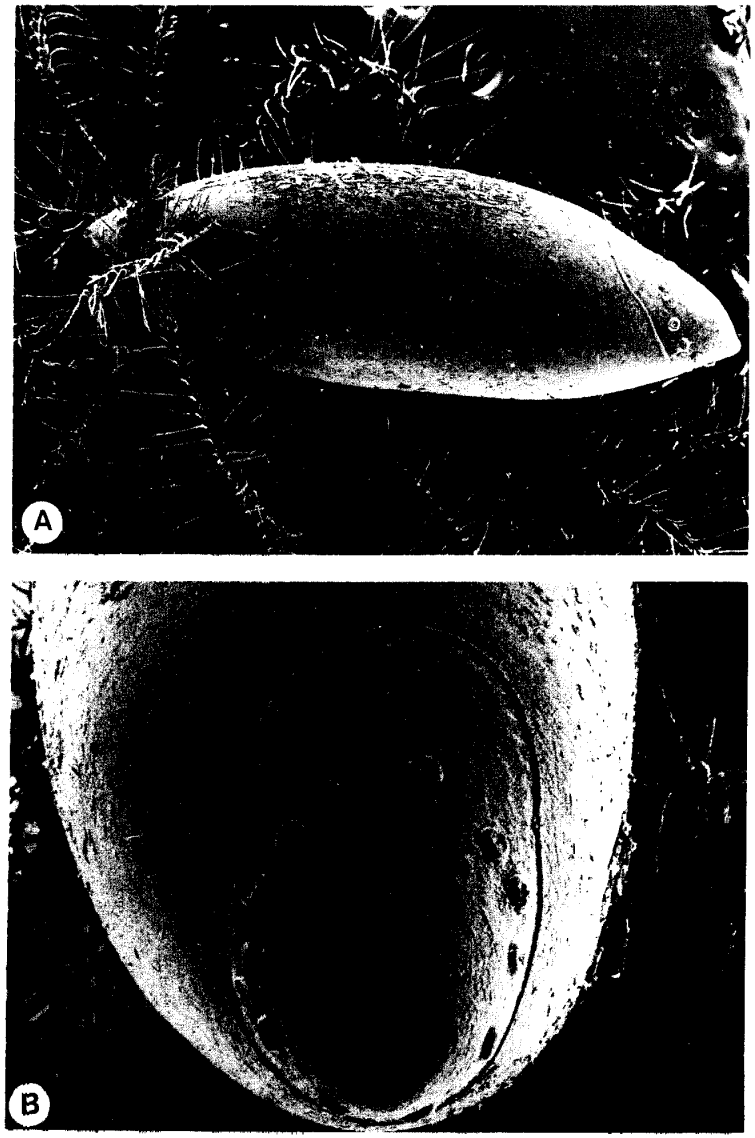

Fig. 1(b). Egg removed from swan's plumage: (A) whole egg with egg cap on right (400 μm); (B) detail of egg cap with twelve micropyles (mp).

Results

1. *The degree of association between insect and host*

A total of 387 swans (*C.olor* = 354; *C.cygnus* (L.) = 9; and twenty-four were of other species held in Wildfowl Trust collections) were searched for lice and nematodes. No regional differences in distribution or infestation levels of louse or worms were evident (Figs 2a, 2b). The high incidence of lice in the Cheltenham area (eleven) is attributable to the density of swans in a wildlife hospital.

T.anserinum were removed from twelve adult and twenty juvenile swans (8.3%). Males and females were infested in equal proportions. Twelve swans harboured larval stages of *S.eurycerca* and 3.1% of swans were host to both louse and nematode.

The mean number of lice on the thirty-two infested swans was 2.0 (range one to twelve). Not included in this sample are four heavily infested swans thought to have died from lead poisoning which had insect loads ranging from twenty-six to 109.

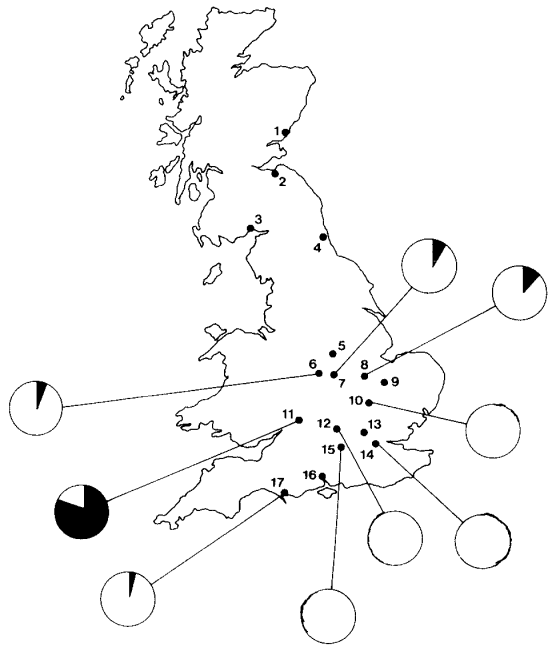

Fig. 2(a). Incidence of *Trinoton anserinum* on swans searched by hand. Number of swans searched = 387; number of swans with *T. anserinum* = 32. Key to locations of swan capture: 1: Montrose; 2: Lothians Region; 3: Caerlaverock (Wildfowl Trust Reserve), Dumfries; 4: Washington (Wildfowl Trust collection), Tyne and Wear; 5: Nottingham region; 6: Alvecote, Staffs. (n = 147); 7: Leicester region (n = 51); 8: Peakirk (Wildfowl Trust collection), Cambs. (n = 18); 9: St Neots, Cambs.; 10: Welney (Wildfowl Trust Reserve), Cambs. (n = 31); 11: Wildlife Hospital, Cheltenham, Glouc. (n = 20); 12: Oxford region (n = 40); 13: Hemel Hempstead; 14: Thames region (n = 14); 15: Reading region (n = 28); 16: Lymington, Southampton; 17: Abbotsbury, Dorset (n = 38). n = numbers of swans hand-searched for *T.anserinum* where sample >5. Swans were caught at a number of sites within the region at locations 2, 5, 7, 12, 14 and 15.

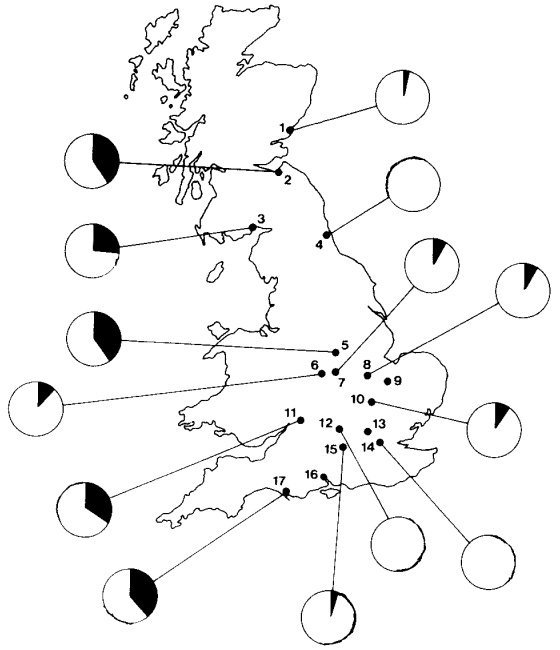

Fig. 2(b). Geographical distribution and incidence of *Sarconema eurycerca* microfilaria in swans. Number of swans sampled = 855; number of swans with *S.eurycerca* = 137 (16% infected). Key to locations of swan capture: 1: Montrose (n = 81); 2: Lothians Region (n = 18); 3: Caerlaverock (Wildfowl Trust Reserve), Dumfries (n = 302); 4: Washington (Wildfowl Trust collection), Tyne and Wear (n = 20); 5: Nottingham region (n = 5); 6: Alvecote, Staffs. (n = 149); 7: Leicester region (n = 51); 8: Peakirk (Wildfowl Trust collection), Cambs. (n = 18); 9: St Neots, Cambs.; 10: Welney (Wildfowl Trust Reserve), Cambs. (n = 56); 11: Wildlife Hospital, Cheltenham, Glouc. (n = 20); 12: Oxford region (n = 41); 13: Hemel Hempstead; 14: Thames region (n = 25); 15: Reading region (n = 28); 16: Lymington, Southampton; 17: Abbotsbury, Dorset (n = 38). n = numbers of swans sampled for *S.eurycerca* at each site. Swans were caught at a number of sites within the region at locations 2, 5, 7, 12, 14 and 15.

The frequency distribution of *T.anserinum* is highly aggregated. An exponent, k, estimated from $k = \bar{x}/(s^2 - \bar{x})$ is 0.054±0.023 SE and the dispersion is adequately described in terms of a negative binomial model (χ^2 = 3.12). The very low value of k reflects a marked skew in the distribution. The population structure of lice from healthy swans was dominated by adults. Lead poisoned swans had higher proportions of nymphs (Fig. 3).

2. *Acquisition of microfilariae by the louse*

The labrum is situated anteriorly and is lined with a row of setae. Some are peg-like, 7–20 μm in length, and are interspersed with needle-like setae 35–40 μm in length. The mandibles are large (approximately 400 μm), asymmetrical and each has two apices. The right mandible is stouter with apices more heavily sclerotized. The left mandible has a deep cavity which

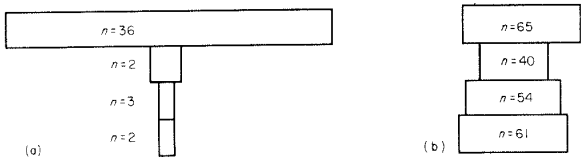

Fig. 3. (a) The population structure of lice from a healthy swan (as a percentage). (b) The population structure of lice showing a change in proportion of size classes taken from four lead-poisoned swans (as a percentage). n = number of lice in each size-class.

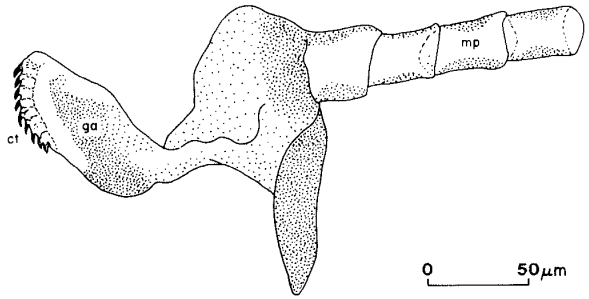

Fig. 4. Maxilla of *Trinoton anserinum* (scale μm). ga = galea, mp = maxillary palp, ct = cuticular teeth.

receives the dorsal tip of the right mandible when they interlock. The hypopharynx consists of a distal tongue-like lobe attached by muscles of the lingual sclerite. The anterior margin of the hypopharynx diverges into two serrated lobes each covered with tufted projections. The maxillae (Fig. 4) are lightly sclerotized. The galea has an inter-cutting surface with a row of strong cuticular teeth which appear well suited to puncture or abrade the skin of the host.

The alimentary canal has a mid gut comprising a crop leading into expanded caecal sacs, a feature illustrated by Waterhouse (1953). A sclerotized proventriculus, present as two semi-circular combs of teeth, separates these regions; the crop retains its function as a storage organ for both blood and feather. Two pairs of malpighian tubules are present leading into the hind gut, in the rectum of which are rectal pads.

Of the 259 lice dissected, the crop contents of fifty-six (22%) contained exclusively blood, eighty-five (33%) blood and feathers and 118 (45%) had feathers alone or an empty gut. The proportions of adult, nymph 3, and nymph 2 lice feeding on blood were not significantly different, but the proportion of first instar lice feeding on blood was significantly lower (z (Ad:N_1) = 6.37 $P<0.001$; (N_3:N_1) = 2.68 $P<0.01$; (N_2:N_1) = 3.08 $P<0.01$).

Blood droplets in contact with the mouthparts immediately induced ingestion. During ingestion the mandibles remained 'open' and flow through the fore-gut was rapid and staccato, possibly due to the action of a cibarial pump. A lapping motion was observed adjacent to the mandibles. It was not clear which structures were involved but from its morphology the hypopharynx is implicated. Blood filled the crop and then the gut caecae; ingestion time was about 15 s to distend the abdomen.

When blood and plasma containing live microfilariae were fed to lice the same mechanism of ingestion was observed. Microfilariae entered the buccal cavity with the flow of ingested blood. The mean ingested volume was 1.42 μdm^3 (n=30; SD=1.19 μdm^3).

Barbs and barbules from down feathers were most frequently found in the crop, whilst hooklets from contour feathers were only found in adult insects.

3. *Development of S.eurycerca within the insect*

Most artificial cultures died after 3–4 days. Survival for 9 days was at 22°C, 65% r.h. Of the 127 preserved specimens of *T.anserinum* dissected, twenty-three had developing stages of *S.eurycerca*. Fifteen of the twenty-three infected lice had blood in their crops and twenty had been removed from swans with microfilariae circulating in the blood. From the twenty-three infected lice, thirty-four developing larvae were removed, twelve larvae from the head, fourteen from the thorax and eight from the abdomen.

4. *Louse mobility*

Five lice, labelled externally with Tc99m, were observed in pill-boxes for 24 h to determine if the isotope caused any observable change in behaviour and survival before experiments were conducted using swans. All lice remained active for 24 h and no observable changes in behaviour were noted.

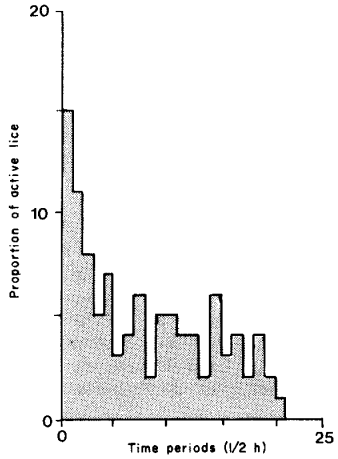

Fig. 5. Activity pattern of *T.anserinum* (n = 20). For each louse an active/inactive score was obtained in each ½ h period of observation.

Initially, activity of the lice released on the swan was high with fifteen out of the twenty individuals moving within the first 30 min, irrespective of time of release. Thereafter, activity declined (Fig. 5).

Lice placed on the back moved onto the wings, up the neck, onto the head and over most of the back and scapular regions (Fig. 6). In general, the direction of movement was towards the scapular region and onto the wing itself where skin temperatures were 33–38°C. Movement of lice placed on the wings was confined to the scapular regions, the middle of the back and the wings, where lice rested on the primary flight feathers. Lice placed on the head moved down the neck to the scapular region, to the top of the back and on to parts of the wings. A mean distance travelled of 121 cm per 30 min (back) compares with means of 44 cm and 35 cm for lice placed on head and wings, respectively.

Discussion

T.anserinum satisfies the four general requirements of an intermediate host. The overall incidence of 8.3% observed in this study probably underestimates the true incidence, due to the inefficiency of hand-searching large birds. Incidence and infestation levels of ectoparasites are, however, dependent upon many factors, e.g. age, health-status and behaviour of the host. Hopkins (1949) observed that there is a tendency for young mammals to be more heavily infested than adults. For swans, it appears that the opportunities for acquiring lice are greatest in young birds. Once juvenile swans leave their natal site, they join immature flocks where there is physical contact between swans and the opportunity for parasite transfer. Host aggregations which increase the probability of bodily contact are critical to the survival of louse populations (Marshall, 1981).

At the British Wildlife Hospital, Cheltenham, 80% of swans examined carried *T.anserinum*. These birds were in poor health through injury or lead-poisoning, and, being crowded together and unable to preen, a build-up in the numbers of lice enhanced the opportunity for transference from swan to swan.

Host behaviour can also affect the incidence and infestation levels of lice in the other ways.

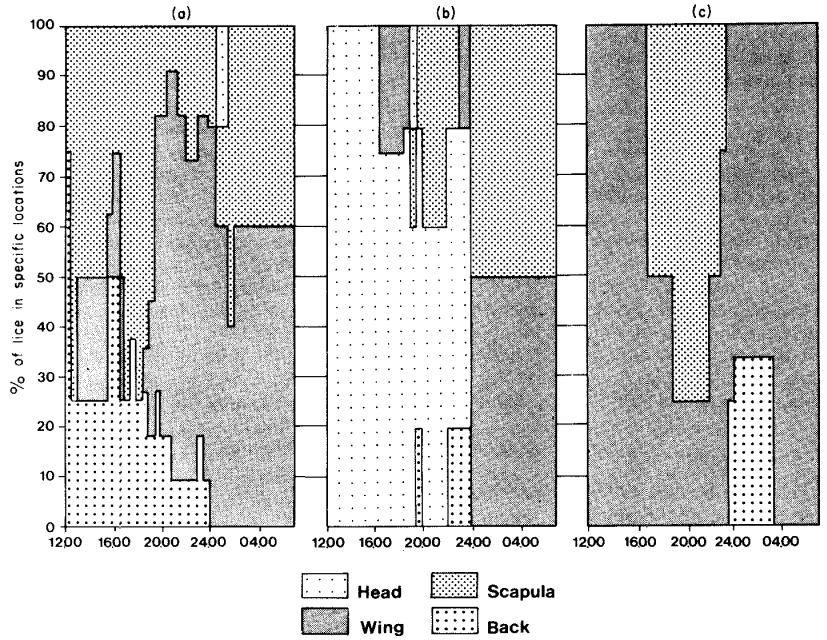

Fig. 6. The location of *T.anserinum* on mute swans in the period 12.00–06.30 hours. (a) Location of lice starting from back; (b) location of lice starting from head; (c) location of lice starting from wings.

Preening reduces the parasite load on birds (Kartman, 1953) and the timing of the moult may also control the numbers of lice. Thus spring moults in bird populations may cause drastic falls in louse populations (Ash, 1960). During moult in July and August, swans are flightless when a great many remiges are lost (Birkhead & Perrins, 1986). It is uncertain to what extent the summer moult affects the population structure of *T.anserinum* but there is evidence of lower infestation rates at this time (S. Cohen, unpublished). Some seasonal check in numbers may arise which may have implications for the transmission rate.

A negative binomial dispersal of feather lice on birds has been reported for a number of host species. Crofton (1971), Randolph (1975) and Fowler & Williams (1985) have postulated a series of situations where a contagious distribution of parasites might arise amongst hosts.

Lice were not observed feeding directly on swans. However, the analysis of crop contents, the structure of the mouthparts and observations of the imbibition of blood show that lice are capable of acquiring microfilariae by feeding on the definitive host. Biting or chewing lice have been regarded as unlikely vectors due to their mechanism of feeding. However, most Amblyceran lice which include blood in their diet, have sharply pointed dimorphic mandibles. Lice which feed exclusively on blood, e.g. *Ricinus carolynae* (Nelson) and *R.sittae* (Nelson), have sharply pointed monomorphic mandibles thought to be an adaptation for piercing (Nelson, 1972).

Associated with the hypopharynx of Phthiraptera (and the closely related Psocoptera) are two structures, the sitophore sclerite and lingual sclerite. Both are considered to be involved in active water-vapour uptake via the mouthparts

and in those species of Phthiraptera with these structures, the uptake performance is exceptionally efficient showing higher rates than other absorbing arthropods (Rudolph, 1983).

In those species of biting lice which have lost the ability to take-up water-vapour, the structural components of the uptake system are modified or reduced. Rudolph (1983) found no water uptake capacity in *Trinoton querquedulae ludwigfreundi* (Eichler), and from the structure of the mouthparts it appears that *T.anserinum* is also unable to absorb water by this method. This may partly explain the difficulties of culturing *T.anserinum in vitro*. Of particular interest is that the typical structure of the sclerites is modified in three genera: *Trinoton*, *Dennyus* and *Heterodoxus*, which are all known to be intermediate hosts to filarial nematodes (Cummings, 1916). *Pseudomenopon pilosum* (Scopoli) and *P.dolium* (Rudow), both Amblyceran lice infesting the coot *Fulica americana*, (Gmelin) and red-necked grebe *Podiceps grisegena* (Boddaert) have been reported as intermediate hosts of *Pelecitus fulicaeatrae* (Diesing), a nematode whose microfilariae are found in the skin of the feathered portions of the legs of infected birds. *Pseudomenopon* is the third Amblyceran genus of birds found to carry nematodes and is the only louse known to act as intermediate host to skin-inhabiting microfilariae (Bartlett & Anderson, 1987). It would be interesting to discover if they have sclerites modified in a similar way.

T.anserinum is a rapid blood feeder and 54.5% of specimens examined had fed on blood, comparable with the 66% reported from *C.c.columbianus* (Seegar, 1977).

Lice labelled with Tc99m were initially active when released on to the swan regardless of the starting location but patterns of movement then appeared markedly different. Two hypotheses might be suggested to account for the observations. (1) Lice move further when released on to less favourable parts of the bird (back) than when released onto more favourable sites (wings and head.) (2) After release, lice take time to locate a suitable resting/feeding site but having done so, they remain there.

These observations show that the louse is mobile amongst the feathers of the host and makes possible the suggestion that *T.anserinum* easily transfers to other swans, a transfer enhanced by the gregarious nature of swans in immature flocks and at times of moult. It is well known to swan-handlers that lice can transfer to man. *T.anserinum* appears active enough to disperse *S.eurycerca* successfully from swan to swan although this was not directly observed in this study. *T.anserinum* has been recorded from five swan species (Seguy, 1944; Seegar, 1977; McKelvey & MacNeill, 1980).

Clearly *T.anserinum* is a highly mobile species preferentially found on the back, wings and scapular regions which may be sites of feeding and/or transfer to other swans. It was found to be active throughout a 24 h period and capable of rapidly ingesting blood and microfilariae. A comparison of the microfilarial density with that reported by Seegar (1977) gives 8 microfilariae per 0.25 cm^3 blood (*C.olor*) (S. Cohen, unpublished) and 82 microfilariae per 0.25 cm^3 blood (*C.c.columbianus*). *S.eurycerca* exhibits a sub-periodic response throughout 24 h, the highest number of microfilariae circulating in the peripheral blood supply being recorded between 11.00 and 19.00 hours (S. Cohen, unpublished).

We suspect that the louse feeds at regular intervals to maintain fluid balance and when doing so imbibes *S.eurycerca*. The absolute proof that *Trinoton* is a cyclodevelopmental vector for *Sarconema eurycerca* would be hard to establish. Nevertheless, the observations made in this paper give strong support to Seegar's original suggestion.

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Glossina fusca group tsetse as vectors of cattle trypanosomiasis in Gabon and Zaire

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Abstract. 1. The significance of *Glossina fusca* group tsetse flies as vectors of cattle trypanosomiasis was examined using biconical traps to survey tsetse populations at one site in Gabon and two sites in Zaire.

2. Mean trypanosome infection rates in *G.tabaniformis* Westwood over the study period ranged from a minimum of 8.9% at one site to a maximum of 17.7% at another. The mean infection rate in *G.nashi* Potts was 6.0%.

3. Up to 49% of bloodmeals of *G.tabaniformis* were from cattle. Trypanosome prevalence in cattle where *G.tabaniformis* appeared to be the main vector was 9.5% and 5.4% at the Mushie and OGAPROV ranches, respectively.

4. A highly significant positive correlation was found between tsetse challenge and trypanosome prevalence in N'Dama cattle across sites. Tsetse challenge was defined as the product of tsetse relative densities, trypanosome infection rates in the flies and the proportion of feeds taken by them from cattle. Thus, *G.tabaniformis* can be an important vector of pathogenic *Trypanosoma* species in cattle.

Key words. *Glossina fusca* group, *G.tabaniformis*, tsetse, vectors, trypanotolerant cattle, trypanosomiasis, Gabon, Zaire.

Introduction

Large areas of tropical Africa are unsuitable for livestock production due to the presence of tsetse flies (Murray & Gray, 1984) and in some tsetse infested areas of west and central Africa, only trypanotolerant breeds of domestic livestock can be kept without chemoprophylaxis.

Glossina fusca group tsetse are, mainly, forest inhabiting species. Although tsetse species of this group inhabit vast areas of the forest zones of west and central Africa, the ecological separation of their habitat and the grazing areas of cattle is such that they have rarely been impli-

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