

Geographical distribution and relative abundance of stock-associated *Culicoides* species (Diptera: Ceratopogonidae) in southern Africa, in relation to their potential as viral vectors

G.J. VENTER¹, E.M. NEVILL¹, and T.C. DE K. VAN DER LINDE²

ABSTRACT

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To determine the geographical distribution and relative abundance of *Culicoides* species associated with livestock, 220-V down-draught light-traps equipped with 8-W blacklight tubes were operated at 34 sites in different climatic regions in South Africa and Lesotho. From January 1984 to September 1986, 3 041 631 *Culicoides*, belonging to at least 50 species, were collected in a total of 959 collections. Of these, 572 412 individuals were identified and sexed.

Culicoides species were found to be widespread in South Africa and were collected in varying numbers at all the sites sampled. The average catch size, however, was larger in frost-free areas than in areas with extreme winters. The more abundant and widespread species, which have the potential to be vectors of stock-associated viruses such as bluetongue and African horsesickness, were *C. imicola*, *C. leucostictus*, *C. schultzei* s.l., *C. pycnostictus*, *C. nivosus*, *C. similis*, *C. zuluensis*, *C. magnus*, *C. bedfordi*, *C. neavei*, *C. brucei*, *C. tropicalis*, *C. expectator*, *C. gulbenkiani*, *C. bolitinos*, *C. ravus*, *C. coarctatus* and *C. onderstepoortensis*. Of these, *C. imicola* was the most abundant species, being dominant at 17 of the 34 sites sampled and accounting for 71,4% of the specimens collected. As *C. imicola* is relatively uncommon in hot and dry as well as cool and wet areas, this species cannot be regarded as the only vector of stock-associated viruses in southern Africa. Future laboratory vector-competence studies, i.e. determination of viral-infection and -transmission rates, should first concentrate on the above-mentioned *Culicoides* species, especially those known to feed on livestock.

Keywords: Ceratopogonidae, *Culicoides*, Diptera, geographical distribution, potential, relative abundance, stock-associated, viral vectors

INTRODUCTION

Bluetongue (BT) and African horsesickness (AHS) occur annually in the northern and eastern parts of South Africa and cause severe disease in sheep and horses (Verwoerd & Erasmus 1994; Coetzer & Eras-

mus 1994). The many serotypes of the orbiviruses that are responsible for these diseases are transmitted between the vertebrate hosts almost exclusively by biting midges of the genus *Culicoides*, which are true biological vectors (Tabachnick, Mellor & Standfast 1992; Mellor 1993).

An initial step in the elucidation of the epidemiology of a viral disease is the identification of all potential vectors. Species with a distribution approximating to or exceeding that of the disease, have to be examined first (Standfast & Dyce 1972). However, very little has been published on the geographical distribution and

¹ Onderstepoort Veterinary Institute, Onderstepoort, 0110 South Africa

² Department of Zoology and Entomology, Faculty of Science UOFS, P.O. Box 339, Bloemfontein, 9300 South Africa

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relative abundance of *Culicoides* species in South Africa. Nevill, Venter & Edwardes (1992) suggested that the seven *Culicoides* species having the highest potential as orbivirus vectors in South Africa, are *C. imicola*, *C. bolitinos*, *C. gulbenkiani*, some members of the *C. schultzei* group, *C. zuluensis*, *C. maganus*, and *C. pycnostictus*. Most of these species have already been shown to be abundant in the winter rainfall region of South Africa (Nevill, Venter, Edwardes, Pajor, Meiswinkel & Van Gas 1988), while *C. pycnostictus* and *C. zuluensis* were shown to be the most common species in the southern Free State and Lesotho, respectively (Jupp, McIntosh & Nevill 1980; Venter & Sweatman 1989). *C. bolitinos* was shown to be the most abundant species in the colder, high-lying eastern Free State (Venter & Meiswinkel 1994). However, information on the abundance of *Culicoides* species in other areas is scanty. The purpose of this study was therefore to rectify this situation by identifying and determining the relative abundance and distribution of the most important stock-associated *Culicoides* species more widely. This was done at 34 sites near livestock in different climatic zones in southern Africa.

MATERIALS AND METHODS

Light-trap collections

Down-draught light-traps (220 V) equipped with 8-W blacklight tubes were used. As collections were also used for virus isolation, they were made into phosphate-buffered saline (PBS) to which 0.5% "Savlon" (manufactured by Johnson & Johnson, and containing Chlorhexidine Gluconate and Cetrimide) antiseptic had been added. Large insects were excluded from the collections by mosquito netting placed around the trap. For a few consecutive nights, collections were made daily, stored at 4°C and then railed or air-freighted to the Onderstepoort Veterinary Institute (OVI) once a week (Nevill, Erasmus & Venter 1992). The results of the virus isolations appear in Nevill *et al.* (1992).

The number of collections made at each site was dependent on the collector present and therefore varied between one and 146 (Table 3); the majority of the collections were made during summer, except at Onderstepoort, Potchefstroom and Eiland (Table 1), where collections were made regularly throughout the year.

The number of *Culicoides* per collection varied between zero and more than 100 000. An attempt was made to identify all the *Culicoides* in a collection before using them for virus isolation, but if this was not possible, a random sample of 1 000 to 2 000 insects was identified and sexed. Identification was accomplished with the help of a slide reference collection, preliminary keys and a wing picture atlas of

Afrotropical *Culicoides* (R. Meiswinkel, OVI, unpublished data 1994). Catches that were not identified immediately, were stored in 80% ethanol.

Study area

From one to 146 collections per site were made at 33 sites throughout South Africa and at one site in Lesotho, between January 1984 and September 1986 (Fig. 1, Table 3). Tables 1 and 2 summarize the location, environmental factors and weather conditions (Weather Bureau 1986) at each site.

Since the main objective of this study was to identify *Culicoides* species which could be vectors of BT, AHS and other stock-associated viruses, most of the collecting was done near various livestock species (Table 1). The four collections made at Tugela (# 26), Loskop Dam Nature Reserve (# 30) and Mtubatuba (# 32) were the only collections where there were no livestock in the vicinity of the light-trap. According to Nevill & Anderson (1972), Dipeolu (1976), Murray (1987) and Nevill *et al.* (1988) the species and number of host animals in the vicinity of the light-trap probably have an influence on the *Culicoides* abundance and species diversity.

Collection sites varied from dry regions with an annual rainfall of only 169 mm (Veekos) (# 16) to high rainfall areas (Allerton) (# 9) with an annual rainfall of 927 mm (Table 2). Stellenbosch (# 6) (annual rainfall 619 mm) was the only site in a winter rainfall region.

The height above sea-level varied between 100 m (Mtubatuba) (# 32) and 2 800 m (Rhodes) (# 34) (Table 1). In addition, the temperature varied between relatively hot areas, e.g. Messina (# 18) with mean annual daily maximum and minimum temperatures of 29.4°C and 17.3°C, respectively, and relatively cold areas, e.g. Rhodes (# 34) with mean annual daily maximum and minimum temperatures of 19.6°C and 4.1°C, respectively (Table 2). Collections were made in frost-free or only light-frost areas, e.g. Ukulinga (# 4), Stellenbosch (# 6), Eiland (# 11), Louis Trichardt (# 14), Dohne (# 15), Messina (# 18), George (# 21) and Loskopdam (# 30), where for less than 1 d/year the minimum temperature is below freezing point, to areas with severe frost, e.g. Middelburg (Eastern Cape) (# 7) and Rhodes (# 34), which have 70.7 and 93.3 d/year, respectively, on which the minimum temperature is below freezing point (Table 2).

Collections were made in 22 of the 70 different vegetation regions of South Africa (Acocks 1975) (Table 1).

Farming activities at the collections sites varied from intensive mixed farming (Stellenbosch) (# 6) to situations where only a few riding horses were kept (Tshipise and Eiland). Apart from farming activities, irrigation also varied at the different sites (Table 1).

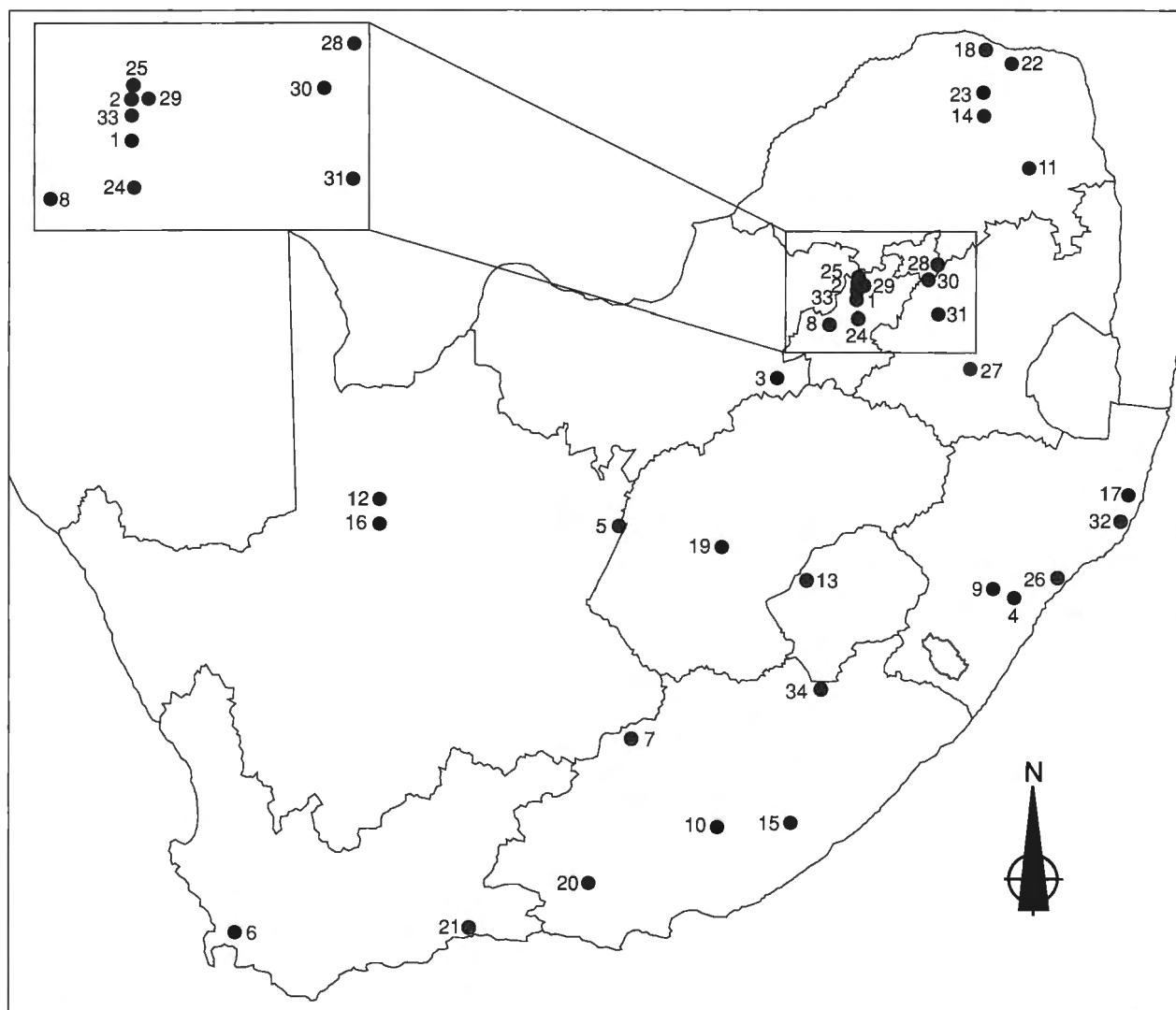


FIG. 1 Distribution of 34 light-traps used in *Culicoides* collections between January 1984 and September 1986. The numbers refer to Table 1. The division into provinces is the revised one of 1994

Value of light-traps as monitoring tool

To determine whether light-trap collections were representative of the *Culicoides* species flying in an area, light-trap collections made at five different sites (Onderstepoort, Kaalplaas, Soutpan, Diepsloot and Tshipise) (Table 1) were compared with vehicle-mounted-trap collections made at the same sites. The vehicle-mounted-trap was based on a design of Dyce, Standfast & Kay (1971). The vehicle was driven at 20 km/h over a fixed route at dusk and occasionally at dawn. In this way flying insects could be sampled randomly by the moving net.

When the total numbers of *Culicoides* of each species collected by means of the two methods were compared, there was a high correlation ($P < 0,001$) between their respective species compositions. At these five sites no single species was active solely

during the day or at dusk, therefore light-trap collections were representative of the species found near livestock in an area. The vehicle-mounted-trap, however, collected many more males than the light-traps. This was expected as, due to limited dispersal, male numbers are usually low in light-traps unless the trap is set very near a breeding site (Kettle 1962).

Representativeness of light-trap locations

At each of the 34 sites light-traps were operated at one permanent point for the duration of the survey. Factors which influenced the choice of sites, were the presence of livestock, the availability of 220-V electricity and easy access to the light-trap for regular collections. To evaluate how representative of an area the results from one permanent site in this area were, more intensive surveys were conducted at three of the 34 sites, namely Eiland, Allerton and Stellenbosch (Table 1).

TABLE 1 Summary of light-trap locations and the main environmental factors applicable at each of the 34 collection sites

Collection site & no.	Grid reference	Height above sea level (m)	Vegetation region (Acocks 1975)	Irrigation	Type of farming	Animals in vicinity of light-trap
1. Onderstepoort VI, stable 3	25°39'S, 28°11'E	1 219	Other turf thornveld	Yes	Experimental animals	Cattle
2. Onderstepoort VI, camp 168	25°39'S, 28°11'E	1 219	Other turf thornveld	Yes	Mixed	Cattle & horses
3. Potchefstroom Agricultural Research Laboratory	26°35'S, 27°14'E	1 345	<i>Cymbopogon Themedaveld</i>	Yes	Mixed	Cattle, sheep & poultry
4. Pietermaritzburg, Ukulinga Experimental Farm	29°40'S, 30°25'E	762	'Ngongoni veld of Natal mist-belt	Yes	Mixed	Cattle
5. Kimberley, "Mauritzfontein"	28°49'S, 24°45'E	1 200	Kalahari thornveld overtaken by karoo	Yes	Horses	Horses
6. Stellenbosch, "Welgevallen"	33°56'S, 18°52'E	119	Coastal renosterveld	Yes	Mixed	Cattle
7. Middelburg, Eastern Cape Grootfontein Agric. Coll.	31°29'S, 25°02'E	1 263	False upper karoo	Yes	Cattle, sheep & horses	Cattle, sheep, horses & goats
8. Diepsloot Nature Reserve, Gauteng	25°50'S, 27°50'E	1 500	Bankenveld	Yes	Cattle	Cattle
9. Pietermaritzburg, Allerton regional laboratory	29°32'S, 30°17'E	684	'Ngongoni veld	Yes	Experimental animals	Sheep & poultry
10. Adelaide Experimental Farm	32°38'S, 26°20'E	763	False thornveld, Eastern Cape	None	Goats & cattle	Goats
11. Eiland, Aventura Resorts	23°40'S, 30°45'E	400	North-eastern mountain sourveld	None	None	Horses
12. Upington Karakul Research Station	28°28'S, 21°20'E	793	Orange River broken veld	None	Karakul	Sheep
13. Roma, St Mary's High School, Lesotho	29°27'S, 27°45'E	1 690	<i>Cymbopogon Themedaveld</i> sandy veld	None	Mixed	Cattle, sheep, poultry & pigs
14. Louis Trichardt, Lot 285 Soutpansberg District	23°03'S, 29°54'E	961	Mixed bushveld	Yes	Maize	Cattle & game
15. Dohne Research Station, Stutterheim	32°31'S, 27°28'E	899	False Eastern Province thornveld	Yes	Cattle & sheep	Cattle
16. Upington, Veekos Experimental Farm	28°28'S, 21°20'E	793	Orange River broken veld	Yes	Sheep	Sheep
17. Hluhluwe, Lot H 110	28°05'S, 32°20'E	125	Coastal forest & thornveld	Yes	Cattle & goats	Cattle & sheep
18. Messina Experimental Farm	22°20'S, 29°55'E	500	Mopani veld	Yes	Cattle	Cattle, sheep & goats
19. Glen Agricultural College, Free State	28°57'S, 26°20'E	1 304	Dry <i>Cymbopogon Themedaveld</i>	Yes	Mixed	Cattle, sheep & goats
20. Steytleville, "Orange Grove"	33°22'S, 24°26'E	600	Succulent karoo	Yes	Sheep & goats	Sheep & goats
21. George, Outeniqua Experimental Farm	33°58'S, 22°28'E	221	Knysna forest	Yes	Sheep & cattle	Sheep & cattle
22. Tshipise, Aventura Resorts	22°33'S, 30°15'E	600	Mopani veld	None	None	Horses
23. Bergpan Salt Works, Northern Province	23°05'S, 29°05'E	961	Mixed bushveld	None	Salt works	Cattle
24. Irene Animal Production Institute	25°50'S, 28°12'E	1 448	Bankenveld	None	Cattle	Cattle
25. Soutpan Experimental Farm, Gauteng	28°22'S, 28°05'E	1 117	Sourish mixed bushveld	None	Cattle	Cattle
26. Tugela, Kwazulu-Natal	29°20'S, 31°28'E	122	Valley bushveld	None	None	None
27. Ermelo, "Ystervarkfontein"	26°31'S, 29°59'E	1 698	North-eastern sandy highveld	None	Mixed	Cattle
28. Groblersdal, "Weber Farm"	25°15'S, 29°26'E	953	Mixed bushveld	Yes	Sheep	Sheep
29. Honingneskrans, Pretoria	25°39'S, 28°11'E	1 219	Sourish mixed bushveld	None	None	None
30. Loskop Dam Nature Reserve	25°28'S, 29°26'E	1 009	Mixed bushveld	None	Game	Game
31. Middelburg, "Springboklaagte", Mpumalanga	25°48'S, 29°44'E	1 447	Bankenveld	None	Cattle & sheep	Sheep, goats & ostriches
32. Mtubatuba, Kwazulu-Natal	28°28'S, 32°10'E	100	Coastal forest & thornveld	None	None	None
33. Onderstepoort, "Kaalplaas"	25°39'S, 28°11'E	1 219	Other turf thornveld	None	Mixed	None
34. Rhodes, Eastern Cape	30°38'S, 27°58'E	2 800	<i>Themeda Festura</i> high mountain veld	Yes	Sheep	Sheep & cattle

Comparison of collections made immediately adjacent to livestock—in the general vicinity of livestock and where livestock were absent—showed that it was only in the latter situation that the light-trap collections were not representative of the *Culicoides* species associated with livestock. Collections made over a wide area, but still in the vicinity of stock, yielded more species, but there was no significant difference between the relative abundance of the various species caught in the different light-traps—as long as the light-traps were sited near stock. Therefore as a livestock-*Culicoides* sampling tool, a light-trap set at one permanent site near livestock could be regarded as a good indicator of the *Culicoides* species abundance for that particular area.

RESULTS AND DISCUSSION

Distribution and relative abundance of the genus *Culicoides*

The number of collections made and the maximum and average catch sizes at each site, are shown in Ta-

ble 3. A total of 3 041 631 *Culicoides* specimens were collected during 959 collections from 34 different sites. From these, 572 412 were identified and sexed (Table 3). *Culicoides* specimens were found in varying numbers at all the collection sites, emphasizing the wide distribution of this genus in southern Africa.

Notwithstanding the different climatic conditions at each site, which would have an influence on the number of *Culicoides* specimens collected, there are several other factors which may also influence the number of these specimens collected on a specific night. These include the presence of breeding sites and other light sources in the vicinity of the light-trap, the height of the light-trap above ground level (Murray 1987), wind-speed (Edwards, Kettle & Barnes 1987) the phase of the moon (Nelson & Bellamy 1971; Barnard 1980; Edwards *et al.* 1987) and even the tides (Reye & Lee 1962). Climatic conditions such as temperature and wind velocity (Murray 1987), and rainfall and relative humidity (Reuben 1963) during the trapping night may also influence the numbers of *Culicoides* collected. Even the physiological condition and the age of the population may influence these numbers (Brenner, Wargo, Stain & Mulla 1984).

TABLE 2 Summary of the main climatic conditions at the respective collection sites (S.A. Weather Bureau 1986)

Collection site	Weather station	Annual mean daily		Lowest mean daily temp. (°C)	Av. no. of days with temp. < 0 °C	Rainfall in mm		
		Max. temp. (°C)	Min. temp. (°C)			Oct.–March	April–Sept.	Total
Onderstepoort	Onderstepoort (agric.)	26,3	9,3	-3,7	32,8	604	102	706
Potchefstroom	Potchefstroom (agric.)	25,1	9,1	-5,4	41,0	517	108	625
Ukulinga	Ukulinga (agric.)	23,9	12,8	3,5	0,0	560	168	728
Kimberley	B.J. Vorster (airport)	26,0	10,8	-3,9	20,6	322	97	419
Stellenbosch	Elsenburg (agric.)	22,5	10,6	2,7	0,0	146	473	619
Middelburg (E. Cape)	Grootfontein (agric.)	23,0	6,1	-8,0	70,7	267	93	360
Diepsloot	Krugersdorp (council)	22,2	9,0	-2,5	13,9	633	134	767
Allerton	Pietermaritzburg (hospital)	24,6	12,3	1,3	1,3	747	180	927
Adelaide	Bedford & Fort Beaufort	23,7	10,1	-2,3	11,4	337	156	493
Eiland	Chester	28,9	14,2	1,9	0,4	449	79	528
Karakul	Upington (airport)	28,3	12,1	-3,2	16,4	147	48	195
Roma	Ladybrand & Modderpoort	22,0	7,6	-4,4	56,8	599	167	766
Louis Trichardt	Louis Trichardt	24,8	12,6	1,6	0,4	639	109	748
Dohne	Dohne (agric.)	21,9	10,6	0,9	0,5	547	212	759
Veekos	Upington (agric.)	28,2	11,4	-4,3	17,9	124	45	169
Hluhluwe	Mkuze	29,0	14,6	0,8	—	416	162	578
Messina	Messina	29,4	17,3	6,4	0,0	315	36	351
Glen	Glen (agric.)	24,8	7,6	-7,0	66,6	423	125	548
Steytlerville	Mentz Dam	26,0	11,1	-2,2	13,0	135	90	225
George	George (weather stat.)	21,4	11,0	2,8	0,1	425	345	770
Tshipise	Pangbourne & Messina	29,1	16,0	4,4	—	315	36	351
Bergpan	Mansfield	28,1	14,6	—	—	—	—	—
Irene	Irene (weather stat.)	23,6	9,7	-2,5	9,1	610	99	709
Soutpan	Onderstepoort (agric.)	26,3	9,3	-3,7	32,8	604	102	706
Tugela	Stanger	26,6	16,3	8,2	—	—	—	—
Ermelo	Ermelo	22,1	7,3	-6,2	25,8	645	110	755
Groblersdal	Oudestad (exp. farm)	26,9	11,7	-0,6	1,2	525	67	592
Honingneskrans	Onderstepoort (agric.)	26,3	9,3	-3,7	32,8	604	102	706
Loskop Dam	Loskopdam (water affairs)	27,9	13,5	3,3	0,3	572	104	676
Middelburg (Mpumalanga)	Middelburg (prison)	23,9	7,1	-6,0	66,0	628	107	735
Mtubatuba	Dukuduku (forestry)	26,6	15,8	7,2	—	—	—	—
Rhodes	Rhodes & Barkly East	19,6	4,1	-3,3	93,3	509	177	686

TABLE 3 Light-trap collections of *Culicoides* biting midges at 34 locations in southern Africa from January 1984 to September 1986. See Table 1 for details of collection sites

Collection site	No. of collections	No. of <i>Culicoides</i> collected	No. of <i>Culicoides</i> identified	Maximum catch size	Average catch size
1. Onderstepoort: Stable 3	146	104 720	88 358	8 320	717
2. Onderstepoort: Camp 168	82	92 540	68 201	5 492	1 129
3. Potchefstroom	77	15 767	15 230	2 942	205
4. Pietermaritzburg: Ukulinga	67	16 235	16 050	2 130	242
5. Kimberley	64	16 524	16 524	1 952	258
6. Stellenbosch	62	145 297	52 039	26 200	2 344
7. Middelburg (Eastern Cape)	61	14 008	13 680	1 407	230
8. Diepsloot	55	30 847	27 889	3 663	561
9. Pietermaritzburg: Allerton	55	25 497	16 360	8 148	464
10. Adelaide	39	57 503	30 149	6 876	1 474
11. Eiland	39	1 730 191	90 752	456 100	44 364
12. Upington: Karakul	35	4 646	4 646	990	133
13. Roma	32	32 778	31 897	3 884	1 024
14. Louis Trichardt	31	115 123	18 685	46 450	3 714
15. Dohne	22	110 161	35 281	40 800	5 007
16. Upington: Veekos	22	23 999	6 678	10 660	1 091
17. Hluhluwe	15	390 613	14 904	173 400	26 041
18. Messina	15	65 317	12 648	33 050	4 082
19. Glen	8	9 468	3 239	6 740	1 183
20. Steytlerville	6	253	253	49	42
21. George	4	312	312	193	78
22. Tshipise	4	24 785	2 191	14 000	6 196
23. Bergpan	3	9 700	1 099	7 860	3 233
24. Irene	3	569	569	246	190
25. Soutpan	2	1 455	1 455	1 228	738
26. Tugela	2	338	338	210	169
27. Ermelo	1	84	84	84	
28. Groblersdal	1	354	354	354	
29. Honingneskrans	1	514	514	514	
30. Loskopdam	1	255	255	255	
31. Middelburg (Mpumalanga)	1	458	458	458	
32. Mtubatuba	1	541	541	541	
33. Onderstepoort: Kaalplaas	1	490	490	490	
34. Rhodes	1	289	289	289	
Total	959	3 041 631	572 412		

When one takes the above into account, it is very difficult to make substantial conclusions on relative abundance from the calculated average catch sizes represented in Table 3. However, the large number of collections made at some of the sites, raised the reliability of the calculated average of the catch sizes for those sites.

The largest *Culicoides* collections were from Eiland ($\bar{x} = 44\ 364$) and Hluhluwe ($\bar{x} = 26\ 041$) (Table 3). Both these sites are in low-lying areas with warm summers and mild winters where frost is seldom experienced. Similar to this, large collections were also made at Stellenbosch ($\bar{x} = 2\ 344$), Louis Trichardt ($\bar{x} = 3\ 714$), Messina ($\bar{x} = 4\ 082$) and Tshipise ($\bar{x} = 6\ 196$) (Table 3). All of these are areas with warm summers and mild, frost-free winters (Table 2).

The average catch size was much smaller in areas with severe winters, such as Potchefstroom (205), Upington (Karakul) (133) and Middelburg (Cape) (230) (Table 3). Notwithstanding the severe winters

at Roma and Glen, the average catch sizes were relatively large, being, respectively, 1 024 and 1 183 (Table 3). The calculated catch size, however, is dependent on the seasonal distribution of the collections made. The Roma and Glen averages, for example, were calculated only on the summer catches as no collections were made during a large part of the winter when *Culicoides* were absent owing to low temperatures.

Karakul (# 12) and Veekos (# 16) Experimental Farms are both in the same climatic region and less than 10 km apart, yet the average catch size of 1 091 at Veekos was significantly larger than that of 133 at Karakul (Mann-Whitney test) (Table 3). Karakul is not irrigated and is 10 km from the Orange River, while Veekos is within 1 km of the Orange River and is irrigated from the river. The presence of the river, irrigation, denser vegetation and higher relative humidity, probably create a microclimate and breeding sites conducive to *Culicoides* breeding and survival.

Distribution and relative abundance of *Culicoides* species

Tables 4 and 5 show the *Culicoides* species composition, expressed as a percentage of the total *Culicoides* collected, at each of the 34 light-trap collection sites. Together with the fluctuation in *Culicoides* numbers, there was also a variation in the species composition at the different sites (Tables 4 and 5). The single most abundant species at each site is printed in bold. Where numbers appear in lieu of names in the tables, the numbering system of R. Meiswinkel is followed (OVI, unpublished data 1995).

Table 6 gives a summary of all the species collected as well as the total of the average number of each species collected per site, their relative abundance (the average number of each species collected as a percentage of the total collected) and the number of sites at which each species was collected. This information is converted to percentages and used to give an indication of possible vector rating for each species by using the average of the sum of the two different values. The purpose of this is to exclude species which, although common, have a very restricted distribution, e.g. *C. kobae* (which was found in very high numbers at only two sites) and to pay more attention to those species which are not only relatively abundant, but also have a wider distribution and are therefore considered better potential vector candidates.

Culicoides belonging to at least 50 species were collected. This is less than 50% of the more than 110 species found in South Africa (R. Meiswinkel, OVI, personal communication 1993). It must be taken into account that collections were made at only 34 sites, mainly near livestock, and that only a relatively small area of South Africa was sampled.

The probability of an insect feeding on a viraemic animal or suitable reservoir, becoming infected, surviving the 4–8-d incubation period, then feeding on a receptive host and transmitting the virus, is low. As a result, rare insects are unlikely to be important vectors (Standfast & Dyce 1972). Therefore the most widespread and abundant species will be better potential vectors than less abundant or localized species. Species which satisfy both these conditions—resulting in a vector rating of more than 25%—were *C. imicola*, *C. leucostictus*, *C. schultzei* s.l., *C. pycnostictus*, *C. nivosus*, *C. similis*, *C. zuluensis*, *C. magnus*, *C. bedfordi*, *C. neavei*, *C. brucei*, *C. tropicalis*, *C. exspectator*, *C. gulbenkiani*, *C. bolitinos*, *C. ravus*, *C. coarctatus* and *C. onderstepoortensis*. Of the above, only those species which were common and predominated at one or more sampling sites, as indicated in Tables 4 and 5, will be discussed further. They are *C. imicola*, *C. schultzei* s.l., *C. zuluensis*, *C. leucostictus*, *C. pycnostictus*, *C. magnus* and *C.*

bedfordi. For various reasons which will be explained later, *C. bolitinos*, *C. milnei* and *C. gulbenkiani* will also be discussed.

C. imicola

With a vector rating of 84,3%, *C. imicola* was the most abundant *Culicoides* species in this survey and accounted for 71,4% of all *Culicoides* collected (Table 6). *C. imicola* has a wide distribution in South Africa and was found at 33 of the 34 collection sites. At 17 of these, it was the single most abundant species (Tables 4 and 5). The highest numbers were collected at Eiland ($\bar{x} = 41\ 272$) and Hluhluwe ($\bar{x} = 23\ 793$). Even if the large numbers collected at these two sites were excluded, *C. imicola* would still form 29,2% of the species composition and remain the most abundant species in this survey.

This species was more abundant in the warm, low-lying areas (e.g. Eiland) than in areas characterized by cold winters and severe frost (e.g. Roma) (Table 4). *C. imicola* was also less abundant in warm/dry areas (e.g. Upington) (Table 4). In the winter rainfall region (e.g. Stellenbosch), where the summers are relative dry and the rainy season relatively cold, *C. imicola* was only the fourth most abundant species (Table 4).

At Middelburg (Eastern Cape), Roma (Lesotho), Vee-kos (Upington) and Ermelo, *C. imicola* made up less than 5% of the species composition (Tables 4 and 5). It was also less abundant in a survey in the colder high-lying eastern Free State (Venter & Meiswinkel 1994) and was rare in the Karoo and southern Free State (Jupp *et al.* 1980). In collections made in the absence of stock (e.g. Tugela and Loskopdam), *C. imicola* was replaced by *C. leucostictus* as the most abundant species (Table 5). A decline in the numbers of *C. imicola* collected in the absence of livestock, was also seen in collections made in the Kruger National Park (Meiswinkel 1989).

Outside the borders of South Africa, *C. imicola* is also widespread. It has been found over the whole of Africa as well as in neighbouring countries (Khamala 1971; Khamala & Kettle 1971; Davies & Walker 1974a; Dipeolu 1976; Dipeolu & Sellers 1977; Walker 1977; Phelps, Blackburn & Searle 1982; Meiswinkel 1989; Venter & Sweatman 1989; Glick 1990; Boorman & van Harten 1992). The most northerly distribution of *C. imicola* was extended to the parallel of 41°17'N after this species had been collected in Portugal following an outbreak of AHS in 1989 (Capela, Sousa, Pena & Caeiro 1993).

According to the results of precipitin tests, *C. imicola* feeds predominantly on cattle and sheep (Nevill & Anderson 1972; Braverman & Phelps 1981; Nevill *et al.* 1988), and is still the only proven vector of BT and AHS in South Africa (Du Toit 1944; Wetzel, Nevill &

TABLE 4 *Culicoides* species composition (%*) at sites 1–18 in southern Africa as determined by more than ten light-trap collections at each site. Full details of each site appear in Table 1

Site no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>Culicoides</i> spp.	98,0	79,9	94,9	58,2	78,5	11,3	1,8	70,7	69,9	83,6	93,0	9,8	1,7	24,5	15,5	4,8	91,4	38,6
<i>C. imicola</i>	0,2	2,1	0,1	3,7	0,4	0,1	5,1	2,9	7,8	2,0	0,1	1,0	1,1	1,4	0,2	1,5	2,1	0,5
<i>C. leucostictus</i>	0,3	2,2	0,1	0,8	4,8	0,0	14,9	0,1	3,1	0,7	5,3	49,4	5,1	7,5	0,0	68,9	1,8	12,8
<i>C. schultzei</i> s.l.	0,1	3,7	0,2	2,2	2,4	2,1	20,6	6,3	0,7	6,9	0,0	1,6	10,0	0,8	1,6	0,3	0,1	0,2
<i>C. pycnostictus</i>	0,1	5,7	0,1	1,2	4,0	0,1	11,8	0,8	0,2	0,8	0,1	16,9	0,9	0,6	0,3	1,6	0,5	0,1
<i>C. nivosus</i>	0,0	0,2	0,0	0,3	0,4	0,0	1,5	0,2	0,1	0,8	0,1	1,2	0,0	4,7	0,1	2,2	0,3	1,4
<i>C. simiis</i>	0,9	2,6	0,3	13,1	1,6	25,7	0,0	4,3	0,4	0,9	0,0	0,0	74,2	0,1	75,8	0,1	1,0	0,2
<i>C. zuluensis</i>	0,2	0,4	1,0	2,1	1,2	29,0	0,1	5,5	0,7	0,1	0,1	0,0	2,6	0,0	0,7	0,0	0,1	0,1
<i>C. magnus</i>	0,0	0,7	0,3	0,3	0,4	0,0	18,8	5,7	0,1	0,1	0,0	14,5	0,1	0,1	0,0	3,5	0,0	0,0
<i>C. bedfordi</i>	0,0	0,1	0,3	4,8	0,2	0,0	0,7	1,8	0,1	0,0	0,0	0,1	0,6	0,0	0,0	0,5	1,1	0,0
<i>C. neavei</i>	0,1	0,3	0,4	0,7	0,0	0,0	0,4	0,8	0,4	0,1	0,5	0,1	0,2	0,0	0,0	0,0	0,4	0,0
<i>C. brucei</i>	0,0	0,1	0,0	0,0	0,3	0,0	3,8	0,1	0,3	0,5	0,1	0,1	0,1	2,2	0,1	0,0	0,1	2,6
<i>C. tropicalis</i>	0,0	0,3	0,0	0,0	0,2	0,0	0,1	0,2	0,0	0,1	0,2	0,3	0,0	2,6	0,0	0,0	0,0	0,2
<i>C. exspectator</i>	0,0	0,0	0,0	1,0	3,0	27,0	0,0	0,2	0,1	0,1	0,0	0,0	0,0	0,0	1,2	0,0	0,0	0,0
<i>C. gulbenkiani</i>	0,0	0,0	2,2	10,0	1,7	4,6	0,4	0,2	6,8	3,8	0,1	1,3	1,3	0,4	3,2	0,2	0,2	2,0
<i>C. bollinos</i>	0,1	0,2	0,2	0,2	0,4	1,0	1,0	0,3	0,3	0,0	0,0	1,3	0,1	9,3	0,0	12,4	0,0	4,4
<i>C. ravidus</i>	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,3	0,0	0,0	0,0	0,2	0,1	0,0
<i>C. coarctatus</i>	0,0	0,0	0,3	0,0	0,1	9,4	0,1	0,1	0,1	0,1	0,0	0,3	0,0	0,0	0,0	0,2	0,8	0,0
<i>C. onderstepoortensis</i>	0,0	0,0	0,0	0,0	0,1	0,0	0,2	0,0	4,8	0,1	0,1	0,0	2,0	0,0	0,2	0,0	0,0	0,0
<i>C. milnei</i>	0,0	0,0	0,0	0,7	0,1	0,0	0,0	0,0	0,1	0,0	0,0	0,0	0,0	0,0	0,0	0,3	0,0	0,0
<i>C. engubandei</i>	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,1	0,0	0,0	0,0	0,0	0,0	0,0	0,3	0,0	0,0
<i>C. nigripennis</i> s.l.	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,1	0,0	0,0	0,0	0,0	0,0
<i>C. micheli</i>	0,0	1,6	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,1	0,0	0,0	0,0	0,0	0,0
<i>C. cornutus</i>	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,1	0,0	0,0	0,0	0,0	0,0	0,1	0,3
<i>C. sp. 30 (Avaritia)</i>	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
<i>C. macintoshi</i>	0,0	0,0	0,0	0,3	0,0	0,0	9,2	0,0	3,3	0,0	0,0	0,3	0,1	0,2	0,0	0,2	0,0	0,1
<i>C. trifasciellus</i>	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,2	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
<i>C. pretoriensis</i>	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,1
<i>C. glabripennis</i> s.l.	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
<i>C. eriodendroni</i>	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	2,9	0,0	0,0	0,0	0,0	0,0	0,0
<i>C. accraensis</i> s.l.	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
<i>C. angolensis</i>	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
<i>C. dutoitii</i>	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
<i>C. herero</i>	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
<i>C. dekeyseri</i>	0,0	0,0	0,0	0,0	0,0	0,1	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
<i>C. kobae</i>	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
<i>C. huambensis</i>	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
<i>C. isiolensis</i>	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
<i>C. moreli</i>	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
<i>C. sp. 66 (Avaritia)</i>	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
<i>C. galliardi</i>	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
<i>C. kibatiensis</i>	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Other <i>Culicoides</i> species	0,0	0,0 ^g	0,0	0,0	0,0	0,0 ^h	0,0	0,0	0,0 ^e	0,3 ^a	0,0	0,0 ^f	0,0	0,0	0,0	0,0	0,0	0,0
Unidentified species	0,0	0,0	0,0	0,1	0,0	0,0	0,0	0,0	0,5	0,0	0,0	0,2	0,0	0,0	0,3	0,3 ^{bcd}	0,0	0,0
										45,9								

* As % of total collection of each species
The single most abundant species at each site is printed in bold
0,0 = species representation < 0,05%

- ^a *C. sp. 54 (Avaritia)* s.l.
- ^b *C. sp. 95 (near bedfordi)*
- ^c *C. sp. 76 (near bedfordi)*
- ^d *C. sp. 89 (near dekeyseri)*
- ^e *C. sp. 65 (near citroneus)*
- ^f *C. sp. 90 (near exspectator)*
- ^g *C. punctithorax*
- ^h *C. sp. 61 (near pretoriensis)*

TABLE 5 *Culicoides* species composition (%*) at sites 19–34 in southern Africa as determined by less than ten light-trap collections at each site. Full details of each site appear in Table 1

Site	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
<i>Culicoides</i> spp.																
<i>C. imicola</i>	27,5	34,0	22,8	25,1	37,5	43,1	19,8	11,8	4,8	82,8	9,0	19,6	8,3	46,0	49,0	0,4
<i>C. leucostictus</i>	3,0	1,0	0,3	0,8	1,9	23,4	26,4	52,1	13,1	0,3	5,1	45,5	9,8	1,9	7,4	
<i>C. schultzei</i> s.l.	1,1	4,3		56,8	21,4	0,1	26,5	19,2		9,3	0,2	0,4	0,2	6,8		
<i>C. pycnostictus</i>	55,8	13,9		3,3	7,0	14,6	19,6	5,3	51,2		6,2	0,8	12,0			
<i>C. nivosus</i>	5,3	1,4	0,6	3,0	11,5	10,4	0,8	0,9		2,8	0,6	0,4			32,2	28,4
<i>C. similis</i>	2,4	1,9	0,3	2,5	0,1		1,8	5,6	9,5	0,9	1,6				8,8	0,7
<i>C. zuluensis</i>	0,2	6,7	60,9	0,2	0,2	1,9				0,3	0,2	4,3	6,3	0,2	0,4	
<i>C. magnus</i>	0,6	3,8	1,0	0,2	0,1	1,1	0,2		8,3		0,2		14,6	8,7	0,2	3,1
<i>C. bedfordi</i>	3,3	2,9	0,3	6,3	1,3	1,8	1,8				74,5		0,2	5,7	0,2	3,8
<i>C. neavei</i>	0,1	1,0	0,6		3,6	1,8	0,1		8,3		2,7		0,7		0,4	0,4
<i>C. brucei</i>		4,3			2,4	0,2	0,8		1,2			17,3	3,1	7,0		1,4
<i>C. tropicalis</i>	0,1	1,9			0,6	0,2	0,3			0,3		7,8				
<i>C. exspectator</i>		5,3	0,3	0,2	9,2	0,4	0,3					3,5			0,4	
<i>C. gulbenkiani</i>			1,6	0,5			0,1									
<i>C. bolitinos</i>		4,8	11,2	1,2		1,8	0,5			2,8			0,2			
<i>C. ravus</i>	0,1			0,0	0,3		0,1			0,3			0,2			0,4
<i>C. coarctatus</i>	0,0				0,2		0,2						0,2			0,4
<i>C. onderstepoortensis</i>		12,0					0,2						44,5	0,2		56,1
<i>C. milnei</i>					0,0			0,3						21,4		0,4
<i>C. engubandei</i>									2,4							5,2
<i>C. nigripennis</i> s.l.				0,0	0,4										0,4	
<i>C. micheli</i>					0,0										0,2	
<i>C. cornutus</i>																
<i>C. macintoshi</i>																
<i>C. pretoriensis</i>					0,2											
<i>C. glabripennis</i>					0,4											
<i>C. accraensis</i> s.l.					0,4		1,0									
<i>C. angolensis</i>					0,0											
<i>C. dekeyseri</i>					1,6											
<i>C. huambensis</i>																
<i>C. isioloensis</i>		0,5			0,3									1,7		
<i>C. galliardii</i>		0,5				0,1										
Unidentified species																0,4

* As % of total collection of each species
 The single most abundant species at each site is printed in bold
 0,0 = species representation < 0,05%

TABLE 6 *Culicoides* species representation, number of positive sites and species vector rating as determined with 959 light-trap collections at 34 sites, mostly near livestock, in southern Africa from January 1984 to September 1986

<i>Culicoides</i> species	Average no. of each sp. collected	% Relative abundance (a)	Positive sites (out of 34)	% Sites positive (b)	Vector rating % (a + b)/2
<i>C. imicola</i>	77 065,1	71,4	33	97,1	84,3
<i>C. leucostictus</i>	1 575,1	1,5	34	100,0	50,8
<i>C. schultzei</i> s.l.	9 115,1	8,5	30	88,2	48,4
<i>C. pycnostictus</i>	2 180,2	2,0	31	91,2	46,6
<i>C. nivosus</i>	1 070,2	1,0	31	91,2	46,1
<i>C. similis</i>	649,8	0,6	31	91,2	45,9
<i>C. zuluensis</i>	5 697,3	5,3	28	82,4	43,8
<i>C. magnus</i>	1 010,4	0,9	29	85,3	43,1
<i>C. bedfordi</i>	1 064,9	1,0	28	82,4	41,7
<i>C. neavei</i>	528,9	0,5	28	82,4	41,4
<i>C. brucei</i>	512,1	0,5	26	76,5	38,5
<i>C. tropicalis</i>	311,2	0,3	26	76,5	38,4
<i>C. exspectator</i>	534,2	0,5	23	67,6	34,1
<i>C. gulbenkiani</i>	715,2	0,7	20	58,8	29,7
<i>C. bolitinos</i>	594,2	0,6	20	58,8	29,7
<i>C. ravus</i>	761,0	0,7	19	55,9	28,3
<i>C. coarctatus</i>	47,7	0,0	19	55,9	28,0
<i>C. onderstepoortensis</i>	196,8	0,2	17	50,0	25,1
<i>C. milnei</i>	526,3	0,5	10	29,4	15,0
<i>C. engubandei</i>	70,1	0,1	10	29,4	14,7
<i>C. nigripennis</i> s.l.	4,7	0,0	9	26,5	13,2
<i>C. micheli</i>	5,5	0,0	7	20,6	10,3
<i>C. cornutus</i>	21,5	0,0	6	17,6	8,8
<i>C. sp. 30 (Avaritia)</i>	88,1	0,1	5	14,7	7,4
<i>C. macintoshi</i>	28,5	0,0	5	14,7	7,4
<i>C. trifasciellus</i>	16,5	0,0	5	14,7	7,4
<i>C. pretoriensis</i>	15,6	0,0	5	14,7	7,4
<i>C. glabripennis</i> s.l.	14,5	0,0	5	14,7	7,4
<i>C. eriodendroni</i>	0,4	0,0	5	14,7	7,4
<i>C. accraensis</i> s.l.	0,8	0,0	5	14,7	7,4
<i>C. angolensis</i>	0,9	0,0	4	11,8	5,9
<i>C. dutoiti</i>	0,9	0,0	4	11,8	5,9
<i>C. herero</i>	19,5	0,0	4	11,7	5,9
<i>C. dekeyseri</i>	52,0	0,1	3	8,8	4,4
<i>C. kobae</i>	3 194,9	3,0	2	5,9	4,4
<i>C. huambensis</i>	10,2	0,0	3	8,8	4,4
<i>C. isioloensis</i>	9,6	0,0	3	8,8	4,4
<i>C. moreli</i>	16,7	0,0	2	5,9	3,0
<i>C. sp. 66 (Avaritia)</i>	0,8	0,0	2	5,9	2,9
<i>C. galliardi</i>	0,2	0,0	2	5,9	2,9
<i>C. kibatiensis</i>	0,1	0,0	2	5,9	2,9
<i>C. sp. 54 (Avaritia) s.l.</i>	120,8	0,1	1	2,9	1,5
<i>C. sp. 95 (near bedfordi)</i>	1,0	0,0	1	2,9	1,5
<i>C. sp. 76 (near bedfordi)</i>	0,7	0,0	1	2,9	1,5
<i>C. sp. 89 (near dekeyseri)</i>	0,6	0,0	1	2,9	1,5
<i>C. sp. 65 (near citroneus)</i>	0,2	0,0	1	2,9	1,5
<i>C. sp. 90 (near exspectator)</i>	0,1	0,0	1	2,9	1,5
<i>C. punctithorax</i>	0,1	0,0	1	2,9	1,5
<i>C. sp. 61 (near pretoriensis)</i>	0,0	0,0	1	2,9	1,5
Unidentified species	41,2	0,0	16	47,1	23,6

0,0 = species representation < 0,05 %

Erasmus 1970). Over the past 20 years, various serotypes of BT virus have been isolated from *C. imicola* in parts of Africa and the Mediterranean (Davies, Walker, Ochieng & Shaw 1979; Mellor, Osborne & Jennings 1984; Blackburn, Searle & Phelps 1985; Braverman, Barzilai, Frish & Rubina 1985). AHS virus serotypes 2, 4 and 7 were isolated from *C. imicola* in South Africa (Nevill *et al.* 1992), while AHS virus serotype 4 has been isolated from *C. imicola* in Zimbabwe (Blackburn *et al.* 1985) and Spain (Mellor,

Boned, Hamblin & Graham 1990). Ephemeral fever virus was also isolated from *C. imicola* in Zimbabwe (Blackburn *et al.* 1985). The laboratory infection rate for a single population of *C. imicola* from the hot, low-lying Northern Province (Eiland) was established at 31 % for BT virus serotype 3, at 24 % for serotype 6 (Venter, Hill, Pajor & Nevill 1991). Other viruses isolated worldwide from *C. imicola*, as reviewed by Meiswinkel, Nevill & Venter (1994), included Akabane, Shamonda, Nyabira and Letsitele. It can also

be mentioned here that *C. imicola* is a member of the subgenus *Avaritia* to which most proven orbivirus vectors belong (Mellor 1992). This, together with the strong association of this species with livestock, the high abundance and wide distribution, rated *C. imicola* as the most important vector of BT and AHS in South Africa. However, the low abundance of *C. imicola* in relatively cold (e.g. Roma) and dry (e.g. Upington) areas, where BT occurs regularly, seems to indicate that this species cannot be the only vector of BT virus in South Africa.

C. bolitinos

C. bolitinos, another member of the subgenus *Avaritia*, was not dominant at any site. It is, however, widespread and was found at 20 of the 34 collection sites, resulting in a vector rating of 29,7% (Table 6). Although the relative abundance of this species was only 0,6%, it is nevertheless strongly associated with livestock, breeding in the dung of the larger herbivores (Meiswinkel 1989) and feeding on both cattle and horses (Nevill *et al.* 1988). In a survey conducted in the colder high-lying eastern Free State, *C. bolitinos* was the most abundant species (Venter & Meiswinkel 1994). *C. bolitinos* is considered to be the morphological and ecological equivalent of the Oriental-Australasian-eastern Palaearctic *C. brevitarsis*, which is an important arbovirus vector in Australia (Meiswinkel 1989). An as yet undescribed orbivirus, provisionally named Letsitele virus, has been isolated from *C. bolitinos* (Nevill *et al.* 1992). *C. bolitinos* must therefore be included in the list of species on which future vector-competence studies must be done.

C. schultzei s.l.

There are at least six closely related species in this group in South Africa. As the taxonomy of this group was clarified only in 1994 (Cornet & Brunhes 1994), these species were grouped together as *C. schultzei* s.l. It has a vector rating of 48,4% and is the second most abundant species and represented 8,5% of the *Culicoides* collected (Table 6). This high representation may probably be due to the fact that at least five different species belonging to this group, were collected.

The group has a wide distribution and was found at 30 of the 34 sites sampled (Table 6). It was the most abundant species at Tshipise (56,8%), Veekos (Upington) (68,9%), Karakul (Upington) (49,4%) and Soutpan (26,5%), and was also collected in large numbers at Middelburg (Eastern Cape) (14,9%) and Messina (12,8%) (Tables 4 and 5).

All of these, except Soutpan, are relatively dry areas with an annual rainfall of less than 360 mm (Table 2). Collections at Soutpan were made at the edge of a saltwater pan. According to Wirth & Dyce (1985),

the breeding sites of this group are the edges of streams and drainage canals which are organically poor and saline. *C. schultzei* s.l. have bred in the mud at the edge of the salt pan and this explains the high numbers of *C. schultzei* s.l. found in the light-trap collections at Soutpan.

Dipeolu (1976) also found that *C. schultzei* is more common in the dry savanna in Nigeria. This group has a wide distribution in Africa and can also be an important vector species of ephemeral fever virus in Kenya (Davies & Walker 1974b) and Nigeria (Dipeolu 1976; Lee 1979; Herniman, Boorman & Taylor 1983). Outside Africa, *C. schultzei* s.l. also has a wide distribution and was found to be the second most abundant species in western Turkey (Jennings, Boorman & Ergün 1983). This species is capable of feeding on cattle, sheep and horses (Braverman & Phelps 1981; Meiswinkel *et al.* 1994) and might therefore be an important vector in dry areas. Letsitele virus has been isolated from the *C. schultzei* group. (Nevill *et al.* 1992).

C. zuluensis and *C. milnei*

C. zuluensis represented 5,3% of the *Culicoides* collected, and was found at 28 of the 34 sites sampled, resulting in a vector rating of 43,8% (Table 6). It was the single most abundant species at Dohne (76,0%), Roma (Lesotho) (75,0%), and George (60,9%), and was also abundant at Stellenbosch (25,7%) (Tables 4 and 5). Suitable areas are therefore either summer rainfall areas with cool summers (mean annual maximum temperature below 22,5°C) and high rainfall or winter rainfall areas with mild winters (Table 2).

C. zuluensis was relatively scarce in the tropical parts of the country (Tables 4 and 5). At sites where more than ten collections were made, *C. zuluensis* represented less than 0,5% of the *Culicoides* species composition. The sites were Allerton (Pietermaritzburg), Eiland, Louis Trichardt and Messina. It was also relatively scarce in dry areas such as Middelburg (Eastern Cape) and Upington, where it accounted for less than 1% of species composition (Table 4).

Very little is known about the distribution and biology of *C. zuluensis*. It has been recorded only from Kenya, South Africa, Zimbabwe (Glick 1990) and Lesotho (Venter & Sweatman 1989). *C. zuluensis* has a wide host preference, which may lower its vector potential for BT and AHS, as it was shown to feed on birds, horses, cattle, sheep and pigs (Braverman & Phelps 1981; Meiswinkel *et al.* 1994). Letsitele virus has been isolated from *C. zuluensis* (Nevill *et al.* 1992).

In contrast to *C. imicola* and *C. schultzei*, which are important in tropical and warm, dry areas, *C. zuluensis* can be a potential vector in cooler areas (compare Tables 2 and 4).

In this study, *C. zuluensis* was found to be much more abundant than the closely related *C. milnei*. *C. milnei* is regarded as an important species in Africa (Glick 1990). During this survey, *C. milnei* was found at only ten of the 34 sites. However, it was abundant (44,6%) only in a collection made at Middelburg in the cold highveld of Mpumalanga. *C. milnei* was shown to feed predominantly on birds, but it can also feed on horses, pigs and bovids (Braverman & Phelps 1981). BT virus serotype 1 (Walker & Davies 1971) and Akabane virus have been isolated from *C. milnei* in Zimbabwe (Blackburn *et al.* 1985). The possibility of *C. milnei* being abundant and a potentially important vector in certain areas that have not yet been thoroughly sampled, cannot be excluded.

C. leucostictus

C. leucostictus has a wide distribution and was the only species found at all 34 collection sites, resulting in a vector rating of 50,8% (Table 6). The species representation, however, was only 1,5% and it was never the most abundant species in collections made near livestock (Tables 4 and 5). However, it was the single most abundant species in two collections made at Tugela (# 26) and Loskopdam (# 30), respectively (Table 5). Both these collections were made in the absence of livestock (Table 1). *C. leucostictus* may be abundant in collections made near birds or poultry (Nevill & Anderson 1972; Nevill *et al.* 1988).

This species utilizes a wide range of breeding sites—from mud and wet ground at the edges of dams and rivers to concentrations of organic waste (Glick 1990; Meiswinkel *et al.* 1994). Owing to its wide distribution, this species is rated as being a good potential virus vector, but the fact that it feeds mainly on birds and poultry (Nevill & Anderson 1972; Meiswinkel *et al.* 1994) lowers its vector potential for stock-associated arboviruses of mammals. There is no record of any virus isolates from *C. leucostictus*.

C. pycnostictus

C. pycnostictus has a vector rating of 46,6% and was found at 31 of the 34 collection sites, representing 2,0% of the *Culicoides* species collected (Table 6). It was the single most abundant species at Middelburg (Eastern Cape) (20,6%), Glen (55,8%) and Ermelo (51,2%) (Tables 4 and 5). Jupp *et al.* (1980) showed that *C. pycnostictus* accounted for 46,6% of the species collected in the southern Free State.

Similar to *C. leucostictus*, this species is mainly a birdfeeder and is usually abundant only in collections made in the vicinity of birds or poultry. The omnipresence of wild birds, although in different concentrations, and the variable breeding sites of *C. pycnostictus*, might be the reason for the wide distribution of this species. However, it was shown that *C.*

pycnostictus may feed on both cattle and horses (Nevill & Anderson 1972; Braverman & Phelps 1981; Meiswinkel *et al.* 1994). BT virus serotypes 6 and 24 have been isolated from *C. pycnostictus* (Nevill *et al.* 1992), which indicates that this species can be a potential vector of at least BT. However, because it is mainly ornithophilic, this species would have a low vector potential for livestock viruses.

C. magnus and *C. gulbenkiani*

Although *C. magnus* has a wide distribution (it was collected at 29 of the 34 sites sampled) it was not abundant and represented only 0,9% of the *Culicoides* species collected, resulting in a vector rating of 43,1% (Table 6). However, at Stellenbosch *C. magnus* (29,0%) together with *C. gulbenkiani* (27,0%) and *C. zuluensis* (25,7%) were the most abundant species (Table 4). This is confirmed by the results of Nevill *et al.* (1988).

C. magnus is not widely distributed in Africa and has been found only in Gambia, Kenya, South Africa, Zimbabwe (Glick 1990) and Lesotho (Venter & Sweatman 1989). It was, however, the single most abundant species in a "bluetongue area" in Kenya (Walker & Davies 1971). *C. magnus* can feed on sheep, cattle and horses (Walker & Davies 1971; Nevill & Anderson 1972; Braverman & Phelps 1981) and should therefore be regarded as a likely vector of stock-associated arboviruses. Letsitele virus has been isolated from *C. magnus* (Nevill *et al.* 1992).

C. gulbenkiani was common only at Stellenbosch (Tables 4 and 5). Nevertheless, it has a wide distribution and was found at 20 of the 34 collection sites, resulting in a vector rating of 29,7% (Table 6). This species breeds in decomposed cattle or horse dung and can feed on cattle, sheep and pigs (Braverman & Phelps 1981; Nevill *et al.* 1988). Both AHS and BT viruses have been isolated from *C. gulbenkiani* (Nevill *et al.* 1992; Meiswinkel *et al.* 1994).

The host preference and wide distribution of both *C. magnus* and *C. gulbenkiani*, enhance the vector potential of these species in South Africa, but they are not abundant enough to be important vectors.

C. bedfordi

C. bedfordi had a vector rating of 41,7%, but was not very abundant, and dominant only in a collection made at Honingneskrans near the OVI (Table 5). It has a wide distribution in South Africa and was collected at 28 of the 34 collection sites (Table 6). The relative abundance was the highest at Middelburg (Eastern Cape) (18,8%), Karakul (Upington) (14,5%) and Tshipise (6,3%)—all relatively dry areas (Table 2).

C. bedfordi has been found in Cameroon, Kenya, South Africa, Sudan, Tanzania, Zimbabwe (Glick

1990) and Lesotho (Venter & Sweatman 1989). According to Glick (1990), the high number of antennal sensilla, similar to that of *C. leucostictus* and *C. pycnostictus*, indicates that this species may also primarily be a bird feeder. However, there are also reports of females taken while they were biting horses in the daytime in Zululand (Glick 1990) and positive blood-meal identifications from sheep (Meiswinkel *et al.* 1994). There is no record of any virus isolates from *C. bedfordi*.

CONCLUSIONS

Although these studies have indicated that *Culicoides* species are widespread throughout southern Africa, and that there are at least 18 stock-associated species which have the potential to be virus vectors, there are a number of additional factors which will determine whether arboviruses may be transmitted to the different livestock species in various parts of the region. Among these are the need for unvaccinated, susceptible hosts and a source of virus to be present; the ability of the particular virus to multiply in and be transmitted by livestock-feeding *Culicoides* species in an area; and for adequate populations of the *Culicoides* vector species of the correct age structure to be present. The latter aspect will form the subject of a subsequent paper.

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