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DISPERSAL, DENSITY AND HABITAT PREFERENCE OF THE BLOW-FLIES *CHRYSOMYIA ALBICEPS* (WD.) AND *CHRYSOMYIA MARGINALIS* (WD.) (DIPTERA: CALLIPHORIDAE)

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ABSTRACT

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16 000 *Chrysomyia albiceps* and 52 000 *C. marginalis* adults were radioactively labelled with ^{32}P-orthophosphate and released in the northern Kruger National Park, South Africa. After a 1-week dispersal period 69 baited blow-fly traps were placed in different habitat types and at varying distances around the release point. *C. albiceps* were subsequently found to have covered up to 37,5 km and *C. marginalis* 63,5 km, suggesting dispersal rates per day of 2,20 km and 2,35 km for the 2 species, respectively. Calculation of density using the Lincoln Index yielded estimates per hectare of 7,56 *C. albiceps* and 29,03 *C. marginalis*. Both species were trapped more numerously in forested environments than in open scrub, and both avoided arid scrubland.

INTRODUCTION

Blow-flies have been considered important in the maintenance and spread of anthrax *(Bacillus anthracis)* during periodic epizootics in the northern Kruger National Park (K.N.P.) (Pienaar, 1961; Braack, 1984). Flies arrive soon after the death of an animal to feed on blood at haemorrhaging body cavities, and deposit large numbers of infective discard droplets on vegetation in the area, thus greatly increasing the probability of herbivorous mammals ingesting the pathogen in fatal doses (Braack, 1984). *Chrysomyia albiceps* and *C. marginalis* are by far the most abundant blow-flies in the northern K.N.P. and are widespread throughout southern Africa and elsewhere (Smit & Du Plessis, 1927; Smit, 1929; Zumpt, 1965). Apart from the findings of Smit (1931) on habitat preferences, no published information exists on the flight patterns and density of these species. Field experiments were therefore conducted to determine their flight range, dispersal, habitat preferences and population densities for use in epidemiological studies of anthrax.

Along with 3 other calliphorid species, *C. albiceps* has established itself in South America during the last decade and appears to be spreading rapidly through the continent (Baumgartner & Greenberg, 1984). The data presented in this paper should facilitate the development of programs to monitor the distribution and spread of such intruder species.

THE STUDY AREA

The investigation took place in the northern K.N.P. (Fig. 1) which is little disturbed by human activity and has been a protected conservation area since 1903 (Stevenson-Hamilton, 1947). It is a semi-arid region with a mean annual rainfall of between 438,1 and 587,8 mm (Gertenbach, 1980), and mean daily maximum and minimum temperatures of 29,4 °C and 16,3 °C, respectively (Van Rooyen, 1978). Most of the central area comprises extensive flat plains dominated by stunted mopane woodland *(Colophospermum mopane)* and localized tall mopane forests. Hilly terrain with mixed woodland occurs especially in the west, north and north-east. In the east tongues of sandy soils with their own characteristic semi-arid open woodland jut in from Moçambique. Two major rivers flow through the area and are fringed by lush riverine forest that generally extends for up to 200 m on either side. Detailed vegetation maps for the area have been published (Van Rooyen, 1978; Gertenbach, 1983).

MATERIALS AND METHODS

A single operation was envisaged to achieve all the aims indicated in the introduction. It depended on the release from a single point of large numbers of reared, radioactively-marked blow-flies and the subsequent placement of blow-fly traps at varying distances and in different habitat types. ^{32}P-orthophosphate was used as the marker because of its relative safety, convenient half-life (14,2 days), and the high degree of success achieved by other investigators using this substance to mark flies (Lindquist, Yates, Hoffman & Butts, 1951; Yates, Lindquist & Butts, 1952; Schoof & Mail, 1953; Quarterman, Kilpatrick & Mathis, 1954; Quarterman, Mathis & Kilpatrick, 1954; MacLeod & Donnelly, 1957; Southwood, 1978).

Full-grown 3rd-stage *C. albiceps* and *C. marginalis* larvae were collected from deliberately-placed impala carcasses and allowed to pupariate separately in sand-filled basins covered with netting against parasite attack. The impala carcasses and surrounding area were burnt to destroy all the remaining larvae, which would have contributed to an unnatural increase in the wild populations under study. A total of 16 000 *C. albiceps* and 52 000 *C. marginalis* puparia were sieved from the sand-basins and placed in batches of 2 000 in spacious gauze-cages each provided with a zipper and 6 Petri-dishes for food and water.

Adult emergence occurred on the 30th and 31st January 1982. Sugar water and a 1:4 mixture of yeast hydrolysate:sugar was provided for initial protein and carbohydrate requirements, but on the 2nd and 3rd days after emergence dishes with standard sugar water were replaced with a solution of 0,74 GBq ^{32}P-orthophosphate per millilitre of sugar water (0,020 milliCuries ^{32}P/mℓ sugar water).

Random sampling of flies during the afternoon of 2nd February indicated that 96,43 % of *C. albiceps* (n = 56) and 90,0 % of *C. marginalis* (n = 40) registered between 1 000 and 80 000 counts per minute. The flies were transferred to the central release point (C.R.P.) in their cages in a covered vehicle to protect them against excessive exposure to the sun and a dehydrating draught. The flies were released at dusk as blow-fly adults are inactive at night (Norris, 1966; Braack, 1981, 1984), so that they would not travel far before settling for the night. By dawn they were presumed to have recovered from any shock-effect or escape-tendency induced by the process of transfer, so that dispersal and further flight-behaviour would approximate to a natural pattern.

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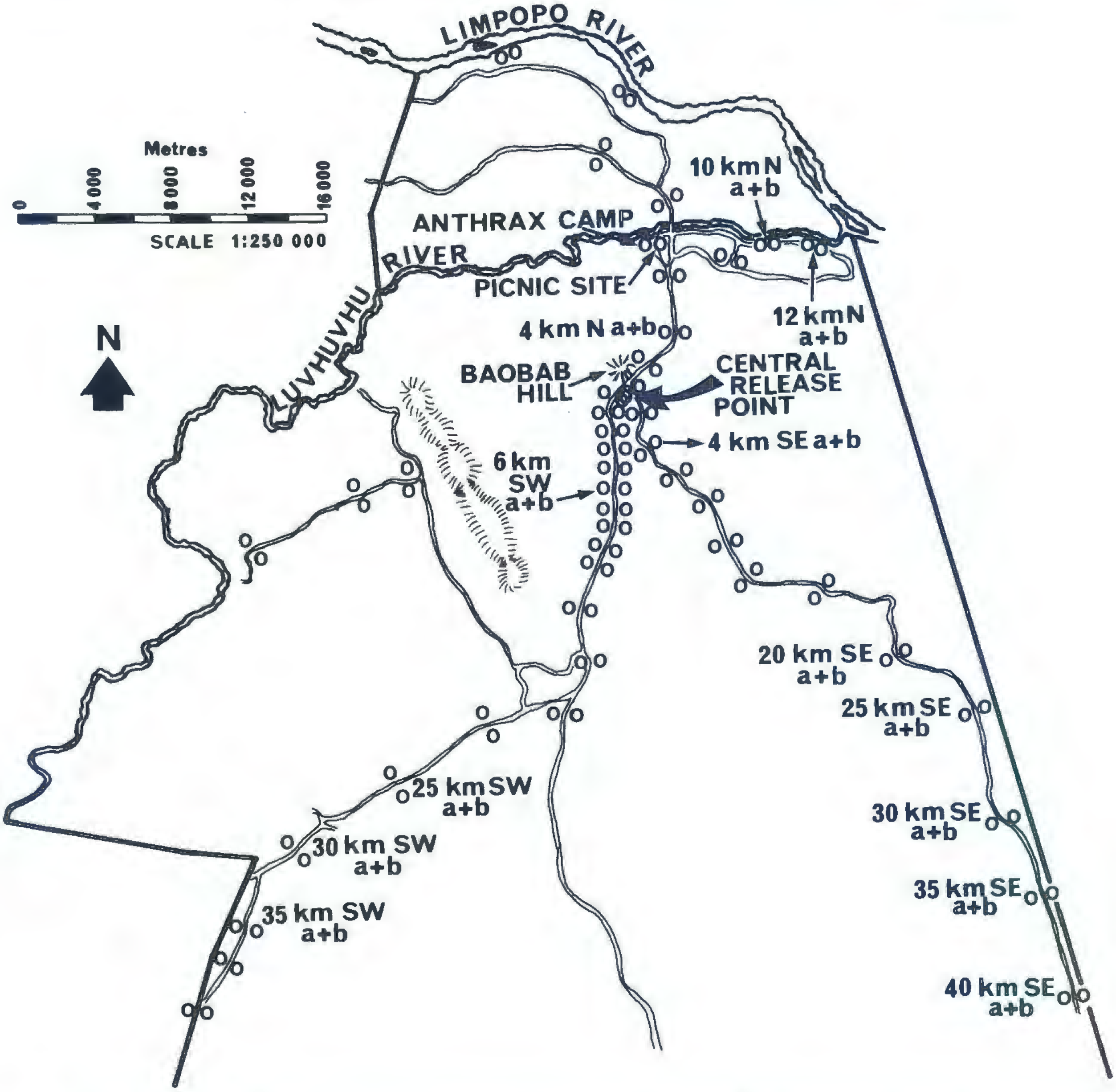

FIG. 1 Map of the northern Kruger National Park to show Central Release Point of radioactive flies and positions of traps for subsequent recapture of blow-flies (each small circle represents one trap)

The flies were left undisturbed for a full week, and baited blow-fly traps were placed on the 10th, 11th and 12th February in 3 main radii around the C.R.P. (Fig. 1), up to a distance of 40 km. On the 15th February a journey had to be made to Shingwedzi (south of the study area) and this opportunity was utilized to place 2 additional traps in mopane shrubveld along the Mphongolo River at a point 63,5 km from the C.R.P. The traps operated on the same principle as the "standardized West Australian" trap, as described by Vogt & Havenstein (1974) but were round in shape and very near double in size and capacity. Each trap was baited with a mixture of 1 kg of fresh, lean buffalo meat, 1 kg of fish, 100 g of buffalo rumen-content, and 2 litres of water from a 200 ℓ drum in which 20 kg of meat had been allowed to decompose for a week. A total of 90 traps were orginally placed, but several were damaged by scavenging mammals so that eventually only 69 remained effective. Trap collection and emptying occurred on the 17th, 18th and 19th February and were performed in the same sequence as placement so that all traps had an equal trapping period. Trap contents were first examined for radio-active flies and then sealed in bags for later counting of total catches.

The Lincoln or Peterson Index was applied for the determination of density during this study, using adjusted values to account for mortality in the marked population and other factors to be mentioned. The limitations of this Index and the conditions for its use are discussed by Southwood (1978). Although it is an estimate, it is the most practical and probably the most accurate method available at present for obtaining some concept of population density in species such as blow-flies. For good accuracy, however, a large number of released flies and also traps for recapture should be used (Vogt, Woodburn & Crompton, 1981).

RESULTS AND DISCUSSION

Dispersal and flight range

A total of 1 625 radioactive blow-flies were recaptured up to 40 km from the release point. Of these, 132

TABLE 1 Captures of radioactive and non-radioactive blow-flies 10–19 February 1982

Distance from central release point (km)	Number of traps	Total number of *Chrysomyia albiceps* captured	Number of radioactive *C. albiceps* recaptured	% of total *C. albiceps* formed by radioactive recaptures	Total number of *Chrysomyia marginalis* captured	Number of radioactive *C. marginalis* recaptured	% of total *C. marginalis* formed by radioactive recaptures
0–4	12	4 066	8	0,20	21 226	133	0,62
6–10	19	14 270	65	0,45	93 698	880	0,93
12–18,5	16	10 801	40	0,37	63 738	379	0,59
20–29	8	5 992	9	0,15	30 904	55	0,18
30–40	12	10 455	10	0,10	34 965	46	0,13
Total	67	45 584	132		244 531	1 493	

TABLE 2 Number of traps and recaptures of radioactively marked flies in different directions around central release point

Direction of trap-line	Number of effective traps in trap-line	Number of marked recaptures of	
		Chrysomyia albiceps	*Chrysomyia marginalis*
North	22	78	1 139
West	5	14	74
South-west	21	29	146
South-east	17	9	112
C.R.P.	2	2	22
Totals	67	132	1 625

were *C. albiceps,* reflecting the low number of flies of this species initially released. Table 1 shows the distribution of recaptures in the distance-classes from the C.R.P. Of the 10 recaptures between 30–40 km, 5 were at a distance of 30 km, 4 at 35 km, 1 at 37,5 km, and none at 40 km. The *apparent* maximum distance covered by this species during the 17 days following the release of the flies and removal of the last trap-line thus appears to have been 37,5 km. High numbers of radioactive *C. marginalis* recaptures were obtained in all distance-classes and, of the 46 caught 30–40 km from the C.R.P., 18 were at 30 km, 16 at 35 km, 4 at 37,5 km and 8 at 40 km.

The furthermost radioactive *C. albiceps* and *C. marginalis* recaptured were in the upper layer of flies in the traps, suggesting that they had arrived close to the time of trap removal. It also indicates a minimum rate of movement of 2,35 km per day for *C. marginalis* and 2,20 km per day for *C. albiceps.*

The 2 traps on the Mphongolo River were recovered on the 24th February (22 days after fly release) and 2 radioactive *C. marginalis* were found in each of them. These flies were also in the upper layer and their presence suggests a minimum rate of movement of 2,88 km per day.

Radio-active *C. albiceps* and *C. marginalis* recaptures were highest in the distance-class 6–10 km from the C.R.P., the next highest being 12–18,5 km (Table 1). Direct comparison of radioactive recaptures in the 2 classes is not valid because different numbers of traps were used, and, more importantly, because the 12–18,5 km swath around the C.R.P. represents a far greater area into which flies could disperse with proportionately fewer traps per unit area and therefore less chance for recapture. The 141 flies (133 *C. marginalis* and 8 *C. albiceps)* recaptured in the 4 km radius around the release point, which was relatively saturated with 12 traps, should be considered a low number of recaptures compared with, for example, the 56 recaptures in the 30–40 km band, which was an enormous area with only 12 traps. Following this line of reasoning the results in Table 1 suggest that the released flies moved away from the area of release and relatively few either remained there or returned to it.

Directional movement by flies subsequent to their release is summarized in Table 2, and indicates a clear preponderance of both species in the northern, western and south-western sectors. Although the prevailing wind at the time was south-easterly, it rarely exceeded a gentle occasional breeze that was unlikely to have influenced blow-fly flight. The low number of recaptures along the south-eastern trap-line most likely reflects the avoidance reaction of these species to arid scrubland areas (as discussed later), resulting in a concentration of flies in more heavily wooded regions. Dispersion appeared to be random, however, as suggested by the capture of marked flies in all directions around the C. R. P., and recaptures even along the south-east trap-line at the furthest points up to 40 km

The vast areas covered by adult *C. albiceps* and *C. marginalis* in a relatively short time period would have considerable adaptive advantage to increase breeding success. Both species are narrow specialists which utilize only carcasses as their breeding medium. They have to contend with severe competition from vertebrate scavengers for such a resource, especially as they require carcasses over a certain size in a fresh or nearly fresh condition (Braack, 1984). Such resources are rare and selection pressure most likely forces these blow-flies to search enormous areas to locate a suitable breeding medium.

The Luvuvhu River, approximately 30 m wide at the time, did not present an obstacle to blow-fly flight or serve as an inhibitory boundary. This was clearly revealed by the 31 *C. albiceps* and 357 *C. marginalis* radioactive recaptures in the 8 traps north of the river (Fig. 1). These figures represent 23,48 % and 23,91 % of the total number of radioactive recaptures of *C. albiceps* and *C. marginalis,* respectively, throughout the study area. The high percentage of recaptures from only 8 traps in a relatively confined area is probably due to the attraction afforded by the lush riverine forest adjoining the Luvuvhu and Limpopo rivers and stands of fairly tall, dense mopane trees in many areas between these 2 rivers.

Mountainous terrain similarly posed no apparent obstacle to flight. A series of hills up to about 192 m in height, and stretching in a nearly continuous north-south line, separated the C.R.P. from 5 traps placed well to the west of these hills. These 5 traps recaptured 14 radioactive *C. albiceps* (10,61 % of all *C. albiceps* radioactive recaptures) and 74 *C. marginalis* (4,96 %), despite the area being predominantly fairly arid mopane shrubveld and Punda Maria sandveld (Gertenbach, 1983). The hilly terrain that is a characteristic feature of much of the region between the C.R.P. and the Luvuvhu River also proved ineffective as a barrier to blow-fly movement. Schoof & Mail (1953) in West Virginia, U.S.A., found that *Phormia regina* blow-flies were not deterred by either rivers or wooded ridges 120 to 150 m in height. MacLeod & Donnelly (1960) similarly found that *Lucilia* *caesar* and *Calliphora erythrocephala* readily crossed a 180 m wide river in England and a steep hill 150 m in height failed to prevent their crossing. The most important factor influencing blow-fly movement would appear not to be of a direct geological nature, but rather the nature of the vegetation in the area. This aspect is discussed later.

Useful reviews by Johnson (1969) and Greenberg (1973) summarize much of the available data on flight distances covered by flies through fixed time periods. No data appear to exist concerning the flight ranges of *C. albiceps* and *C. marginalis*. Gurney & Woodhill (1926) found that *Chrysomyia rufifacies* (which they mistakenly referred to as *C. albiceps)* covered 16 km in 12 days in Australia, while Norris (1959) found the same species covering over 6,4 km in 24 hours. Most of the studies recorded in the leterature were undertaken on a small scale and provide limited results, although some findings indicate that species such as *Calliphora vicina* could cover 70 km (Lempke, 1962), while a record dispersal distance of 289 km within 2 weeks was reported for *Cochliomyia hominivorax* (Hightower, Adams & Alley, 1965). No previous work on flight range in blow-flies appears to have been done in Africa.

By extrapolation from the dates of their 1st arrival in newly colonized areas in South America, Baumgartner & Greenberg (1984) estimated a maximum dispersal rate of 1,5 km/day for *C. albiceps*, while the closely related *C. rufifacies* spread at a rate between 0,77 to 3,2 km/day. This compares favourably with the figure of 2,20 km/day obtained for *C. albiceps* during the present study.

Population densities

After placement of the 16 000 *C. albiceps* and 52 000 *C. marginalis* puparia in rearing cages, separate samples of 200 puparia of each species revealed an adult emergence success of 97 % in *C. albiceps* and 96,65 % in *C. marginalis*. This theoretically reduced the caged population of *C. albiceps* to 15 520 and *C. marginalis* to 50 258.

After 2 feeds of 0,74 GBq ^{32}P-orthophosphate per mℓ sugar water, random pre-release sampling indicated that only 96,43 % of *C. albiceps* and 90 % of *C. marginalis* exceeded 1 000 cts/min, thus further reducing the effectively marked populations to 14 965 and 45 232, respectively.

Mortality of marked flies from the time of release to eventual trap collection could be inferred from separately caged, marked populations (200 of each species), in which 38,54 % of *C. albiceps* and 82,47 % of *C. marginalis* survived by the *last* day of trap removal. Extrapolated to the released population, this implies that 5 767 *C. albiceps* and 37 302 *C. marginalis* survived to the last day of trapping. Statistically, however, the population surviving midway through the trapping period was preferable for use in the Lincoln Index, and by extrapolation from known mortality curves for each species (Braack, 1981, unpublished data) this could be determined. Calculation indicated that 7 862 *C. albiceps* and 40 921 *C. marginalis* adults would have survived, and these figures were accepted as representing the marked populations available for trapping.

A potential problem arose in that the available evidence indicated that marked flies arrived at the outer periphery of the trapping area only during the final days of the trapping period, so that significantly more time was available for trapping unmarked flies by these peripheral traps than marked flies. To negate this bias we used only the values of marked and unmarked captures in an inner circle around the release point with 19,25 km as radius (midway between the 18,5 and 20,0 km series of traps). This necessitated calculation of the number of marked flies presumed to have migrated from this inner area, so that they could be excluded from the working population of marked flies under consideration, and was deduced as follows:

$$M_o = \frac{m_o}{m_i} \times \frac{A_o}{A_i} \times M_i$$

where M_o = total number of marked flies in the outer circle,

M_i = total number of marked flies in the inner circle,

m_o = mean number of marked recaptures per trap in the outer circle,

m_i = mean number of marked recaptures per trap in the inner circle, and

A_o and A_i = the areas in km^2, covered by the outer and inner circles, respectively.

In this calculation it is assumed that the recaptures per trap estimate relative density per unit area, and that the traps were not so close that they affected each other.

For *C. albiceps* the computation is as follows:

$$\begin{aligned} M_o &= \frac{0{,}95}{2{,}40} \times \frac{3\ 862{,}39}{1\ 164{,}16} \times M_i \\ &= 1{,}3133\ M_i \end{aligned}$$

By mathematical substitution and entering the total number of marked *C. albiceps* we find:

$$\begin{aligned} M_o &= 1{,}3133\,(7\ 862 - M_o) \\ &= (1{,}3133)(7\ 862) - 1{,}3133\ M_o \\ 2{,}3133\ M_o &= (1{,}3133)(7\ 862) \\ M_o &= \frac{(1{,}3133)(7\ 862)}{2{,}3133} \\ &= 4463 \end{aligned}$$

By subtracting this from 7 862 we derive a figure of 3 399 marked *C. albiceps* in the inner circle.

By employing the same method for *C. marginalis* a figure of 26 134 was obtained. The values for the 2 species as derived above were then substituted into the Lincoln Index, generally written as:

$$N = \frac{an}{r}$$

where N = the estimate of the number of individuals in the population,

n = total number of flies captured,

a = number of marked flies and

r = total marked recaptures.

For *C. albiceps*, we obtained an estimate of:

$$N = \frac{(3\ 399)(29\ 137 + 113)}{113}$$

= 879 899 flies in the inner circle with 19,25 km as its radius (1 164,16 km^2), which gives a figure of 756 *C. albiceps* per km^2 or 7,56 adults per hectare.

The corresponding values for *C. marginalis* were:

$$N = \frac{(26\,134)(178\,662 + 1\,392)}{1\,392}$$

= 3 380 410 flies, i.e. an estimated 2 903 *C. marginalis* per km^2 or 29,03 adults per hectare.

The above estimates are rather low when compared with some of the results achieved for a range of other blow-fly species by investigators in other countries. Working in Australia, Gilmour, Waterhouse & McIntyre (1946) released large numbers of *Lucilia sericata* at the centre of an area (6,4 km radius) throughout which they had distributed 100 traps. By correcting for death rate end emigration from the study area they calculated a density of 0,7 to 14 flies per hectare. Norris (1959), who also worked in Australia, used a similar technique, but he failed to take into account fly mortality. He obtained tentative densities for the following species: *Calliphora stygia* 247/ha, *C. augur* 864/ha, *Chrysomyia ruficacies* 123/ha, and *Microcalliphora varipes* 24–49 flies per hectare. Cragg & Hobart (1955) also attempted population estimates of blow-flies in England but dit not correct for such factors as mortality or emigration. They arrived at tentative densities of 56 *Lucilia sericata* per hectare, and between 14 and 588 females of the "*L. caesar* group" per hectare. MacLeod (1958), who used another method with several assumptions regarding rates of mortality, dispersal, and zones of influence of traps, showed that densities in England varied markedly at different times of the year. He measured densities of *Calliphora vicina* in 1 year as 123–494/ha in August; 988–2 471/ha in September, and 1 729–2 471/ha in October, whereas in another year he recorded only 27–66/ha in August and 165/ha in October. For *Lucilia sericata* he computed densities of 6,9 and 1,9/ha in August and 2,4/ha in October.

The value of the present estimates of *Chrysomyia albiceps* and *C. marginalis* in the northern K.N.P. is that these figures reflect blow-fly population densities in an undisturbed natural environment. The density estimates by the other workers discusses above are for economically important species which in many instances cause myiasis either in sheep or cattle. Almost certainly these have elevated population levels as a result of agricultural practices.

Habitat preferences

In Table 3 the catches for 6 traps in each of 4 different habitat types are given. These traps were selected because they were located completely within a particular habitat type and not because they made either particularly high or low catches.

The trap catches indicate larger concentrations of both *C. albiceps* and *C. marginalis* in densely wooded forest environments such as the reverine forest along the Luvuvhu River and the tall mopane forest in the south-west near Punda Maria. Very low numbers of flies were captured in the arid south-eastern sandveld. Intermediate, although still somewhat low, numbers of blow-flies were captured in the mopane shrubveld in the area around Baobab Hill. The short stunted mopane scrub in the southern plains also yielded a very low number of blow-flies. Statistical analysis using the Mann-Whitney U test reveals that for both species the populations in densely wooded environments are significantly different from those in semi-arid open woodland (P = 0,036).

A possible cause of the aggregating behaviour of *C. albiceps* and *C. marginalis* adults in well-wooded, forested environments is their need for moisture. During earlier experiments, when adult blow-flies were kept in cages for reproductive and other studies, it became clear that they were subject to rapid dehydration, especially in summer, and that they required daily access to liquid to obviate fatal dehydration. On hot summer days the adults generally had several drinks of water at the dishes provided. Another likely influence is an avoidance reaction displayed by the flies to excessive radiation intensity from the sun.

TABLE 3 Trap catches of *Chrysomyia albiceps* and *C. marginalis* in differing landscape zones to indicate habitat preference (trap numbers indicate distance, e.g. 20 km, and general direction, e.g., SW = south-west, in relation to central release point)

Trap number	Landscape	Total number of *C. albiceps* captured	Total number of *C. marginalis* captured
Anthrax Camp 7,5 km N	Riverine forest	2 716	14 817
Picnic Site 7,5 km N		693	4 012
Luvuvhu 10 km Na		1 418	5 702
Luvuvhu 10 km Nb		1 091	8 527
Luvuvhu 12 km Na		1 047	7 856
Luvuvhu 12 km Nb		616	4 171
	Totals:	7 581	45 085
25 km SWa	Generally tall, dense mopane forest, no river nearby	1 936	9 756
25 km SWb		2 743	15 701
30 km SWa		2 841	5 159
30 km SWb		1 164	2 853
35 km SWa		749	3 914
35 km SWb		1 606	6 932
	Totals:	11 039	44 315
20 km SEa	Arid Wambiya sandveld	30	217
20 km SEb		59	322
25 km SEa		69	440
30 km SEa		47	374
35 km SEb		11	198
40 km SEb		166	1 905
	Totals:	313	3 456
4 km Na	Mopane shrub-veld representative of large part of study area	973	4 590
4 km Nb		556	4 341
4 km SEa		228	890
4 km SEb		141	442
6 km SWa		222	1 595
6 km SWb		157	754
	Totals:	2 277	12 612

Observations revealed that, when resting, adults rarely remained for long in positions where they were directly exposed to the sun on hot days, although they would rest for lengthy periods in the shade. Earlier experiments (Braack, 1984) revealed that *C. albiceps* and *C. marginalis* have a bimodal daily activity peak in summer, with depressed activity at noon, whereas this pattern is not evident in late autumn. Forested environments allow a greater proportion of adult activities to take place in the shade.

Although it is difficult to prove, probably the greatest single factor attracting blow-fly adults to well-wooded environments is the greater probability of finding carcasses. Arid, sparsely vegetated environments generally support a reduced mammal population compared with better vegetated environments, so that the likelihood of a carcass occurring in an arid environment is decreased. Even more important is that any carcasses occurring in such open arid environments are soon discovered by vultures, which rapidly strip the carcass of soft tissues. The probability of locating a carcass suitable for oviposition is increased in riverine or forested environments.

In comparison, Smit (1931) placed a series of blow-fly traps, over a 3-year period, in a semi-arid region of the Cape Province to establish habitat preferences. His results were inconclusive, probably because of the lack of well-defined habitat types covering significant areas. His results did suggest, however, that blow-flies were attracted to areas of moisture and shelter afforded by vegetation, and avoided open plains.

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