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African horsesickness epidemiology: five species of *Culicoides* (Diptera: Ceratopogonidae) collected live behind the ears and at the dung of the African elephant in the Kruger National Park, South Africa

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ABSTRACT

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During the culling of elephants *(Loxodonta africana)* at five sites in the Kruger National Park, South Africa, a total of 682 *Culicoides* of five species of the subgenus *Avaritia* were found live either behind the ears of elephants or attracted to the freshly disembowelled intestinal dung of elephants. The species are *Culicoides tororoensis* Khamala & Kettle, 1971; *C. kanagai* Khamala & Kettle, 1971; *C. loxodontis* Meiswinkel, 1992, and two undescribed species, i.e. *Culicoides* sp. #50 and *Culicoides* sp. #54 pale form (p.f.). Of 511 female midges found behind ears, 39,9 % were nulliparous, 57,3 % empty parous, 2,5 % freshly bloodfed and 0,2 % gravid. The age composition of this subpopulation indicates that the *Culicoides* were behind the ears to suck blood and, furthermore, would do so in broad daylight. The age composition of 171 *Culicoides* of three species attracted to dung was entirely different: 1,8 % nulliparous, 14,6 % empty parous, and 83,0 % gravid, indicating that the great majority of midges captured at dung were about to oviposit or had just oviposited.

Immediately after culling, light-traps were operated at two of the sites. Of 4 023 *Culicoides* of 21 species captured, 93 % were of the same five species found on the ears and at the dung of elephants. Using these and other unpublished data pertaining to the rearing of these five *Avaritia* species from elephant dung over the past seven years, we broadly sketch the life cycle of these *Culicoides*, the first for any Afrotropical species of the genus. We also discuss the implications the close association between elephant and midge has for the dispersal and geographic distribution of the latter, and how it may influence the involvement of midges in the transmission of diseases such as African horsesickness. Owing to difficulties in identifying species of the subgenus *Avaritia* in the Afrotropical Region, the taxonomy of each of the five above-mentioned species is briefly appraised. Of the remaining 16 species (7 %) captured in light-traps 15 (6 %) belong to that sector of the genus *Culicoides* whose immature stages develop in groundwater habitats and include *C. imicola*, which comprised only 2 % of the light-trap collections. The large disparity in the adult abundance patterns of the "dung" and "groundwater" species in the middle of dry bushveld, is probably the result of differences in host and larval habitat preferences, and is briefly discussed. Finally, the few reports extant on the wild-host preferences of Afrotropical *Culicoides* are reviewed. Five tables and five figures accompany the text.

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INTRODUCTION

In the Afrotropical Region certain arboviruses are biologically transmitted by bloodsucking *Culicoides* midges, the most important being those of bluetongue in sheep, African horsesickness and, to a lesser extent, bovine ephemeral fever and Akabane. Since these viruses appear to be endemic to Africa, wild ungulates must act as reservoir and amplifying hosts. Many game animals at least circulate the viruses as indicated by antibody surveys (Walker & Davies 1971; Davies & Walker 1974a, b; Davies, Shaw & Ochieng 1975; Davies & Otieno 1977; Simpson 1978; Davies & Jessett 1985; Hamblin, Anderson, Jago, Mlengeya & Hirji 1990; Binepal, Wariru, Davies, Soi & Olubayo 1992; Barnard 1993), and by transmission and infectivity trials such as those conducted on blesbuck (*Damaliscus albifrons*) by Neitz (1933), and on zebra and elephants by Erasmus, Young, Pieterse & Boshoff (1976). In many parts of the continent these natural hosts have been eradicated and, in the case of bluetongue, the reservoir role has now been taken over by cattle (Du Toit 1962; Nevill 1971). As regards African horsesickness virus, limited data gathered over the past 20 years indicate that the African elephant may be a reservoir. As summed up by Lubroth (1992), "experimental inoculations ... did not equivocally exonerate the elephant having a role in AHS epizootiology but did underline the need for further field and experimental studies". The further elucidation of the epidemiology of AHS can best be achieved against a backdrop of knowledge gleaned from a natural situation such as occurs in the Kruger National Park (KNP), South Africa, where large numbers of Africa's major savanna herbivores still abound.

Since 1979 we have been involved in piecemeal studies, mainly light-trapping, on the *Culicoides* biting midges of the KNP. It was in 1983 that one of us (L.E.O. Braack), while searching for the elephant louse, *Haematomyzus elephantis* Piaget, 1869 (Mallophaga, Haematomyzidae), found seven females of the undescribed *Culicoides* species #54 pale form (p.f.) behind the ears of an elephant culled in the Pafuri area, northern KNP, but the significance of this finding was not fully appreciated at the time. Two years later a six-month study was initiated to rear *Culicoides* species from the dung of elephants and other large herbivores in the KNP. This project was largely inspired by unpublished data assembled by Mr Alan Dyce of Sydney, Australia, during a four-month fellowship to South Africa in 1973/1974, and later presented in a short communication (Dyce & Marshall 1989). The rearing of *C. kanagai* and four other species of the subgenus *Avaritia* from elephant dung led Meiswinkel (1987) to contend that an intimate relationship seemed to exist between these biting midge species and *Loxodonta*. He had found that *C. kanagai*, and a few other dung-inhabiting *Culicoides* species, were always caught in higher numbers in the immediate vicinity of elephants, and that the near absence of these midge species throughout the rest of South Africa, in parallelling the disappearance of elephants from the same locales, further supported the idea of mutualism. However, more conclusive data were needed.

Since then information has been gathered by us that supports the view that a close relationship exists between five dung-inhabiting species of *Culicoides* of the subgenus *Avaritia*, and the African elephant. Especially revealing were observations made in 1988, 1990 and 1992 when we examined 14 elephant carcasses for *Culicoides* in the southern, northern and central areas of the KNP. These data are here given in detail. To bring home more clearly the relationship that exists between the elephant and these biting midge species we also draw on unpublished notes made on their larval habitat, i.e. elephant dung, and their geographic distribution and abundance gained from more than ten years of light-trapping. This has culminated in what we believe is a fairly complete understanding of the life-cycle of these *Avaritia* species, and appears to be the best evidence yet gathered on the wild ungulate hosts preferentially fed on by any species of Afrotropical *Culicoides.*

MATERIALS AND METHODS

Culling sites, vegetation and prevailing weather

According to White (1983) the Kruger National Park falls into two major phytochoria: II (Zambezian regional centre of endemism) and XV (Tongaland-Pondoland regional mosaic). The northern three-quarters of the KNP falls into phytochorion II, comprising vegetation units 28 and 29d, the former described as *Colophospermum mopane* woodland and scrub woodland, the latter as South Zambezian undifferentiated woodland. The southern quarter falls into phytocorion XV, vegetation unit 29e, known as a transition from the above-mentioned 29d to Tongaland-Pondoland bushland. Colloquially, these are respectively referred to as lowveld, arid lowveld and mopani veld (Acocks 1975). Gertenbach (1983) introduced detail into the above categories by zoning the KNP into 35 landscapes, each of these defined as an area "with a specific geomorphology, climate, soil and vegetation pattern together with an associated fauna".

Culling of elephants during the present study occurred at five sites in four of these landscapes (Fig. 1). These are briefly described to pinpoint our areas of activity rather than to imply that the vegetational and climatic patterns solely dictate the distribution of the elephants and their associated *Culicoides* species. Brief descriptions of each site, weather conditions and temperature at the time of culling, are given.

Culling site 1

James Windmill, southern KNP; landscape 5: mixed *Combretum* spp./*Terminalia sericea* woodland; covers 8 % of the KNP; topography undulating with dense bush savanna vegetation on the uplands, open tree savanna in the bottomlands and with dense riparian vegetation on the banks of rivers and streams; altitude 350–500 m a.s.l.; climate temperate with sporadic frost in the bottomlands; rainfall 550–600 mm/annum.

Elephants are commonly found in this landscape. Time and date of culling: 16:00; 22.iv.1988. Weather: windless; clear, blue autumn sky; temperature ± 28 °C. No light-trap collection made.

Culling site 2

Langtoon dam area, northern KNP; landscape 23: *Colophospermum mopane* shrubveld; is the largest and most homogeneous landscape covering 10 % of the KNP; consists of flat to concave plains with a number of drainage channels often ending in marshes; woody vegetation is dominated by multi-stemmed mopane shrubs 1–2 m in height; altitude 300–400 m a.s.l.; summers very hot; rainfall 450–500 mm/annum. Zebra and buffalo are found in the largest numbers; elephant bulls are common, while breeding herds occasionally move through to other landscapes. Time and date of culling: 15:15; 24.iv.1990. Weather: windless, clear blue sky; temperature 31 °C. Light-trap operated from 17:00–22:00.

Culling site 3

Mooigesig dam area, northern KNP; landscape 12: *Colophospermum mopane/Acacia nigrescens* savanna; covers 5,5 % of the KNP; topography relatively flat; four rivers drain this landscape, while three hot springs and a number of pans occur; vegetation is an open tree savanna with occasional low shrubs; grass cover dense; altitude 400–460 m a.s.l.; temperatures a little milder than in landscape 23, frost seldom occurs; rainfall 500–600 mm/annum. This landscape is a preferred habitat for a variety of game, with large numbers of zebra, buffalo and elephant present. Time and date of culling: 14:50; 25.iv.1990. Weather: windless, blue sky with much scattered cloud, but sun shone throughout collection period until 16:45; temperature 28 °C. Light-trap operated from 17:00–22:00

Culling site 4

Masala koppie, 30 km west of Satara, central KNP; landscape 5: see under culling site 1. Time and date of culling: 14:45; 28.iv.1992. Weather: blue sky with scattered cloud, periodic wisps of breeze; temperature 31 °C. No light-trap collection made as strong winds from the south began blowing at 17:30.

Culling site 5

Houtboschrand, north-west of Timbavati, central KNP; landscape 6: *Combretum* species/*Colophospermum mopane* woodland of the Timbavati area; covers 2,4 % of the KNP; topography undulating, and drained by a number of tributaries of the Timbavati River; vegetation on uplands open bush savanna with a moderate shrub layer and dense grass cover; altitude 300–500 m a.s.l.; hot summer and cool winters with

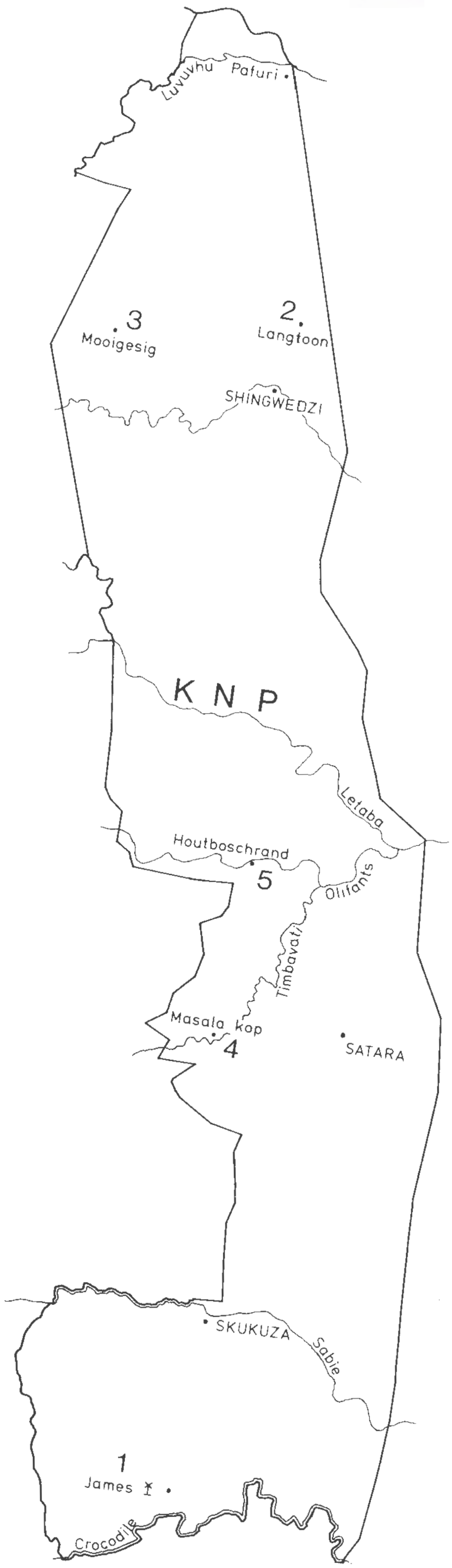

FIG. 1 Map of the Kruger National Park detailing elephant culling sites 1–5, major rivers and camps

frost an exception; rainfall 450–550 mm/annum. Habitat suitable for sable antelope, elephant, buffalo, kudu and impala, while zebra occur in small groups of about six individuals. Time and date of culling: 14:30; 14.iv.1992. Weather: windless; clear blue sky; temperature 32 °C. No light-trap collection made.

Elephant culling

As part of the KNP's annual culling programme to restrict the number of elephants to ± 7 500 in the 20 000 km^2 national park, small family groups of eight to 20 animals are randomly tracked down, rounded up by helicopter, and destroyed. This is done each year during the autumn and winter months. Within minutes after being drug-darted from the air, the elephants are bled (throats severed) and disembowelled. Over the next 1–2 h various data pertaining to their age, size and sex are collected, and the elephants are then loaded onto flatbed trucks to be taken to the abattoirs at Skukuza. During the short period the elephants lay in the field we examined as much of the body of 14 elephants as possible for *Culicoides* midges.

Collection of *Culicoides*

Behind elephant ears

Live *Culicoides* were collected off ears with a suction pooter comprising a 50 cm rubber tube connected to a 30 cm glass tube, the joint interrupted by a fine gauze net preventing *Culicoides* from being swallowed during collecting. After five to ten midges had been collected, they were blown into a small bottle of 70 % ethyl alcohol. As elephants usually lie on their side, only half the anatomy and one ear were examined; only at Mooigesig could both ears of one elephant be examined as it had died on its haunches. Owing to a shortage of collecting time, no effort was made to establish exactly which part of the ear carries the majority of *Culicoides*.

At intestinal dung

Soon after culling all elephants are disembowelled. In six animals a slit was made in the large intestine near the anus to expose the fully digested bronze-coloured browse. These ruptures were monitored for 10–25 min and as many as possible of the *Culicoides* seen attracted to the dung were collected with a suction pooter. In two animals a slit was also made higher up in the small intestine to reveal a large amorphous mass of partly digested pale green browse in the very early stages of fermentation. On each occasion this "young" dung was monitored for 10 min.

Light-trapping

Immediately after the culling operation had been completed and all personnel had departed, light-traps were operated at the Langtoon and Mooigesig culling sites. One commercially available New Jersey-type down-draught trap equipped with an 8-W UV light was run at each site between 17:00–22:00. A small generator was used to provide 220-V electricity.

Age-grading

Each and every *Culicoides* of a total of 4705 collected behind ears, at dung and in light-traps was identified and sexed. All females were graded as either nulliparous, empty parous, gravid or freshly bloodfed, using the method of Dyce (1969).

Taxonomy

More than 500 males and females of the five *Avaritia* species collected were slide-mounted in Canada balsam and provide the data on which the discussion of their taxonomy is based.

Finally, where we refer to a *Culicoides* species as having been reared from the dung of elephants and other herbivores, most of the information is drawn from unpublished data accumulated by us in the KNP over the past seven years, and from miscellaneous findings made elsewhere in South Africa.

RESULTS AND DISCUSSION

What is known about the wild-host preferences of Afrotropical *Culicoides*?

Very little is known about the preferred wild hosts of *Culicoides* in Africa south of the Sahara. It must be appreciated that the collection of an unbiased sample of such small, 1-mm-sized, primarily nocturnal midges off Africa's wild animals is difficult to achieve.

The host data that do exist reflect a strong veterinary bias in that they nearly all originate from domesticated animals (Walker & Davies 1971; Nevill & Anderson 1972; Walker & Boreham 1976; Braverman & Phelps 1981; Nevill, Venter, Edwardes, Pajor, Meiswinkel & Van Gas 1988). Besides these studies there are, however, nine reports which in one way or another deal with *Culicoides* and Africa's endemic mammals, but they either contain limited data resulting from opportunistic collecting, or the data are slanted as the host animals were either tamed or kept away from their natural habitats in man-made environments.

In their introduction to a taxonomic study of 61 East-African *Culicoides* species Khamala & Kettle (1971) refer to specimens received from Mr T.N. Kangwagye that were collected off tame African buffaloes *(Syncerus caffer)*. This note is best ignored as the authors do not name the *Culicoides* species involved, make no further textual reference to these host records and, furthermore, appear to have misquoted the data assembled by Kangwagye (1973, 1974). The latter author, in a study conducted at Katookye on the River Ntungwe, western Uganda, collected biting Diptera off "four tethered, brown Ankole longhorn bullocks *(Bos taurus)*" and from "two juvenile buffaloes *(Syncerus caffer caffer)*". His results reveal that 109 specimens of four species of *Culicoides (C. fulvithorax, C. grahamii, C. pallidipennis* and *C. schultzei)* were found only on the *Bos taurus* bullocks, and that the two *Syncerus buffaloes* examined for biting flies were sampled only during the day and yielded no *Culicoides* whatsoever. Elsewhere this information was corroborated by Khamala (1968) who states that "Mr T.N. Kangwagye ... sent specimens of *Culicoides* collected off bullocks ... along the River Ntugu". The data *re Culicoides* presented in Kangwagye's second study (1974) is inconclusive, as under Ceratopogonidae he lists the same four species he collected off bullocks at Katookye (Kangwagye 1973) but gives no clue as to where, how or off which host these specimens were caught. It appears, therefore, that these data were merely transcribed from his 1973 study.

In another study on Kenyan biting midges, Walker & Boreham (1976) identified the bloodmeal source of 682 *Culicoides* belonging to 21 species collected with light-traps. Eighteen of these species, comprising 390 specimens, had fed on bovids, i.e. "any member of the Bovidae family except sheep and goats but includes cattle and wild Bovidae". Although their collections were made at sites where "there was a wide and plentiful variety of other hosts including humans, wild and domestic birds, rodents, dogs, wild Bovidae, viverrids, rabbits and reptiles," Walker & Boreham (1976) add that "there was a deliberately strong bias towards sheep and cattle as potential hosts; the traps were usually at or near their pens and other livestock were ignored". These results are therefore inconclusive as regards the wild-host preferences of African *Culicoides*.

In a study purporting to deal with wild-host-associated *Culicoides* in Nigeria, Dipeolu (1976) collected 33 biting midge species around two sitatungas *(Tragelaphus spekei)*, two crowned duiker *(Cephalophus rufilatus)*, two Maxwell's duiker *(Philantomba maxwellii)*, six kob *(Kobus kob)*, two red-bellied monkeys *(Cercopithecus erythrogaster)*, four cherry-crowned mangabey *(Cercocebus tergautus)* and 58–60 giant rats *(Cricetomys gambianus* or *emini)* in the zoological gardens of the University of Ibadan. The animals were held in three enclosures, two of which were vegetated. At best, such situations must be considered man-made and whether stocked with exotics or endemics displaced from their natural habitat, would probably attract only a specific range of *Culicoides*, i.e. those species which do not succumb to or, alternatively, respond positively to man's manipulation or "development" of the surrounding environment.

A similar, but less severe, bias is to be found in Meiswinkel (1989) who recorded eight females each of *C. (Avaritia) bolitinos* and *C. (A.) imicola* taken off a darted specimen of an African buffalo kept in man-made bomas at Skukuza in the KNP. However, we classify this finding as only partly artificial as the bamboo-fenced bomas are small in area (± 1 000 m^2), open above, and are situated in undisturbed bushveld thickets where much game abounds, including buffalo. Furthermore, there is little doubt that *C. bolitinos* does enjoy a close association with buffalo as it has on numerous occasions been reared from buffalo dung (Meiswinkel 1989; Dyce & Marshall 1989) and also from the dung of the blue wildebeest *(Connochaetes taurinus)* and domesticated cattle (Meiswinkel 1989). A two-year unpublished light-trapping survey has shown that the strongly mammalophilic *C. imicola* is one of four dominant species at the bomas and, in the KNP, is the site with the highest known *C. imicola* population. This herd of ten to 15 buffaloes has been held in these bomas for some eight years; the maintenance of this sedentary "bloodbank" is probably responsible for the *C. imicola* focus.

The last reference to *Culicoides* and wild hosts, and the one most pertinent to this study, concerns the following important note made by de Meillon & Hardy (1953) on *C. (Avaritia) grahamii*: "several females, Entebbe, Uganda, 1949, from under an elephant's ear where they were firmly attached. Forwarded ... for identification by Dr O. Fiedler of Onderstepoort. Some of these females had blood in their intestines and there seems little doubt that they were feeding on the elephant". Unfortunately there is no record as to how these *Culicoides* were collected. The identity of these midges will be discussed elsewhere. This note was only recently (1990) brought to our attention by Mr Alan Dyce of Sydney, Australia. Until that time we had thought that our findings on *Culicoides* behind the ears of elephants reported herein were unique, as Sikes (1971), in her "Natural History of the African elephant", recorded only the bloodsucking fly genera *Haematobia* and *Stomoxys (Muscidae)*, and *Glossina (Glossinidae)* as attacking elephants.

Live *Culicoides* found behind the ears of elephants (Fig. 2, 3 and 4; Table 1)

After the first collections of *Culicoides* were made from behind elephant ears in the northern KNP in 1983 one of us (L.E.O. Braack), in the ensuing years, examined the entire anatomy of another 30 elephants either culled or darted at a variety of sites in the KNP. When *Culicoides* were present they occurred only behind the ears. Here the skin is at its thinnest and smoothest, and, being liberally supplied with blood vessels, would seem to be the area most suitable for biting midges from which to obtain their bloodmeals. As described by Bannister & Skinner (1987), the elephant's bulk makes heat loss difficult, especially as it has no sweat glands. Cooling is achieved through the enormous ears. Weighing only 20 kg apiece, but

TABLE 1 *Culicoides* females found on the ears of elephants culled at four sites in the Kruger National Park, 1988–1992

Site Date Time No. of elephants Position	James Windmill 22.iv.1988 16:00–16:40 4 Behind ears	Mooigesig Dam 25.iv.1990 15:30–15:45 1 Base of ear	Mooigesig Dam 25.iv.1990 15:00–15:20 1 Behind ears	Mooigesig Dam 25.iv.1990 15:00–15:15 1 Behind ears	Houtbosch-rand 14.iv.1992 14:30–14:55 4 Behind ears	Masala Kop 28.iv.1992 14:55–15:35 3 Behind ears	TOTAL 14
Species: *C. kanagai*							
Nulliparous	15	87	11	3	0	0	116
Parous	25	61	23	12	0	1	122
Gravid	0	0	0	0	0	0	0
Bloodfed	0	2	1	0	0	0	3
TOTAL	40 (33,3 %)	150 (67,0 %)	35 (59,3 %)	15 (33,3 %)	0	1 (2,2 %)	241 (47,2 %)
Species: *C.* sp. #54 p.f.							
Nulliparous	29	17	4	6	9	14	79
Parous	47	46	18	18	4	31	164
Gravid	0	0	0	1	0	0	1
Bloodfed	0	3	0	2	2	0	7
TOTAL	76 (63,3 %)	66 (29,5 %)	22 (37,3 %)	27 (60,0 %)	15 (88,2 %)	45 (97,8 %)	251 (49,1 %)
Species: *C. tororoensis*							
Nulliparous	0	1	0	0	0	0	1
Parous	3	0	0	0	0	0	3
Gravid	0	0	0	0	0	0	0
Bloodfed	0	0	0	0	0	0	0
TOTAL	3 (2,5 %)	1 (0,4 %)	0	0	0	0	4 (0,8 %)
Species: *C.* sp. #50							
Nulliparous	0	6	0	1	0	0	7
Parous	1	1	0	1	0	0	3
Gravid	0	0	0	0	0	0	0
Bloodfed	0	0	1	0	0	0	1
TOTAL	1 (0,8 %)	7 (3,1%)	1 (1,7 %)	2 (4,4 %)	0	0	11 (2,1 %)
Species: *C. loxodontis*							
Nulliparous	0	0	0	0	1	0	1
Parous	0	0	0	0	1	0	1
Gravid	0	0	0	0	0	0	0
Bloodfed	0	0	1	1	0	0	2
TOTAL	0	0	1 (1,7 %)	1 (2,2 %)	2 (11,8 %)	0	4 (0,8 %)
GRAND TOTAL	120	224	59	45	17	46	511

comprising some 20 % of the elephant's surface area, the ears provide the major avenue for heat loss. Blood passes through them at a rate of 5–12 *ℓ*/min, and this is responsible for as much as three-quarters of the heat loss needed to maintain a normal body temperature. Although *Culicoides* were found on almost any part of the back of the ear, there appeared to be a preponderance of midges on the upper half of the ear where they were often congregated in groups of eight or more (Fig. 3 and 4). It is interesting to note that all elephants, young and old, have the characteristic ear "turnover" where the upper margin of the ear limply folds back (Fig. 2). Under this fold the ear will be almost permanently shaded, and this may further suit the needs of bloodfeeding *Culicoides*. On one of the Mooigesig elephants a large number of midges were also collected at the base of the ear. Although it is noted by Young (1972) that elephants' ears "exude a large quantity of moisture" and that elephants captured on hot days are "usually noticeably wet behind the ears", none of the ears examined by us were damp or moist, and the 2–3-mm thick layer of clay that caked variable parts of the ear was always dry (Fig. 4). During the cooler autumn months (when obligatory culling is done in the KNP), moisture loss from the ear surface might be reduced.

Table 1 gives the exact number and age status of a total of 511 *Culicoides* of five species found live behind the ears of 14 elephants culled at the four sites of James Windmill, Mooigesig, Houtboschrand and Masala. Of these, 204 individuals (39,9 %) were nulliparous, 293 (57,3 %) empty parous and 13 (2,5 %) freshly bloodfed, while only one female (0,2 %) was gravid. The age composition of the *Culicoides* found behind the ears clearly indicates that the *Culicoides* are there to feed; in all biting Nematocera (Diptera) it is the empty parous and nulliparous individuals that are hungry. This interpretation agrees with that made by Downes (1950) and Reuben (1963) on the Palaearctic species *C. nubeculosus* and *C. impunctatus*, respectively, and more recently, is supported by Braverman (1992) who found that of 522 *C. imicola* captured on a calf in Israel, 65,5 % were nulliparous and 34,5 % parous; of these 11 % were freshly bloodfed.

The presence of only one gravid female *Culicoides* behind elephant ears suggests strongly that once midges have fed, they vacate the host to digest the blood and develop their ovaries in a suitable microhabitat which is apt to be in the nearby vegetation. Besides constantly fanning themselves with their ears during the hottest hours of the day, elephants are also "partial to wallowing in mud or dusting themselves to protect the skin from the hot sun or to rid themselves of parasites" (Smithers 1983). It seems realistic to suggest that these activities of pachyderms must be

FIG. 2 Upper margin of an elephant's ear showing venation, flecks of dried mud, and shaded area beneath characteristic "turnover"

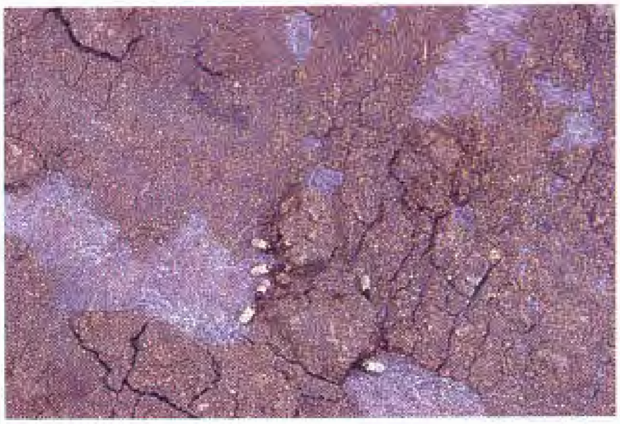

FIG. 4 Mooigesig culling site: eight *Culicoides* females behind elephant's ear, with grey areas of smooth skin between thin layer of cracked mud; though not clearly visible, one of the central group of six midges is freshly bloodfed (see Fig. 3); obvious wing pattern indicates all except one to be *C.* sp. #54 p.f.; patternless species *C. kanagai*

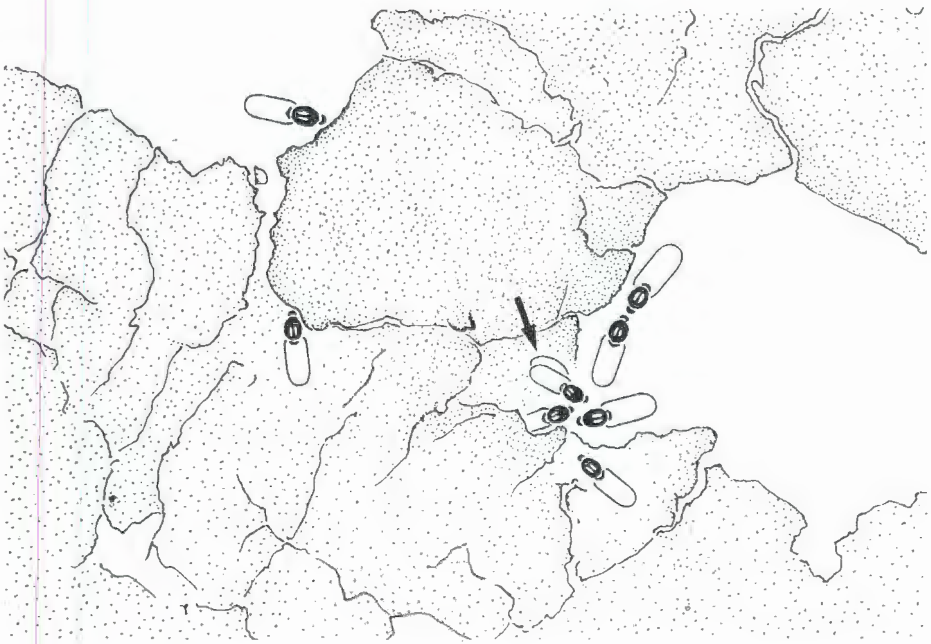

FIG. 3 Pen sketch of Fig. 4: arrowed *Culicoides* sp. #54 p.f. freshly bloodfed

hazardous for tiny biting midges and, as ovarian development in *Culicoides* in hot climes takes 2–3 d, it seems unlikely that the midges would hold on grimly behind the ears of a very active host for so long to achieve full gravidity. We also discount the possibility that, having taken blood, *Culicoides* will migrate to other parts of the elephants' anatomy, such as near the anus, to develop their ovaries while awaiting the evacuation of dung. As stated before, one of us (L.E.O. Braack) has, over the years, examined the entire anatomy of 30 elephants for various biting arthropods and has always seen *Culicoides* only behind the ears. Finally, the capture of large numbers of gravid females in light-traps further indicates that *Culicoides* mature their ovaries away from the host. We therefore have no evidence that gravid females of the various *Culicoides* species remain on the host as apparently is the case with the adult hornfly *Haematobia irritans* (Muscidae: Stomoxyinae) which "remains on the host day and night, the females leaving only briefly to deposit their eggs" (Harwood & James 1979).

Of some interest is the fact that 13 freshly bloodfed *Culicoides* were captured off ears in broad daylight. In the photograph (Fig. 4), taken in full sunshine at 15:00 at the Mooigesig dam site, it can be seen, albeit faintly, that one of the *Culicoides* is still feeding and is almost fully engorged. This individual is arrowed in Fig. 3. This gainsays the general belief that all *Culicoides* are exclusively nocturnal in their activity patterns, especially during that of bloodsucking.

Although four elephants were examined at Langtoon, only one nulliparous specimen of *C.* sp. #54 (p.f.) was found (not tabulated). This finding must be interpreted with caution. It is quite possible that not all individuals in a herd of elephants need have attendant *Culicoides*, but it must also be noted that culling is a deeply traumatic experience for these animals as they are herded into a tight group by a noisy helicopter mere metres above them. In addition, the vortex created by the helicopter blades raises clouds of dust and even lifts the ears of some elephants. Under these circumstances it is indeed remarkable that any *Culicoides* remain attached behind the ears, as to do so they must undergo a frenzied period of herd panic that may last from 1–5 min. However, some of our observations left us in no doubt as to the tenacity of these tiny insects. For example, at the Mooigesig culling site, where 328 *Culicoides* were collected off three elephants, we found it extremely difficult to suck the midges up with a pooter. Even when they were "tickled" with the tip of the pooter, and sucked at simultaneously, they still would not release their foothold, but would either remain motionless or would walk away to creep and hide between the cracks in the mud which thinly layers large areas of the ears (Fig. 4). Only midges which were seen to alight during collecting periods were easily disturbed and would fly away. In fact, these *Culicoides* seemed very aware of any movements one made, and were difficult to capture.

From Table 1 it can be seen that *C. kanagai* and *C.* sp #54 p.f. made up 96,3 % of all midges found behind elephant ears. We are unable to explain why *C. loxodontis*, *C. tororoensis* and *C.* sp #50 were so rare. Judging from the high numbers caught in light-traps, *C. loxodontis* may be more nocturnal in its feeding habits, but the capture of similarly large numbers of *C.* sp. #54 p.f. in light-traps, a species also found commonly behind elephant ears by day, indicates that factors other than nocturnalism/diurnalism may be at play. *C. kanagai* presents yet another problem with interpretation: while it was a co-dominant species behind elephant ears it was rare in the light-trap collections (2,28 %). What seems evident, is that *C. loxodontis*, *C. kanagai* and *C.* sp. #54 p.f., in being common near elephants, feed on them too, and in this broad sense they can be said to occupy the same niche. However, the disparities in their prevalence and abundance patterns imply that each species differs from the next in certain unknown details of its life-cycle. Finally, as many other game species occupy the same territory as elephants, we remain open to the possibility that these may also provide bloodmeals, but we strongly doubt whether any of them play a more important role in the life-cycle of these *Avaritia* species than the elephant does.

Live *Culicoides* attracted to the intestinal dung of disembowelled elephants (Fig. 5; Table 2)

At the Langtoon, Mooigesig and Masala culling sites the large intestines of six elephants were slit near the anus to leave the fully digested, bronze-coloured dung exposed (Fig. 5). These ruptures were monitored for 10–25 min and as many as possible of the *Culicoides* seen attracted to the dung were collected with a suction pooter.

While these ruptured entrails were being monitored, *Culicoides* could be seen approaching upwind on an

FIG. 5 Mooigesig culling site: slit intestines of elephant exposing partly digested, pale green browse (left) and mature, fully digested, bronze-coloured browse (right); gravid *Culicoides* females only attracted to the latter for ovipositing

TABLE 2 *Culicoides* females attracted to the intestinal dung of six elephants disembowelled at three sites in the Kruger National Park, 1990–1992

Site Date Time No. of elephants	Langtoon Dam 24.iv.1990 16:10–16:35 2	Langtoon Dam 24.iv.1990 16:00–16:25 1	Langtoon Dam 24.iv.1990 16:40–16:50 1	Mooigesig Dam 25.iv.1990 16:15–16:30 1	Masala Koppies 28.iv.1992 15:40–16:00 1	TOTAL 6
Species: *C. kanagai*						
Nulliparous	0	0	0	1	0	1
Parous	0	1	0	1	0	2
Gravid	1	1	0	0	0	2
Bloodfed	0	0	0	0	0	0
TOTAL	1 (3,2 %)	2 (3,7 %)	0 + 1 male	2 (4,2 %)	0	5 (2,9 %)
Species: *C.* sp. #54 p.f.						
Nulliparous	0	0	2	0	0	2
Parous	2	9	6	5	2	24
Gravid	26	42	5	41	22	136
Bloodfed	0	0	0	0	0	0
TOTAL	28 (90,3 %)	51 (94,4 %)	13 (100,0 %)	46 (95,8 %)	24 (100,0 %)	162 (95,3 %)
Species: *C. loxodontis*						
Nulliparous	0	0	0	0	0	0
Parous	0	0	0	0	0	0
Gravid	2	1	0	0	0	3
Bloodfed	0	0	0	0	0	0
TOTAL	2 (6,4 %)	1 (1,9 %)	0	0	0	3 (1,8 %)
GRAND TOTAL	31	54	13	48	24	170

almost imperceptible breeze (exact windspeed unknown but certainly < 1 m/s). They would then fly around actively and soon alight on the neighbouring whitish intestine or on the dung itself. Most midges would swiftly enter the crevasses in the dung, presumably to oviposit. With the use of a suction pooter about 30 female *Culicoides* could be collected in 20 min. However, they were not easy to harvest, as most of the females either entered the dung quickly, or gripped firmly on to the wet areas. Still others had alighted on blood on the ruptured intestine, where they struggled to free themselves. A fourth category consisted of those walking actively on the sun-dried parts of the intestines, but these were easily disturbed and therefore difficult to approach and collect by pooter. During the 15–25 min of collecting a slight decrease occurred in the number of *Culicoides* visiting the dung, but there was never a total absence. It appears, therefore, that dung remains attractive to ovipositing *Culicoides* for at least an hour.

At the Mooigesig and Masala sites a slit was also made higher up in the small intestine of two elephants to reveal a large amorphous mass of partly digested, pale green browse in the very early stages of fermentation (Fig. 5). This "young" dung was, on both occasions, monitored for 10 min, but not a single *Culicoides* was seen. This dung probably lacks the necessary attractant volatiles that emanate from the darker and more mature khaki-coloured dung that is found lower down the intestine near the anus, where it is already compressed into boli ready for evacuation.

Elephant dung, after being dropped to the ground, is invaded within minutes by tens to thousands of arthropods, principally larger Diptera and Coleoptera. Their presence, especially during the height of summer, makes close observation difficult as they get into the eyes, nose and throat of the observer. From our present observations, made during the autumn months when insect activity is on the decline in the KNP, it now seems evident that *Culicoides* midges are amongst the first insects to arrive at dung, and therefore may also be amongst the first to leave. Quick oviposition may be part of an evolutionary adaptation enabling the now empty parous females to locate an elephant before it, or the herd, has moved 100 m or more. In this way the cycle of feeding behind the ear can begin again. The quick arrival of gravid *Culicoides* at dung also implies that they must all the while have been in close attendance to the elephants. As our search has thus far failed to reveal gravid female midges on any part of the anatomy of elephants, we suggest that they most probably reside in a suitable microhabitat in the vegetation, and will be stimulated into activity only when the elephants pass in close

TABLE 3 Comparison of gonotrophic status of *Culicoides* (all species) from behind the ears and attracted to the intestinal dung of elephants in the Kruger National Park, 1988–1992

Gonotrophic status of *Culicoides*	Behind ears of elephants	Attracted to intestinal dung of elephants
Nulliparous	204 (39,9 %)	3 (1,8 %)
Parous	293 (57,3 %)	26 (14,6 %)
Gravid	1 (0,2 %)	141 (83,0 %)
Bloodfed	13 (2,5 %)	0
Males	0	1 (0,6 %)
TOTAL	511	171

proximity, in which case they will follow the elephants to await the evacuation of dung.

Table 2 gives the exact number and age status of 171 *Culicoides* of three species caught live at dung. Of these, three individuals (1,8 %) were nulliparous, 25 (14,6 %) were empty parous, 142 (83,0 %) were gravid, while one male (0,6 %) was captured. The results are extremely interesting in that they reveal the age structure of this part of the population of *Culicoides* collected to be diametrically opposed to the age structure of that part found at the same time behind the ears of elephants. These two samples are compared in Table 3. As the clear majority of females at dung were gravid (83,0 %), it seems superfluous to say that they were there to lay eggs. However, it may be argued that these midges were visiting dung to obtain moisture in an environment that is very dry at this time of the year. But if this is indeed part of the survival strategy of *Culicoides*, one would expect nulliparous females, and also males, to take part. Perhaps the most cogent evidence against the argument that these midge adults are at the dung solely to imbibe moisture, is that during studies done in the KNP from 1985–1992, one of us (R. Meiswinkel), reared all the presently tabled *Avaritia* species from elephant dung, proving beyond doubt that this is the preferred larval habitat of their immature stages. The 25 empty parous females (14,6 %) captured at dung are probably individuals that had just completed ovipositing.

From the data contained in Tables 1–3 the adult ecology of these five *Culicoides* species can broadly be sketched as follows:

(i) After feeding behind the ears of elephants, the females

(ii) vacate this host to develop their ovaries in a suitable microhabitat in the nearby vegetation.

(iii) Once fully gravid, 2–3 d later, they may disperse in search of elephants; alternatively, they may be stimulated into flight and egg-laying activity only when elephants pass nearby.

(iv) An elephant, or a herd, is then followed and eggs are laid immediately dung is evacuated.

(v) Within minutes the task of egg-laying is complete and the now empty parous female *Culicoides* leaves the dung to find an elephant that would not have progressed more than ± 100 m, and

(vi) when the midges once again feed behind the ear, the cycle is repeated.

The question remains as to how nulliparous female *Culicoides*, newly mated and freshly emerged from dung, locate their hosts. Though further research is needed here, we surmise that host location by nullipars is a fairly random exercise and that dispersion in search of hosts may take place towards dusk when local conditions, such as relative humidity, are more conducive. Alternatively, as suggested above for gravid females, they may also rest in vegetation to await the passing of elephants. Such strategies may be considered far too disadvantageous for such tiny insects, giving them little chance of success in a continent as large as Africa. However, elephants are "gregarious and live in family groups", while a number of groups "may coalesce to form herds" (Smithers 1983). In the KNP the 7500 elephants comprise at least 22 clans, each clan having a distinct home range or territory (A. Hall-Martin, unpublished data 1984; Whyte 1993). Depending upon the whereabouts and availability of watering points, elephants will criss-cross this clan range in an almost predictable pattern. As stated by Smithers (1983), elephants create "well worn paths which are regularly used over many years and are a feature of elephant country". It is certain that their dung will be randomly dropped along these routes, at feeding points and at watering holes. The existence of clan ranges thus leads to a build-up of coprophilic *Culicoides* species and also means that newly emerged midges stand a reasonable chance of making contact with an elephant.

Similarly, if freshly engorged *Culicoides* abandon a host after taking a bloodmeal to develop their ovaries in the surrounding vegetation, it seems likely that a good proportion of them, when fully gravid and ready to lay eggs, will quite easily locate an elephant two or three days later and follow it until dung is evacuated. Grown elephants eat, on average, between 170 and 300 kg of green food per day (Moss 1976; Guy 1975, cited in Smithers 1983), approximately half of which will be dropped as dung daily. Dougall & Sheldrick (1964), in Kenya, observed a ten-year-old elephant male, weighing a little over 1800 kg, to evacuate 75 kg of dung in 12 h (diurnal). Coe (1972), also in Kenya, observed a ten-year-old captive elephant, over four days and three nights, to evacuate an average of 100,36 kg every 24 h. He found that the time between each defaecation for four age groups of elephants varied from 1,41–1,91 h, and this revealed "no significant difference between the grouped rates for day and night, suggesting that digestive activity and perhaps feeding do not change appreciably". Such a consistent rate of defaecation means that within each elephant clan range, dung will be plentiful and, furthermore, will be more or less evenly distributed along all regularly used paths. It is along these selfsame routes that a large percentage of blood-engorged *Culicoides* would originally have abandoned their hosts, and they would therefore have been in the near vicinity two or three days later when the elephants revisited the area. Our observations, recorded above, as to how quickly gravid *Culicoides* come to the dung of freshly disembowelled elephants, seems to bear out this supposition. Furthermore, our failure to find, behind elephant ears, either gravid females or individuals with partly digested, blackened blood in their abdomens, seems to further reinforce the notion that they do not stay on the elephant to develop their ovaries.

Geographic distribution of dung-inhabiting *Culicoides* species

Unpublished data reveal that two of the commonest species in the KNP, *C. loxodontis* and *C.* sp. #54 p.f., are very resource-specific as regards their larval habitat as they will rarely, if ever, oviposit in dung other than that of the elephant. As reported by Meiswinkel (1992) *C. loxodontis* is found exclusively in "elephant country" where it is often the dominant *Culicoides* amongst 20 or more species recorded in light-trap catches. Outside the range of larger elephant groups, i.e. in lone-bull territory, *C. loxodontis* declines markedly in numbers, to disappear entirely from areas where elephants do not occur, even if those areas are only a few kilometres distant. Because of this strong dependence on elephant dung, *C. loxodontis* has never been found in those parts of South Africa where Man husbands cattle, horses, sheep, etc., and where he, in the process of establishing his farms, has exterminated Africa's game animals. There is mounting evidence that most *Culicoides* species relying on the dung of these herbivores have undergone a parallel extinction in the farming arena, and this explains why *C. kanagai*, *C. tororoensis*, *C. loxodontis*, *C.* sp. #50 and *C.* sp. #54 p.f., are either new records or only recently discovered taxa in South Africa.

From the foregoing it seems clear that the geographic distribution of coprophilic *Culicoides* is unequivocally dependent on the whereabouts and availability of herbivore dung, and that this association is the primary factor determining the geographic distribution of the five *Avaritia* species concerned. Climate probably plays a secondary role, but here more evidence is needed.

Light-trapping (Tables 4 and 5)

At two of the five culling sites light-trap collections were made from 17:00–22:00; each specimen was sexed, and the females age-graded (Tables 4 and 5).

Based on their known larval habitat preferences, the 21 species captured split neatly into the dung- and groundwater-inhabiting sectors of the genus *Culicoides*. While it is premature to speculate too deeply on what has been collected in 10 h on two consecutive nights at two sites 35 km apart, the significant disparity

TABLE 4 Mooigesig Dam elephant culling site, KNP; analysis of species and age-grading of *Culicoides* caught in light-trap, 25.iv.1990

Culicoides species	Females				Males	TOTAL	%
	Nullipar	Parous	b/f	Gravid			
*C. loxodontis**	383	369	5	404	132	1293	53,47
C. sp. #54 p.f.*	101	94	5	535	11	746	30,85
C. imicola	1	0	0	63	0	64	2,65
C. kanagai *	11	8	0	33	6	58	2,40
*C. tororoensis**	33	4	0	3	16	56	2,32
C. kobae	2	0	1	39	0	42	1,74
C. ravus	3	0	2	27	3	35	1,45
C. tropicalis	1	0	3	19	0	23	0,95
C. sp. #50*	4	6	0	6	2	18	0,74
C. bolitinos	2	7	0	8	0	17	0,70
C. leucostictus	1	0	1	9	3	14	0,58
C. similis	2	0	0	6	3	11	0,45
C. nigeriae	6	0	0	2	2	10	0,41
C. sp. #3 (Schultzei group)	1	0	0	8	0	9	0,37
C. walkeri	0	0	1	6	1	8	0,33
C. pycnostictus	1	0	0	3	0	4	0,16
C. dutoiti	1	0	0	2	0	3	0,12
C. schultzei s.s.	0	0	0	2	0	2	0,08
C. micheli	0	1	0	1	0	2	0,08
C. sp. #110 (Schultzei group)	0	0	0	2	0	2	0,08
C. nivosus	0	0	0	1	0	1	0,04
TOTAL						2418	

**Culicoides* species caught behind elephant ears and reared from their dung

TABLE 5 Langtoon Dam elephant culling site, KNP; analysis of species and age-grading of *Culicoides* caught in light-trap, 24.iv.1990

Culicoides species	Females				Males	TOTAL	%
	Nullipar	Parous	b/f	Gravid			
*C. loxodontis**	206	199	1	322	27	755	47,04
C. sp. #54 p.f.*	391	63	1	247	40	742	46,23
*C. kanagai**	9	4	0	20	2	35	2,18
*C. tororoensis**	6	9	0	13	1	29	1,81
C. imicola	1	1	0	13	0	15	0,93
C. bolitinos	0	5	0	7	0	12	0,75
C. sp. #50*	5	6	0	0	0	11	0,68
C. ravus	1	0	0	1	0	2	0,12
C. pycnostictus	1	0	0	1	0	2	0,12
C. kobae	0	0	0	1	0	1	0,06
C. leucostictus	0	0	0	0	1	1	0,06
TOTAL						1605	

**Culicoides* species caught behind elephant ears and reared from their dung

in abundance between the "dung" and "groundwater" groups of *Culicoides* in dry, open bushveld warrants brief comment:

1. The light-trap catches were dominated by the same five *Avaritia* species found live behind the ears and at the dung of culled elephants, i.e. 89,8 % at Mooigesig and 97,9 % at Langtoon. Similarly 96 % of the 250 males found in the traps also belonged to these species, proving that in the preceding weeks elephants had been resident in the area and had dropped fair amounts of dung.
2. Of the remaining 16 species caught in light-traps, 15 (6,24 %) rely solely on groundwater for their larval habitat, and include *C. imicola* (1,96 %). Their low prevalence is probably the result of limited breeding sites in predominantly dry bushveld, this rarity perhaps exacerbated by a feeding preference for other hosts. Two aspects of the biology of the "groundwater" species restrict their ability to disperse widely or rather, once dispersed, would prevent them from establishing viable populations in a new locale. The first is the utter dependence of the immature stages on moist habitats such as found on the edges of rivers, dams and marshes. Secondly, in these situations, the adults would in all likelihood obtain their required bloodmeals as there is an assured and varied biomass of game that visits daily because of their reliance on water. For this reason it seems unnecessary for "groundwater" *Culicoides* to disperse widely from their riverine habitats. However, if they should, it is probable that the mortality rate amongst gravid females would be high because of the distances involved to locate suitably moist oviposition sites in large expanses of dry bushveld. There is no evidence that "groundwater" *Culicoides* species will utilize animal dung as an alternative larval habitat.

It is untrue that the relative scarcity of this "groundwater" group in the present collections is due solely to their populations being low during the autumn months of the year, or to their not being attracted to light-traps. Much unpublished light-trap data collected by us over the years reveal that most of these species can be abundant at any time of the year, but mostly along the larger sand rivers such as the Luvuvhu, Shingwedzi, Letaba, Olifants and Sabie (Fig. 1), and that their numbers decline as one collects further away from water into the drier bushveld.

As regards the coprophilic *Avaritias* found in the light-trap collections, it is sufficient to note that *C. loxodontis* and *C.* sp. #54 p.f. are amongst the most abundant species of *Culicoides* found in the KNP, and that *C. kanagai*, *C. tororoensis* and *C.* sp. #50 are always caught in light-traps, or reared from dung, in low numbers. In fact, the highest numbers of *C. kanagai* yet collected in the KNP are the 200 females presently recorded from behind elephant ears at Mooigesig.

As already indicated elsewhere, explanations for the differences observed in the prevalence and abundance patterns of these five elephant-dung-inhabiting *Avaritia* species require further investigations into their bionomics. Light-traps are too one-sided in the data they provide and, for obvious reasons, would help little to establish whether a particular species is more diurnal than nocturnal in its habits. Furthermore, they cannot clarify why some species persist at such low population levels. Species may also be rare because they cannot tolerate the predominantly dry conditions that persist in the KNP, and if there are indeed preferences in terms of climate, it needs to be recognized that the KNP may be too small and homogeneous a fragment of Africa to enable us to fully probe such trends. In addition, the severe depletion in numbers of the African elephant and the fragmentation of its distributional range into ever smaller enclaves throughout the continent would further complicate such investigations. Taking the argument in another direction, one may also ask: in the process of maintaining a constant number of 7 500 elephants on 2 000 000 ha, and in preventing them from moving further afield, is Man not creating unnaturally high populations of some elephant-associated *Culicoides*? There is much unpublished data indicating that when Man maintains large numbers of domestic stock in confined spaces, and irrigates pastures and builds dams, he works against those natural laws that use animal migration and drought cycles to suppress escalating parasite populations.

Taxonomy

All five species of *Culicoides* found on elephants and reared from their dung, belong to the subgenus *Avaritia* Fox, 1955. This subgenus comprises some 70 species worldwide; these fall into ten or more groups, at least six of which occur in the Afrotropical Region (Meiswinkel 1991). However, taxonomic understanding of the subgenus is far from complete; more than half the African species still need to be described, and the six species groups to be defined. Until this is done we restrict ourselves to only briefly discussing each species below.

1. *C. kanagai* Khamala & Kettle, 1971, has on a few occasions been reared from elephant dung. It is rarely caught in light-traps, and, in fact, the largest numbers taken are those herein reported from behind elephant ears. *C. kanagai* was originally described from two females from Kenya; later both sexes of *C. kanagai* were described and brief notes given on its distribution and biology in the KNP (Meiswinkel 1987). However, there is still some doubt as to its taxonomic status as it is very similar to *C. dasyops* (Clastrier, 1958), described from a single male from the Niokolo-Koba National Park, Senegal.
2. *C. tororoensis* Khamala & Kettle, 1971, is another species rarely caught in light-traps and it has, on a few occasions only, been reared in low numbers from elephant, zebra and white-rhinoceros dung (R. Meiswinkel & H. Nevill, unpublished data 1985–1992). Glick (1990) placed *C. tororoensis* in synonymy with *C. gulbenkiani* Caeiro, 1959, but our unpublished data indicate that these are two valid but closely related species that need to be re-examined both biologically and taxonomically. Dyce & Marshall (1989) reared *C. gulbenkiani* from elephant dung in the KNP but probably had *C. tororoensis* before them.
3. *C. loxodontis* (Meiswinkel 1992) is a member of the Imicola group that can be abundant, and also appears to be exclusively associated with the African elephant. Certain aspects of its biology and geographic distribution were touched upon during its recent description.

   Because *C. loxodontis* is morphologically very similar to *C. imicola*, these two species can easily be misidentified. However, while they may occur sympatrically, major differences in their larval habitat—and most probably host preferences—have meant that these two species have never been found to be co-dominant at any site in South Africa.
4. *C.* sp. #54 *sensu lato* (s.l.) is common and widespread in the KNP. It consists of two species very closely related taxonomically. These have been provisionally dubbed as *C.* sp. #54 pale form (p.f.) and *C.* sp. #54 dark form (d.f.). Morphologically, they differ in that the latter is generally smaller and has a darker wing pattern. They also differ in aspects of their biology (R. Meiswinkel, unpublished data 1985–1992) and pupal morphology (H. Nevill, unpublished data 1991). *C.* sp. #54 p.f. appears also to be exclusively associated with the elephant, and has been reared in large numbers from its dung. The dark form, however, has been reared from a variety of dung types including elephant, zebra, white and black rhinoceros (R. Meiswinkel, L.E.O. Braack & H. Nevill, unpublished data 1985–1992). Dyce & Marshall (1989) reared *C.* sp. #54 (s.l.) from elephant and zebra dung, and while their series from elephant dung might have included both forms, that from zebra would probably have been only the dark form. Taxonomically *C.* sp. #54 (s.l.) is closely related to *C. kanagai*, the major difference being that the former has strongly patterned wings whereas the latter possesses two pale spots along the costal margin only.
5. The fifth and last species found behind elephant ears, *C.* sp. #50, is a small member of the Grahamii group. It is uncommon in light-trap collections, and has on only a few occasions been reared from elephant dung in the KNP. Here it is important to re-examine the note made by de Meillon & Hardy (1953) that they had seen "several females of *C. grahamii* from under an elephant's ear" from Entebbe, Uganda. They were "forwarded ... for identification to Dr O. Fiedler of Onderstepoort". This note prompted us to search through the original manuscript of Fiedler's 1951 revision of 22 South African *Culicoides* species. In it a page of drawings was found, labelled: "*Culicoides* species from ear of elephant, Uganda." The sketches show two views of the female palp, one each of spermathecae, apex of hind tibia and the lengths and outline of the distal four segments of the antenna. Although these resemble *C.* sp. #50, to be expected as they are both members of the Grahamii group, Fiedler's measurements of the antennal segments do not tally at all with those of *C.* sp. #50. One of us (R. Meiswinkel) is aware of other undescribed species belonging to the problematical Grahamii group, and it is possible that one of these may be associated with elephants further north in equatorial Africa.

It is probable that the species recorded by de Meillon & Hardy was not *C. grahamii sensu stricto* (s.s.), as this species is known to be strongly anthropophilic in Central and West Africa. It is also true that females of the Grahamii group are particularly difficult to identify as, between species, there are only minute differences in the wing pattern. Ultimately, accurate identification of species of this group depends strongly on detailed examination of the various sensillae found on the antennae of both sexes, and the male genitalia.

CONCLUSIONS

Studies in the Kruger National Park, South Africa, show that five species of *Culicoides* of the subgenus *Avaritia* require the blood and dung of elephants to complete their life cycles, and that they will also feed in broad daylight. One consequence is that the midges will be found wherever elephants occur, and, in tandem with pachyderms, will penetrate even the driest tracts of savanna where they can comprise up to 90 % of all *Culicoides* captured in light-traps.

It is therfore reasonable to deduce that the geographic distribution of all coprophilic *Avaritias* in the Afrotropical Region will be found to mimic the movement of those animals that produce copious quantities of dung; the latter would include elephants, rhinoceroses, buffaloes, cattle, zebras, horses and wildebeests. This union between midge and mammal not only gives the relevant *Culicoides* a unique dispersal capability, but also brings them into play as potential vectors of disease. As regards the elephant, certain studies indicate it to be a possible reservoir host for African horsesickness virus (Mirchamsy & Hazrati 1973; Davies & Lund 1974; Erasmus *et al*. 1976; Davies & Otieno 1977; Binepal *et al*. 1992).

This host-mediated dispersal of *Culicoides* invites us to re-examine the statement by Hess (1988) that "it is unlikely that the host animals of *C. imicola* are involved in their dispersal over any more than relatively short distances". This may be so in the farming arena where sedentary domesticates facilitate the build-up of large foci of *C. imicola*, but while the need for any long-distance flights is obviated in such situations, the converse appears to be true for species like *C. kanagai*, *C. tororoensis*, *C. loxodontis*, *C*. sp. #54 p.f. and *C*. sp. #50 which have to be in the same locale as their roaming hosts. Unfortunately too little is known about the dynamics of this association to establish what distances are involved, what the midge mortality rates are, and what influence seasonal and climatic fluctuations have on their populations. In addition, the confinement of herds in national parks will also neutralize the negative impact that animal migrations and long-term droughts probably have on dung-inhabiting *Culicoides*, and may, instead, lead to an increase in their numbers. Whatever the realities, it remains true that coprophilic midges are widespread and can be both abundant and dominant in areas where "groundwater" *Culicoides*, including *C. imicola*, are virtually absent.

This association between a midge and a host also partly undermines the hypothesis that each season infective *Culicoides* need to be transported on the wind to cause disease outbreaks in distant places as was suggested for bluetongue in Malawi (Haresnape, Taylor & Lungu 1988). Hosts with attendant *Culicoides* could ensure that a cycle of orbivirus infection is maintained year-round whatever the movement patterns of the hosts are.

Most of the seven species of the subgenus *Avaritia* treated here are poorly understood taxonomically, and so will be confused with other apparently better known African species, e.g. *C. loxodontis* as *C. imicola*, *C. tororoensis* as *C. gulbenkiani*, and *C*. sp. #50 as *C. grahamii*. While the taxonomic differences between each species pair at first glance appear negligible, there are major differences in their bionomics. This has interesting and important implications as regards the epidemiology of certain viral and filarial pathogens.

If elephants do play a role in the epizootiology of African horsesickness, as has been mooted by several studies, it now seems probable that other *Avaritia* species besides *C. imicola* would be involved in the transmission of this virus.

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