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SEASONAL ABUNDANCE OF CARRION-FREQUENTING BLOW-FLIES (DIPTERA: CALLIPHORIDAE) IN THE KRUGER NATIONAL PARK

L. E. O. BRAACK and V. DE VOS, National Parks Board, Department of Research and Information, Skukuza 1350

ABSTRACT

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Monthly population fluctuations of carrion-frequenting blow-flies over a 24-month period were monitored using 2 carrion-baited traps in the southern Kruger National Park (KNP) and 3 in the northern KNP. All species displayed a clear seasonality. *Chrysomyia marginalis* and *Chrysomyia albiceps* were by far the most abundant. *C. marginalis* attained maximum abundance between November and March, with relatively low numbers present between May and September. *C. albiceps* maintained high population numbers between January and March in the northern KNP, with minimum numbers between May and August. In the southern KNP, *C. albiceps* became abundant from November to February, with low population levels between April and September. Although present only in relative low numbers, populations of *Lucilia cuprina* showed a clear increase in winter. *Chrysomyia chloropyga, Chrysomyia putoria* and *Chrysomyia bezziana* were trapped in significant numbers in the southern KNP, the latter 2 species reaching relative abundance in the warmer months, whereas *C. chloropyga* increased in cooler months from June to September. Graphic illustrations of monthly abundance are provided for all species.

INTRODUCTION

Several authors (Smit & Du Plessis, 1927; Smit, 1931; Hepburn, 1943 a & b; Mönnig & Cilliers, 1944) have indicated that there is a marked seasonality in the abundance of blow-flies, with different species having periods of distinct population growth which do not necessarily coincide with that of others. The periods of population increase and the extent of increase obviously vary according to geographic locality, climatic factors and the availability and accessibility of food.

The results reported in this paper form part of a larger study on the epidemiology of anthrax in the Kruger National Park (KNP). Pienaar (1961) and De Vos (1973 a & b) indicated that carrion-frequenting blow-flies have a significant role in the dissemination of this disease which, during periodic epizootics, results in high mortality among wildlife species. Flies feeding on blood at such anthrax mortalities deposit large numbers of infective discard droplets (Braack, 1984) on leaves and other vegetation which are then ingested by susceptible herbivores. This study was therefore initiated to monitor the seasonal population fluctuation of blow-flies and to provide a better concept of blow-fly numbers during the dry post-winter months when the risk of an anthrax epizootic is at its greatest.

MATERIALS AND METHODS

Five traps were used to monitor on a monthly basis blow-fly abundance in different habitat types. The traps operated on the same principle as the so-called "West Australian" trap (Vogt & Havenstein, 1974), but were larger and were suspended from tree-branches. The traps are fully described by Braack (1984). Two traps were placed in the southern KNP near Skukuza, one being within 100 m of a small series of stables for horses (*ca.*5) on the periphery of the large rest-camp. The other trap was removed some 2 km from Skukuza and placed among lush riparian vegetation along the Sabie River. Skukuza consists of a large tourist camp and a staff village, the total number of persons approximating 2 100. The camp is located in Landscape Type 4 of Gertenbach (1983), comprising dense woody vegetation dominated by *Acacia nigrescens* and *Combretum apiculatum*. The riverine forest adjoins the Sabie River as a band approximately 70 m wide on either side, common trees being *Ficus sycomorus, Breonadia microcephala, Nuxia oppositifolia, Diospyros mespiliformis* and *Trichilia emetica*.

The remaining 3 traps were placed in the endemic area for anthrax in the extreme northern KNP. The northernmost trap was placed near Hape Pan approximately 1 km south of the Luvuvhu River on a flat expanse dominated by near-uniformly distributed *Colophospermum mopane* trees, averaging between 4 and 6 m in height. Another trap was located at Baobab Hill in a shallow valley with mixed vegetation consisting of mainly *Colophospermum mopane, Terminalia prunioides, Commiphora* spp., *Adansonia digitata* and *Combretum imberbe* trees which ranged between 4 and 15 m in height. The remaining trap was placed farther south at Nwashitsumbe in a grass-filled scrub-mopane plain dominated by stunted *Colophospermum mopane* varying from 1,5–4 m in height with occasional larger *Combretum imberbe* and *Sclerocarya birrea*.

The traps were all suspended from branches such that the lower end was approximately 1,75 m above the ground, out of reach of hyaenas. Each trap was baited with a mixture comprising 1 kg fresh lean impala meat and 1 kg fresh fish, both cut into small golf-ball-sized chunks, and this then mixed with 2 ℓ of water into which 135 g of impala rumen-content had been stirred. The traps were left in position for a full seven-day period generally during the last week of each month, after which the flies were killed with aerosol insecticide before removal. The traps were washed to remove traces of insecticide.

Monitoring in the southern KNP commenced in November 1982 and continued until November 1984. The Hape Pan and Baobab Hill traps were placed from January 1983 to March 1985, while the Nwashitsumbe trap functioned from April 1983 to March 1985. All the traps were therefore used for a minimum period of 24 months.

RESULTS

These are graphically represented in Fig. 1–12. From these it is evident that a clear seasonality also exists in the carrion-frequenting blow-fly populations of the KNP.

Chrysomyia albiceps and *Chrysomyia marginalis* were the most abundant of the various species trapped, with the latter species being considerably more numerous. In the northern KNP *C. albiceps* reached maximum population numbers generally between January and March, with minimum numbers between May and August (Fig. 1). Their seasonality in the southern KNP differs slightly in that they attained maximum numbers somewhat earlier, between November and February, and maintained low population levels for a longer period, generally lasting from April to September (Fig. 2).

C. marginalis followed a similar pattern, with maximum numbers in both the southern and northern KNP

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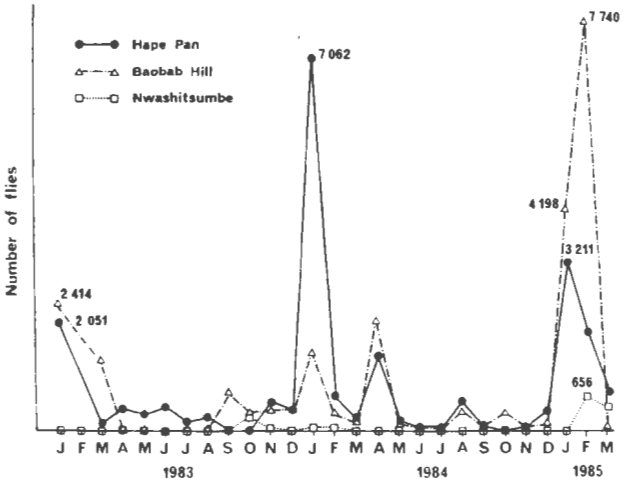

FIG. 1 Monthly trap-captures of adult *Chrysomyia albiceps* (Wd.) in the northern Kruger National Park

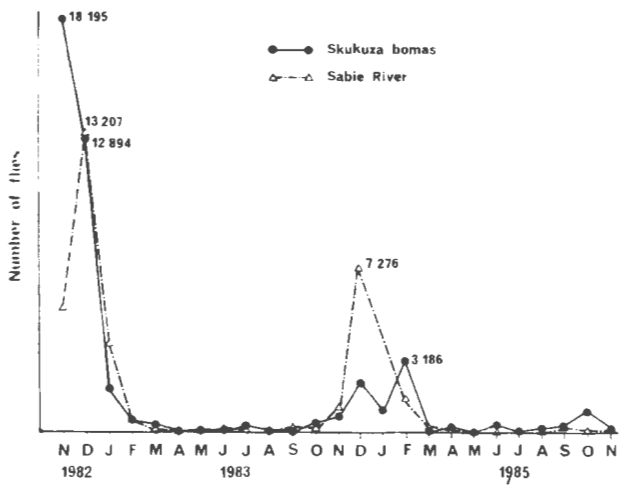

FIG. 2 Monthly trap-captures of adult *Chrysomyia albiceps* (Wd.) in the Skukuza area, southern Kruger National Park

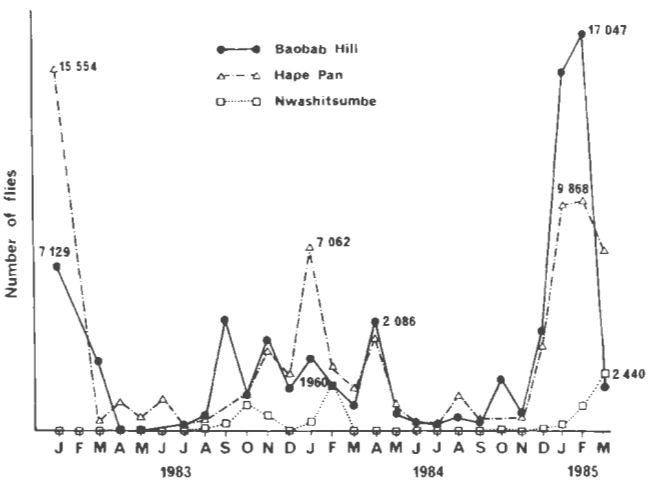

FIG. 3 Monthly trap-captures of adult *Chrysomyia marginalis* (Wd.) in the northern Kruger National Park

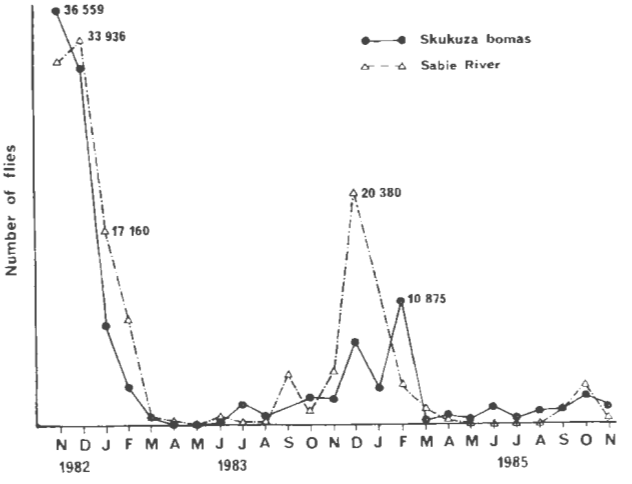

FIG. 4 Monthly trap-captures of adult *Chrysomyia marginalis* (Wd.) in the Skukuza area, southern Kruger National Park

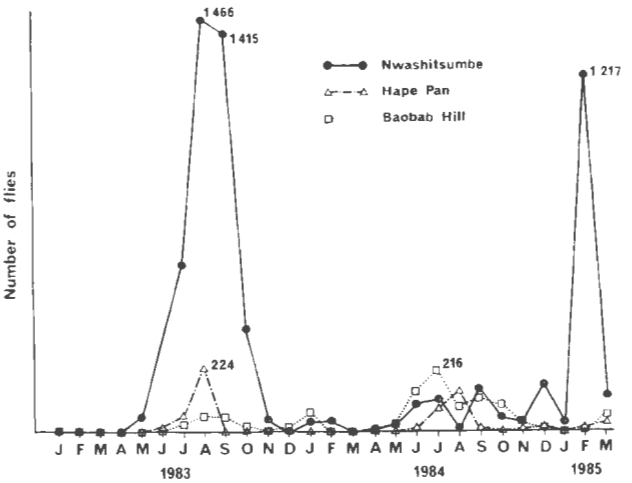

FIG. 5 Monthly trap-captures of adult *Lucilia* spp. in the northern Kruger National Park

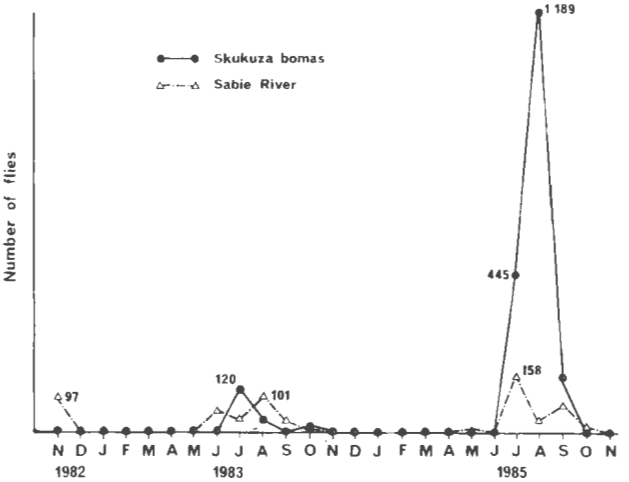

FIG. 6 Monthly trap-captures of adult *Chrysomyia chloropyga* (Wd.) in the Skukuza area, southern Kruger National Park

being reached between November and March, with April also occasionally having elevated numbers (Fig. 3 & 4). Low population levels existed between May and September in the northern KNP, while this period was extended in the southern KNP and lasted from April to August.

Lucilia spp. were generally present only in low numbers, and although both *Lucilia cuprina* and *Lucilia sericata* were recorded, well over 99 % of the specimens captured were *L. cuprina*. In the northern KNP *Lucilia* were recorded only in very low numbers in both the Hape Pan and Baobab Hill traps (Fig. 5), but were more numerous at times in the Nwashitsumbe and southern KNP traps. At Nwashitsumbe the highest numbers were recorded between June and August, with low population levels from November to May. Around Skukuza fairly high numbers were generally maintained between April

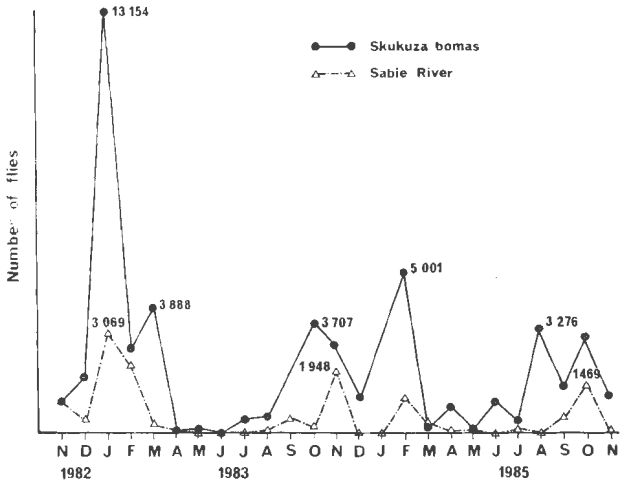

FIG. 7 Monthly trap-captures of adult *Chrysomyia putoria* (Wd.) in the Skukuza area, southern Kruger National Park

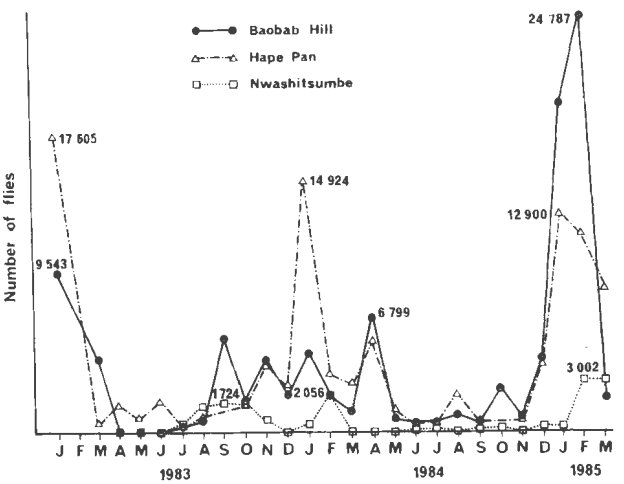

FIG. 8 Monthly trap-captures of adult blow-flies (Calliphoridae) in the northern Kruger National Park

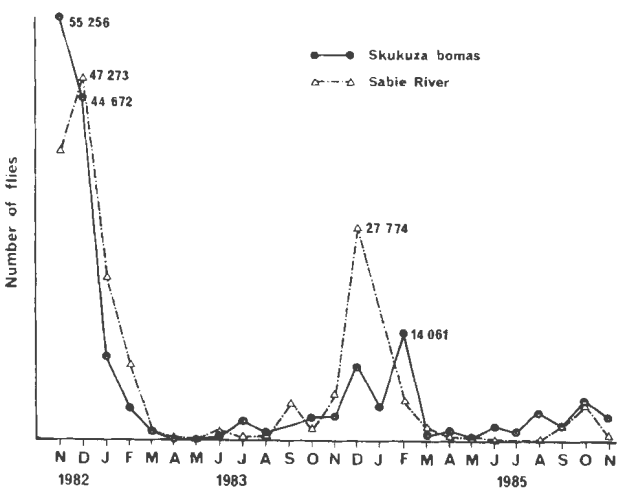

FIG. 9 Monthly trap-captures of all adult blow-flies (Calliphoridae) in the Skukuza area, southern Kruger National Park

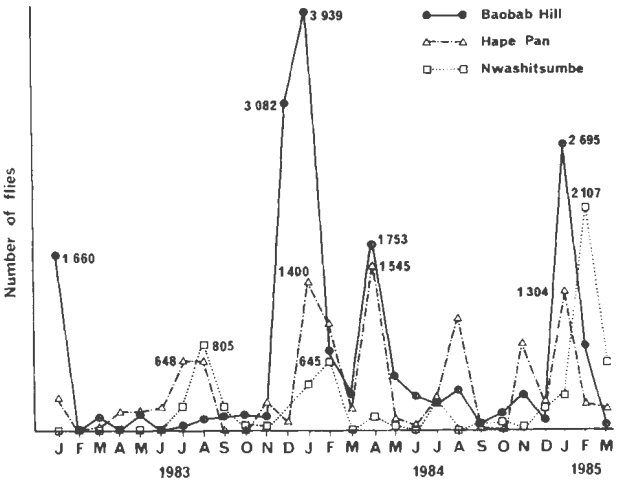

FIG. 10 Monthly trap-captures of all *Musca* spp. (Muscidae) in the northern Kruger National Park

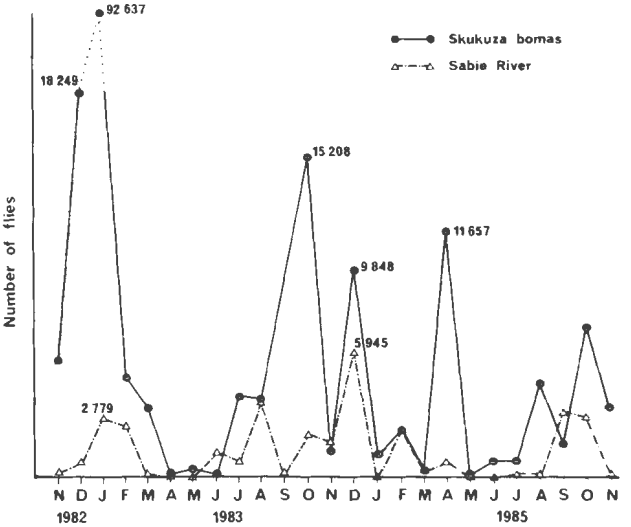

FIG. 11 Monthly trap-captures of all *Musca* spp. (Mucidae) in the Skukuza area, southern Kruger National Park

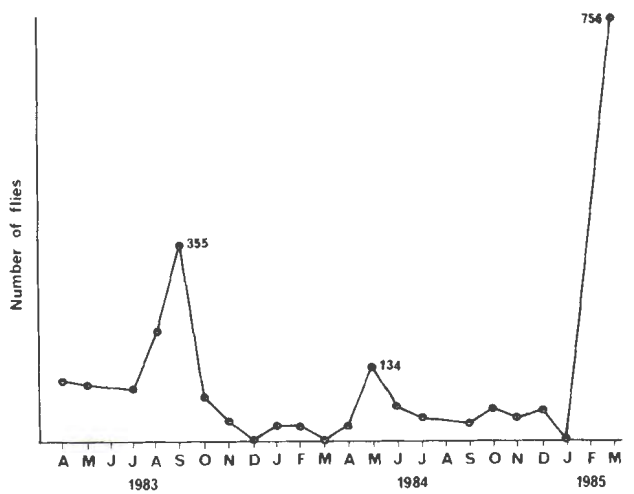

FIG. 12 Monthly trap-captures of *Sarcophaga* spp. (Sarcophagidae) at Nwashitsumbe in the northern Kruger National Park

and November, with a maximum around August/September, while the population reached a minimum in summer and autumn.

Occasional individuals, less than 10 in total, of *Chrysomyia chloropyga* were captured in the northern KNP, but were recorded in significant numbers around Skukuza. Although present in relatively low numbers (Fig. 6), the species appeared to reach maximum population levels between June and September, with minimal presence from November to May.

In addition to the above-mentioned blow-fly species which breed in carrion, others were also attracted to the traps in sufficient numbers to allow some generalization about population abundance. Only infrequent low captures were made of the dung-breeding *Chrysomyia putoria* (Wd.) in the northern KNP, but this species main-

TABLE 1 Periods of peak abundance of carrion-frequenting blow-flies in various localities in South Africa

Locality	Periods of peak population numbers of				Conclusions based on	Author(s)
	C. albiceps	*C. marginalis*	*C. chloropyga*	*Lucilia* spp.		
Bredasdorp (Cape)	Warmer months December–April	Warmer months January–April	September–December	September–October	Trap-captures of adult flies	Mönnig & Cilliers (1944)
Bredasdorp (Cape)	Warmer months	Warmer months	Colder months	Breed throughout year on live sheep. Succesfully breed in large carcasses in winter	Breeding experiments on carcasses	Mönnig & Cilliers (1944)
Northern Karoo (Grootfontein)	November–January April–May	March–May	October–December March–May	October–December April–May	Trap-captures of adult flies	Smit (1931)
Northern Karoo (Grootfontein)	Summer peak in January	Summer peak December–Febr.	Winter and early spring peak June–September	May–September	Breeding experiments on carcasses	De Vries (Unpublished), in Ullyett (1950)
Middelburg (Cape)	Midsummer	Midsummer	Winter	Winter peak June–August	Breeding experiments on carcasses	Hepburn (1943b)
Onderstepoort	Summer	Summer	June–August	Winter and cooler months, but unable to breed successfully in carcasses in summer	Breeding experiments on carcasses	Hepburn (1943b)
Onderstepoort	October–December May	October–February	September–October	July–September 1940 December 1940 February–April 1941	Trap-captures of adult flies	Hepburn (1943a)

tained a steady presence around Skukuza and was occasionally recorded in fairly high numbers (Fig. 7). It reached maximum numbers in the warmer months, generally from October to February, and was present only in low numbers between April and August.

Chrysomyia bezziana was also rarely captured in the northern KNP, but the Skukuza trap-catches indicate a fairly strong presence during the warmer months, generally from November to April.

Apart from the various blow-fly species, the only other flies attracted to the rotting meat bait were *Musca* spp. These flies became very abundant at times but no clear pattern of seasonality could be detected. No attempt was made to separate the various species of *Musca*, and it may be that individual species have non-overlapping periods of peak abundance which collectively result in the erratic pattern presented in Fig. 10 & 11.

Significant numbers of *Sarcophaga* (Sarcophagidae) were captured only at Nwashitsumbe, all other traps attracting only very low numbers of fleshflies, or none at all (Fig. 12).

The results for especially, *C. albiceps, C. marginalis* and *Musca* during November and December 1982 and January 1983 are abnormally high. This stems from the exceptionally severe drought experienced during 1982 which caused the death of hundreds of animals, especially during the final months of that year, and provided vast larval resources for carrion-breeding flies (De Vos, Braack, Rogers, Boomker, Horak & Kriek, 1983).

Discussion

The results support the findings of most previous workers in other parts of South Africa (Table 1). *C. albiceps* and *C. marginalis* reach maximum abundance during the warmer months throughout the country, whereas *C. chloropyga* and *Lucilia* spp. are most numerous during the cooler months.

Of the species trapped in the KNP, the most numerous by far were *C. marginalis,* followed by *C. albiceps*. Despite these trap-catches being capable of providing at most only a rough *index* of abundance in this study they nevertheless did appear to reflect correctly the general proportionate abundance of each species and their seasonal fluctuation.

This contrasts with the findings of Hepburn (1943a) and Mönnig & Cilliers (1944), who captured low numbers of *C. marginalis* in meat-baited traps, but the latter authors suggest that this may be due to differential attractiveness of the bait. Unfortunately none of these workers provided details of the quantity and preparation of the bait. Our own experiments have shown that quantity and composition of bait are crucial for effective trapping, especially for *C. marginalis*. Braack (1984) indicated that this species is only attracted in large numbers to fresh bait, and that the bait must exceed at least 500 g to be maximally effective. The bait should also be kept wet. Small quantities of bait tend to attract a different guild of flies as shown by Mönnig & Cilliers (1944) and our own unpublished results; this fact also explains why Meskin (1980) found *C. marginalis* to be absent from his laboratory rat carcasses.

Braack & Retief (1986) calculated the population densities of *C. albiceps* and *C. marginalis* in the northern KNP, using radioactively marked flies and applying the Lincoln Index, and their results clearly showed *C. marginalis* to be far more abundant than *C. albiceps*. Other studies in mopane woodland of the far northern KNP (Braack, 1981, 1984, 1986) also showed that *C. albiceps* and *C. marginalis* were significantly more numerous in riverine and other well-wooded environments, whereas they tended to shun arid, sparsely vegetated areas. Although *C. albiceps* is known occasionally to breed in sheep fleece as a secondary fly (Smit, 1931; Hepburn, 1943a; Zumpt, 1965), they only breed in carcasses in the KNP and it is in wellwooded and riverine areas where most breeding is likely to occur (Braack, 1984). Vultures and other vertebrate scavengers rapidly detect and consume carcasses in more exposed environments. Other factors, such as moisture and shade, are also important in the survival of these species (Braack, 1984) and contribute to decreased numbers in more arid, open situations.

Lucilia cuprina accounted for practically all the captures of *Lucilia* in the KNP, a finding which tends to support the statement by Meskin (1980) that *Lucilia cuprina* is "restricted" to rural habitats whereas *Lucilia sericata* is "restricted" to disturbed, man-made habitats. *L. cuprina* is the most important myiasis-producing fly responsible for so-called "sheep-strike" in South Africa and Australia (Hepburn, 1943a; Zumpt, 1965).

Braack (1984) found no *Lucilia* breeding in 9 impala carcasses placed seasonally or in any other medium-sized to large-mammal carcasses in the Pafuri area of the KNP. Hepburn (1943b), however, found in experiments at Onderstepoort that *Lucilia* breed in sheep carcasses in winter, but not in summer. Several authors (Holdaway, 1930; Mönnig, 1942; Hepburn, 1943b; Mönnig & Cilliers, 1944), have indicated that *Lucilia* are unable to compete successfully with larvae of *Chrysomyia*, especially *C. albiceps*, which in its 2nd and 3rd instars is a facultative predator on other blow-fly larvae (Ullyett, 1950; Zumpt, 1965) which may account for the low numbers of *Lucilia* during the months when *C. albiceps* and *C. marginalis* are abundant.

In experiments in the Cape winter-rainfall area, Mönnig & Cilliers (1944) found that not a single *L. cuprina* bred from sheep carcasses placed in all seasons, and that *L. sericata* were reared only in very low numbers. They state that *L. sericata* is a "small-carcass breeder" (cats, pheasants, larger snakes, etc.), whereas the *L. cuprina* population is sustained by breeding in the fleece of live sheep. Addressing the fact that Hepburn (1943b) found large numbers of both *L. cuprina* and *L. sericata* breeding in sheep carcasses in winter in the summer-rainfall area at Grootfontein (Cape Province), Mönnig & Cilliers (1944) attributed this contrasting evidence to the fact that "*Chrysomya* species are inactive and conditions are unfavourable for the occurrence of strike" (on sheep) during winter in the summer-rainfall region when conditions are dry and cold. They state that in the winter-rainfall region the climate is temperate and moist in winter so that *L. cuprina* is preferentially drawn to live sheep and avoids carcasses placed in winter. Should *Lucilia* indeed have a preference for breeding in live sheep, their explanation does not answer the obvious question why *Lucilia* does not maintain itself equally well in the Bredasdorp or Swellendam area where rainfall is distributed more or less evenly throughout the year and where temperature and sheep availability are optimal, or why *Lucilia* does not increase in the warmer months in the summer rainfall areas where conditions for sheepstrike are favourable.

The general opinion that it is the competitive influence of *C. albiceps* and *C. marginalis* larvae that precludes *Lucilia* from effectively utilizing carrion in the warmer months (Mönnig, 1942; Howell, 1969; Howell, Walker & Nevill, 1978) is questioned by Ullyett (1950) who found contrasting evidence. His extensive competition experiments indicated that *Lucilia* are not nearly as competitively inferior as is generally believed, and that ". . . although *Lucilia* is not as capable of producing large

populations under optimum condition as are the *Chrysomyia* species, it is nevertheless more adapted to adverse conditions engendered by severe larval competition. It has, consequently, a better chance of survival" (p.98). Ullyett also provides evidence to show that populations of *Lucilia* are often in decline before those of *Chrysomyia* increase. As Richardson (1980) also indicates, the factors influencing population fluctuations in *Lucilia* therefore remain unclear.

C. chloropyga and *C. putoria* were formerly regarded as con-specific although polymorphic (Zumpt, 1956; 1965), but Paterson (1977) conclusively showed that they are 2 ecologically and morphologically separate species. *C. chloropyga* commonly breeds in carcasses whereas *C. putoria* breeds in faeces and the larvae are most commonly found in pit-latrines. *C. chloropyga* is also an important fly responsible for sheep-strike in South Africa (Smit, 1931; Hepburn, 1943a), ranking second in importance to *L. cuprina*. Hepburn (1943b) found *C. chloropyga* bred in large numbers during winter, in sheep carcasses at Onderstepoort (Tvl) and Grootfontein (Cape Province), but not in the warmer months. Mönnig & Cilliers (1944) confirmed these findings in the Bredasdorp (Cape Province) area, where *C. chloropyga* was also present in large numbers at carcasses only in winter. The almost complete absence of this species in the dry northern KNP and its relatively low presence in the southern KNP can almost certainly be ascribed to the area being a marginal habitat for the species. Zumpt (1956, 1965) states that this species (referred to by him as *C. chloropyga* form *typica*) predominates in the southern tip of the continent but is also present at some higher altitudes in the tropics. This suggest a preference for a cooler climate. It is not certain whether the specimens trapped at Skukuza originated from carcasses in the KNP or from live sheep in adjoining tribal homelands.

Although only rarely recorded in the 3 traps in the northern KNP, *C. putoria* occasionally did gain abundance at the Pafuri Anthrax Research Camp and Pafuri Picnic site, where inadequate care sometimes allowed large numbers of larvae to utilize pit-latrines. As this species has never been recorded as breeding in carcasses, but only in human faeces, it follows that the population around Skukuza in the southern KNP must have resulted from pit-latrines or other accumulations of human faeces in the area. The species would of necessity also be restricted to areas of human concentration, and this is confirmed by the pattern presented in the northern KNP.

C. bezziana, also known as the Old World screwworm or cattle screwworm, breeds in wounds on living animals (Zumpt, 1965; Howell *et al.*, 1978) and has never been recorded from carcasses. Such larval-infected wounds appear to be rare in the KNP and no opportunity has arisen to collect such larvae. It is therefore not certain whether the adult specimens trapped in the Skukuza area arose from within the KNP or were migrants from domestic animals in adjoining agricultural areas.

Aside from low numbers of *Sarcophaga* (Sarcophagidae), the only other calliphorid flies recorded were low numbers of *Auchmeromyia bequaerti*, *Hemigymnochaeta* spp. and *Tricyclea* spp.

Because of the numerical dominance by *C. albiceps* and especially *C. marginalis*, the collective seasonal abundance of all carrion-attracted blow-flies presents a pattern similar to that of these 2 species. Blow-flies are most numerous in the northern KNP from November to March and least numerous from May to September. In the southern KNP, they are most abundant from November to February and least numerous between April and August. Blow-flies are more numerous in well-wooded environments and are present only in relatively low levels in arid, open, mopane scrub-plains.

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populations under optimum condition as are the *Chrysomyia* species, it is nevertheless more adapted to adverse conditions engendered by severe larval competition. It has, consequently, a better chance of survival" (p.98). Ullyett also provides evidence to show that populations of *Lucilia* are often in decline before those of *Chrysomyia* increase. As Richardson (1980) also indicates, the factors influencing population fluctuations in *Lucilia* therefore remain unclear.

C. chloropyga and *C. putoria* were formerly regarded as con-specific although polymorphic (Zumpt, 1956; 1965), but Paterson (1977) conclusively showed that they are 2 ecologically and morphologically separate species. *C. chloropyga* commonly breeds in carcasses whereas *C. putoria* breeds in faeces and the larvae are most commonly found in pit-latrines. *C. chloropyga* is also an important fly responsible for sheep-strike in South Africa (Smit, 1931; Hepburn, 1943a), ranking second in importance to *L. cuprina*. Hepburn (1943b) found *C. chloropyga* bred in large numbers during winter, in sheep carcasses at Onderstepoort (Tvl) and Grootfontein (Cape Province), but not in the warmer months. Mönnig & Cilliers (1944) confirmed these findings in the Bredasdorp (Cape Province) area, where *C. chloropyga* was also present in large numbers at carcasses only in winter. The almost complete absence of this species in the dry northern KNP and its relatively low presence in the southern KNP can almost certainly be ascribed to the area being a marginal habitat for the species. Zumpt (1956, 1965) states that this species (referred to by him as *C. chloropyga* form *typica*) predominates in the southern tip of the continent but is also present at some higher altitudes in the tropics. This suggest a preference for a cooler climate. It is not certain whether the specimens trapped at Skukuza originated from carcasses in the KNP or from live sheep in adjoining tribal homelands.

Although only rarely recorded in the 3 traps in the northern KNP, *C. putoria* occasionally did gain abundance at the Pafuri Anthrax Research Camp and Pafuri Picnic site, where inadequate care sometimes allowed large numbers of larvae to utilize pit-latrines. As this species has never been recorded as breeding in carcasses, but only in human faeces, it follows that the population around Skukuza in the southern KNP must have resulted from pit-latrines or other accumulations of human faeces in the area. The species would of necessity also be restricted to areas of human concentration, and this is confirmed by the pattern presented in the northern KNP.

C. bezziana, also known as the Old World screwworm or cattle screwworm, breeds in wounds on living animals (Zumpt, 1965; Howell *et al.*, 1978) and has never been recorded from carcasses. Such larval-infected wounds appear to be rare in the KNP and no opportunity has arisen to collect such larvae. It is therefore not certain whether the adult specimens trapped in the Skukuza area arose from within the KNP or were migrants from domestic animals in adjoining agricultural areas.

Aside from low numbers of *Sarcophaga* (Sarcophagidae), the only other calliphorid flies recorded were low numbers of *Auchmeromyia bequaerti*, *Hemigymnochaeta* spp. and *Tricyclea* spp.

Because of the numerical dominance by *C. albiceps* and especially *C. marginalis*, the collective seasonal abundance of all carrion-attracted blow-flies presents a pattern similar to that of these 2 species. Blow-flies are most numerous in the northern KNP from November to March and least numerous from May to September. In the southern KNP, they are most abundant from November to February and least numerous between April and August. Blow-flies are more numerous in well-wooded environments and are present only in relatively low levels in arid, open, mopane scrub plains.

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