ESTIMATION OF POPULATION SIZE AND DISPERSAL IN *ANOMALIPUS MASTODON* FÅHRAEUS, 1870 (COLEOPTERA: TENEBRIONIDAE: PLATYNOTINI)

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A population of the tenebrionid species *Anomalipus mastodon* Fåhraeus, 1870, was studied particularly in respect of population density and characteristics of movement. A total of 332 individuals was marked throughout the season. At the peak of surface activity the population was estimated at 350 adults, equivalent to 23 800/ha or 148,8 kg/ha. The main daily movement of individuals was calculated at 6 metres, and the maximum displacement (between first and last sightings) at less than 10 metres.

Keywords: Southern Africa, Coleoptera, Tenebrionidae, *Anomalipus mastodon*, population size, dispersal, vagility.

INTRODUCTION

The genus *Anomalipus* is composed of 51 species distributed from equatorial East Africa (one species) to the southeastern Cape (three species) and throughout the Kalahari to Namibia (two species). The geographic ranges of individual species vary from a single locality to areas with a radius of over a thousand kilometres. The preferred climate varies from semiarid to moderately mesic, but excludes deserts and mesic forests. Individual species occupy a restricted and specific habitat within their geographic ranges, most species preferring dense bush-covered patches of woody savanna (personal observation).

Field observations suggest that surface activity usually occurs after rain and during relatively cool and humid hours of the day and that local density may be high and clearly demarcated, even under the same bush cover. For example, over a period of six years *A. endroedii* Endrödy-Younga was only found in the same stretch of about 80 metres in a bush-covered ravine two kilometres in length.

All *Anomalipus* species are heavily built with strong legs. If undisturbed they move little and slowly, spending most of their active periods feeding, either motionless or in slow motion. They feed on dead plant material, especially fallen dry leaves. Their sound production, and courting and mating behaviour, is species-specific and might be complex (Endrödy-Younga, 1988).

The geographic range of *Anomalipus mastodon* Fåhraeus, 1870, coincides largely with the Trans-vaal Province of South Africa. It has a mosaic distribution pattern, primarily following the patchy bush growth of the Highveld, but within this range it is often absent from apparently suitable habitats. *Anomalipus mastodon* often occurs together with one to three of its congeners. It is a large (24–33 mm), wingless species.

The presence of *A. mastodon* in the senior author's garden provided a unique opportunity to study the habits and movements of this species and to estimate the density of the adult population.

Data on the biology of *Anomalipus* species were obtained from a breeding programme in the insectary of the Transvaal Museum. The longevity of adults is quite remarkable. A specimen kept in captivity died in the laboratory 5 years and 8 months after its capture, and in the study area about 20 % of the marked specimens survived for at least three years. Females lay one egg at a time throughout most of the active season, and egg-laying may take place several years in succession. Detailed accounts on the biogeography and ecoethology of *Anomalipus* species appear in Endrödy-Younga (1988).

METHODS

The surface activity of *Anomalipus mastodon* was observed in the senior author's garden in Waterkloof (stand 512), Pretoria, beginning in

1975. The garden has a picket fence on the eastern and wire mesh on the southern boundary, but these did not restrict the movement of individuals into neighbouring gardens. On the nothern side movement was restricted by a brick wall. A mark and recapture study of the population was carried out during the summer of 1979/80 for estimates of population size and dispersal capacity.

The largest number of beetles frequented the bush-covered (mainly exotic ornamentals) south-eastern corner of the garden. Leaf litter was not removed from this area during the observation period. A swimming pool surrounded by slate paving is situated in the same corner, separated from the bushes by a strip of lawn. A broad stretch of lawn flanked the bushes in the rest of the garden (Fig. 1). The bush-covered area was divided into twelve 7 × 3 m plots, nine of them along the picket fence on the east side and three along the wall on the north side. Bush cover in this area was uniform but the deep clay soil reverted gradually to harder and stonier ground from plot no. 4 towards plot no. 1. As the study progressed, observation of plots 1 to 3 was discontinued because of the lack of sightings. The two plots (6 and 9) with the highest population density of beetles also had the best shade. Every 'sample-day' (defined below) the adjoining lawn and pool were also checked and occasional sightings recorded.

Observations started on 18 November 1979, after the first substantial summer rain, and continued till 1 February 1980 when the surface activity of adults declined markedly. There is no adult activity during the dry late summer and in winter. A break in observations between 5 and 24 December coincided with the calculated peak of adult activity.

When first captured, each individual was marked with a serial number in white acrylic paint. Sex and the block in which each individual was found were recorded. At subsequent sightings the serial numbers and block locations were recorded with as little disturbance to the beetles as possible. Active specimens are easily spotted because of their large size. Thus no trapping that might bias the results was necessary. Individuals that were inactive for one or more days shelter rather superficially, thus no leaf litter or stones were moved in order to find such individuals. Sampling was carried out regularly between 18:00 and dusk. Seventy-one percent uf the samples was taken at daily intervals, the other 29 % at intervals of 2–4 days, averaging 1,4 days. Ninety-two percent of the intervals between samples was either 1 or 2 days. We will refer to the interval between subsequent samples as a 'sample-day'.
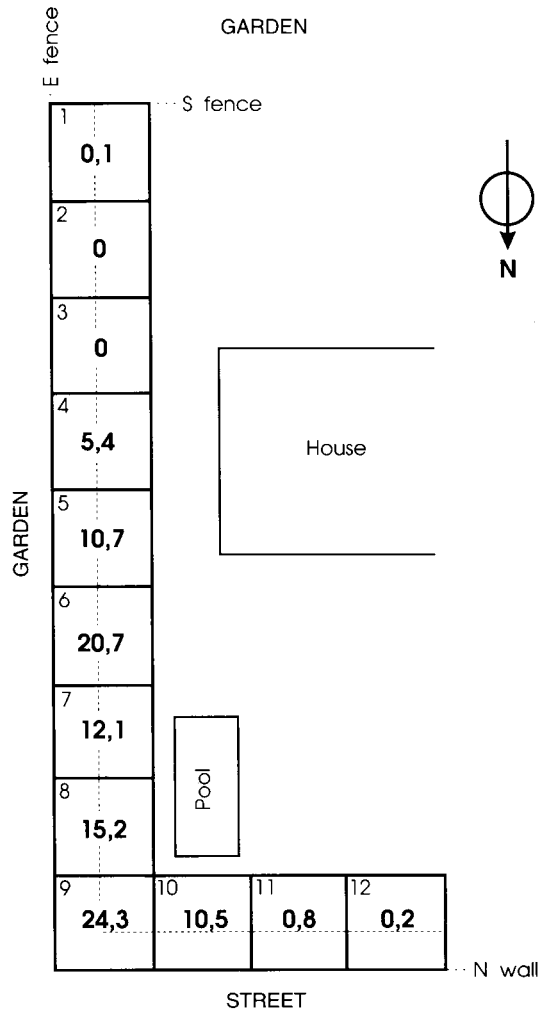

Fig. 1

A diagram of study site showing the layout of observation blocks and adjacent portion of the garden in Waterkloof, Pretoria. In blocks 1 to 12 the capture frequencies (%) within the study area are indicated. Most captures occurred in the seven blocks near the pool.

Population estimates were made using the method of Jolly (1965) and Southwood (1966), which is based on a probalistic model and estimates the population from the number of marked individuals captured at the sample time before and after the day in question. This method also allows the estimation of the mark dilution rate (immigration + natality) and the loss rate from the population (emigration + death).
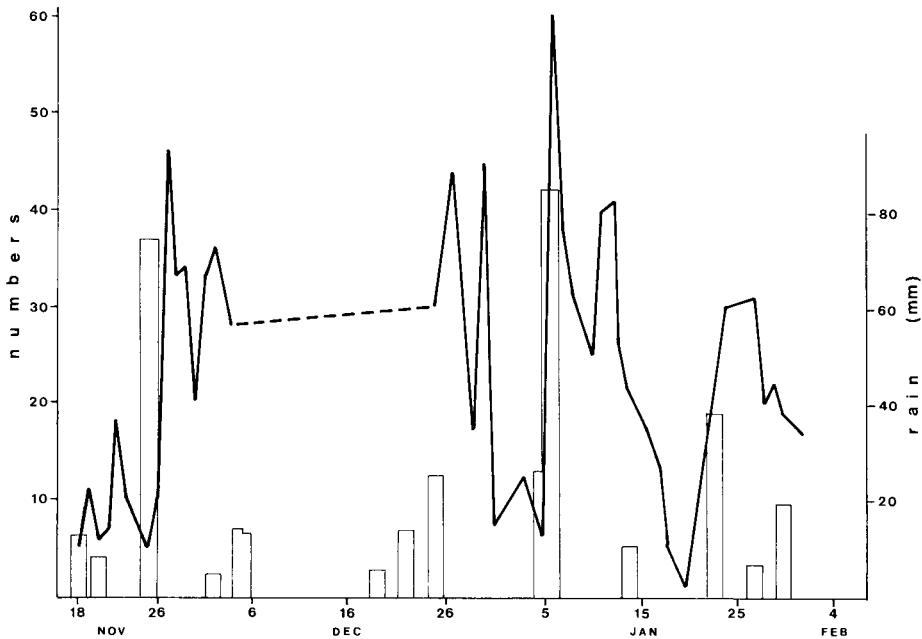
Fig. 2

Total number of beetles captured on each sample-day throughout the study. Rainfall is indicated by the vertical bars. Beetles are more active after significant rainfall.

RESULTS

Population size estimation

Figure 2 shows the marked population size for all sample-days. The active population (those available for marking) increased rapidly in early summer following the first major rain. It probably peaked sometime between 4 and 25 December and gradually dropped throughout the summer. Because of the sampling gap in December, maximum population size could not be estimated, but it probably exceeded 300. The population remained responsive to rainfall throughout the summer and the estimates generally increased following rainfall of more than 20 mm.

The number of beetles captured (Figs 2, 3) clearly shows the dramatic effect that rainfall had on beetle activity (capturability). Every rainfall event of 20 mm or more was followed within one or two days by a large increase in the number of beetles captured. Activity then gradually declined until the next major rain.

Estimation of the number of new animals (= natality + immigration + beetles active for the first time) in the population showed that by far the largest increase occurred after the first summer

rain on 26 November. At this time it is estimated that over 200 new beetles appeared in the population (Figs 2, 3). Many of these were newly eclosed (teneral) adults which continued to appear until the end of December. The estimates of new adults later in the summer were highly variable, and generally below 25 or 30 per sample period (three-point moving average). Thus the great bulk of the increase in the capturable population occurred early in summer, with low rates of addition to the population after that. The estimates of losses (death + emigration + beetles becoming inactive) from the population (Fig. 4) showed that the probability of survival of marked animals from one sample time to the next was generally quite high ($\bar{x} = 0,96$; $S.E. = 0,041$), and therefore the rates of death and emigration were both low.

The intervals between recaptures indicate that individuals may be active for short periods, and then inactive for longer periods. Figure 5 shows the proportion of recaptures which were 1, 2, 3, ... n days after the previous capture. Only beetles marked before 28 November were used for this analysis so that the results would not be skewed by a decreasing opportunity for longer intervals between captures. The mean number of sample-days between captures was 4,51 for males and
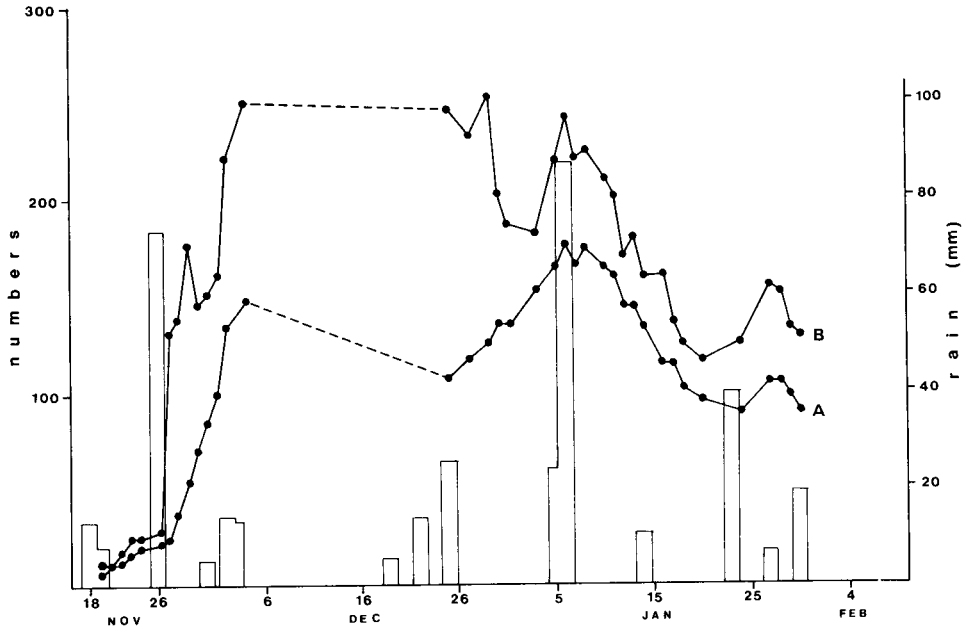
Fig. 3

Three-point moving average of captures (A), and population estimates (B). Total population size increased during early summer and after each rainfall event of more than 20 mm. The marked population increased steadily until early January, then declined. Peaks between 4 and 25 December were not recorded.

5,01 for females. For comparison, Poisson distributions with these means show the expected distribution of intervals between captures for each sex, if recapture interval were a random variable (Fig. 5).

The frequency distribution of capture intervals for both males and females was dramatically non-random [$P < 0,001$; chi-square test with $d.f.$ 145 and 134, respectively (Fig. 5)]. Males and females did not differ significantly, but both showed a much higher than expected frequency of short intervals (1 to 2 sample-days) and long intervals (> 10 days), and much lower than expected frequency of intermediate (3 to 10 days) intervals. This indicates that the beetles were captured in widely spaced bursts, as though they were active for a few days, then inactive and unavailable for recapture for many days.

Figure 6 shows the frequency distribution of the number of captures for all beetles during the entire study. Once again, this function differed greatly from a random Poisson distribution. Beetles were much more likely to be captured a small number of times than the random distribution predicted. This was similar to the patterns for intervals be-

tween captures (Fig. 5) and probably has similar causes.

Recaptures did not occur randomly throughout the study area, but were concentrated in certain parts of it. Figure 1 shows that 99 % of the captures were made in the 7 blocks near the northeastern corner. The low number of beetles in the three southern blocks may be attributable to the hard and stony ground there. Such soil is not suitable for egg-laying or the underground life of larvae and may also be less suitable for sheltering inactive adults. There is no obvious explanation for the low numbers in the two northwestern plots, where soil conditions and bush cover were similar to those of the best-inhabited plots.

Estimates of movement and dispersal

An analysis based on beetles recaptured on the very next day (Fig. 7) shows the frequency distribution of blocks moved between captures. This is a good estimate of distance moved per day, but because beetles tend to move back and forth, it cannot be converted into a directional movement
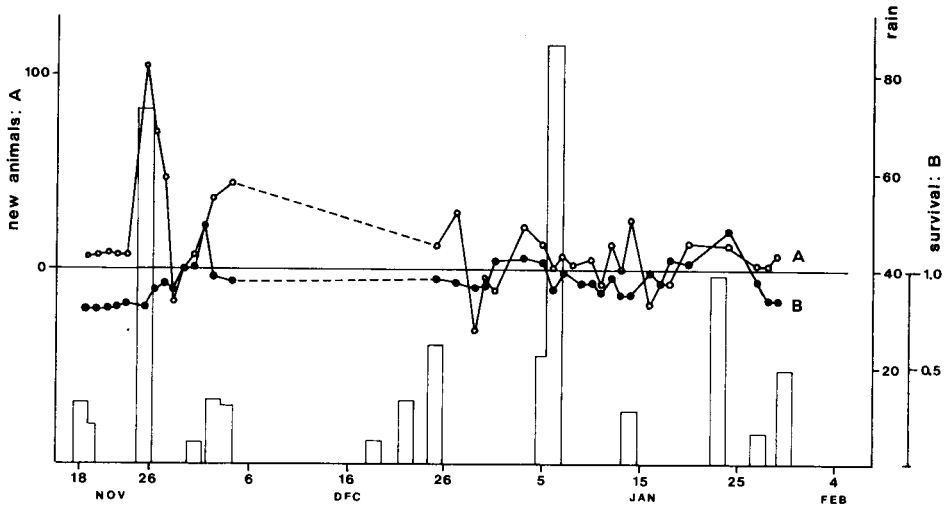
Fig. 4

Estimates of new animals in the population (A) and probability of survival (B) from the last sample-day during the study. New animals include immigration, natality and animals active for the first time. Survival probability includes loss from emigration, death or inactivity. Rainfall is indicated by the bars. The greatest burst of new animals occurred during the early summer. Survival is high throughout.

by multiplying it by the number of days between recaptures. Figure 8 shows that beetles move an average of only 6 metres in a day (0,85 blocks). About 82 % of the population moves less than two blocks (14 metres) and 94 % less than three blocks (21 metres). When the frequency distribution of blocks moved (Fig. 7) was compared to that expected on the basis of a Poisson distribution with the observed mean (0,85 blocks), the difference was found to be not significant (chi-square test). Thus, the distance moved by the beetles in one day is a random variable with the observed mean. No individuals are likely to move farther or less far than randomness would predict.

Having estimated typical vagility for the population, the question that arises is how this is reflected in the dispersal within, and emigration from, the observed area.

It has already been shown that the rate of loss from the population is low. That loss by emigration is low was suggested by the low numbers of individuals observed outside of the bush cover. This, however, does not necessarily mean that dispersal was similarly low within the preferred habitat. Figure 8 shows the distance (in numbers of blocks) between the first and last sightings of individuals, together with the total number of sightings between the first and last. In the same figure

the total movement of individuals is given as the sum of all movements between sightings, irrespective of the direction of those movements, and the maximum displacement of individuals is shown, irrespective of whether the beetles were also recorded at smaller displacements.

DISCUSSION

Population size estimation

The following conclusions about the population and activity of *Anomalipus mastodon* can be drawn from our data. Capturable beetle populations increased in a large burst following the first major summer rains. While beetles remained responsive to rain and continued to enter the population throughout the summer, they did so at much lower rates. After peaking at about 2 beetles per m^2, presumably between 4 and 25 December, populations declined throughout the summer. Neither mortality nor emigration were high. Beetles had a very high probability of being recaptured (i.e., did not die or emigrate) on the next sample date ($\bar{x} = 0,96$). For a beetle captured at the beginning of the study, the probability that it was still recaptured at the end of the study, 35 sample-days (74 calendar days) later, was 0,24 ($0,96^{35}$). The low
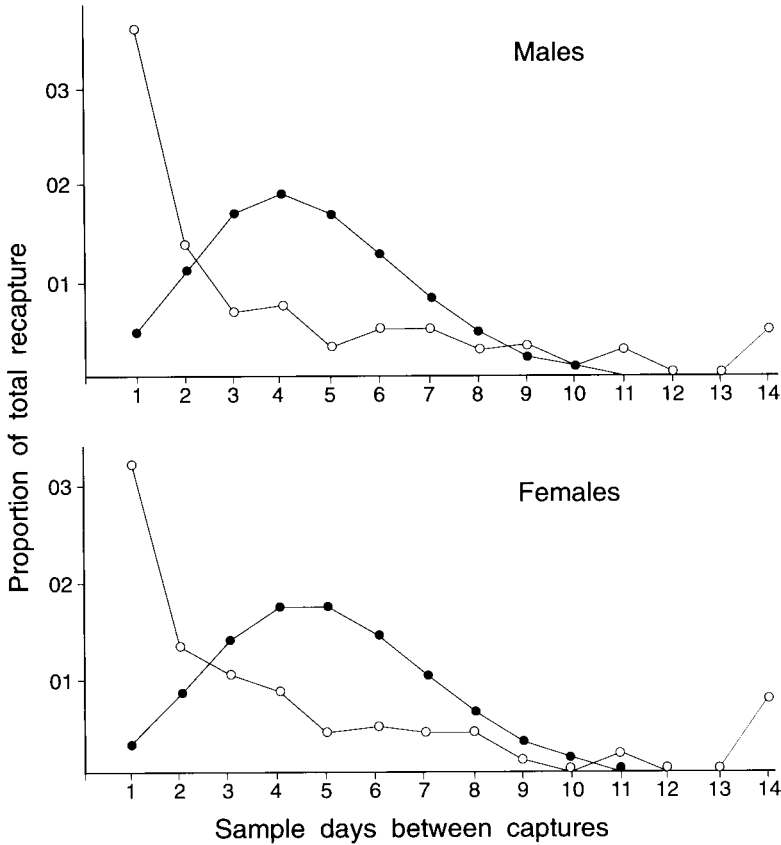
Fig. 5

Comparison of the interval between captures (open circles) for males and females with that expected on the basis of the random Poisson distribution. Males and females do not differ significantly, but are both highly non-random, showing much higher than expected short and long intervals between captures, and lower intermediate intervals.

probability of emigration was confirmed by the short distances moved by beetles in a single day. The beetles appeared to be active for a short period, then inactive for longer periods before becoming active again. During the cold, dry winter months there is no surface activity at all when adults are hibernating underground.

The Jolly (1965) method makes certain assumptions which warrant discussion. Only the population of beetles *available for capture* is estimated. Those which are dormant or otherwise unavailable are not estimated. New animals can be immigrants, animals present but previously inactive, and newly eclosed adults. The method also assumes that capturability of marked and unmarked animals is the same and remains constant over time. This is clearly not the case with *Anomalipus*

mastodon, but what effect this has on the population estimates is uncertain.

A limitation of this study is that beetles were not sampled at equal intervals. Thus the analysis was in terms of 'sample-days' rather than actual days. Because most samples were taken 1 to 3 days apart, the values in actual days were somewhat larger than those in sample-days. The overall patterns were not affected by this limitation.

In the laboratory females mature their very large eggs (about 6 mm), and lay them one at a time, no more than one per week. Direct egg counts by dissection were not made. Females in captivity laid 2 to 18 eggs ($\bar{x} = 9,2$) in a season. Egg-laying during our observations occurred over a period of at least four months, starting soon after the first females appeared and peaking at the same time
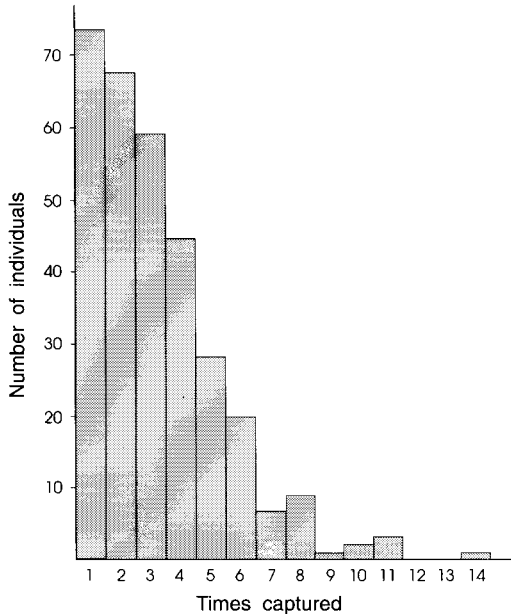
Fig. 6

Frequency distribution of numbers of captures for individual animals over the entire study.

Fig. 7

Frequency distribution of distance moved in one day, compared to expected distribution based on the random Poisson. The two distributions are not significantly different, indicating that distance moved in one day is a random variable. Both sexes are combined. Beetles move an average of about 6 m per day; 94 % of the population moved between 0 and 21 m per day and 82 % less than 14 m per day.

as did general activity, and then declined rapidly after February. *Anomalipus* females must be able to store sperm for a long period of time, as solitary females laid fertile eggs in the laboratory for up to 19 months after capture. The development period of larvae in the laboratory varied from 9 to 14 months after laying but it is not known if such variability is typical of wild populations.

The unusually great longevity of individuals of *Anomalipus* and related genera is important to this study because new adults entering the population can be survivors of previous years as well as newly eclosed beetles. Some adults marked during the 1979/80 season were recaptured three seasons later in 1982/83. Of those, one female and three males were in pre-copula, all with unmarked partners.

Survival of American adult tenebrionids under either natural or laboratory conditions (Kramm and Kramm, 1972; Doyen and Tschinkel, 1974) might be extended into the second season but usually a few individuals survive a second winter. In populations that consist of only a low rate of surviving adults from the previous season or none at all, peaks can be observed in late autumn, made up by the accumulation of new eclosures (Rickard and Haverfield, 1965).
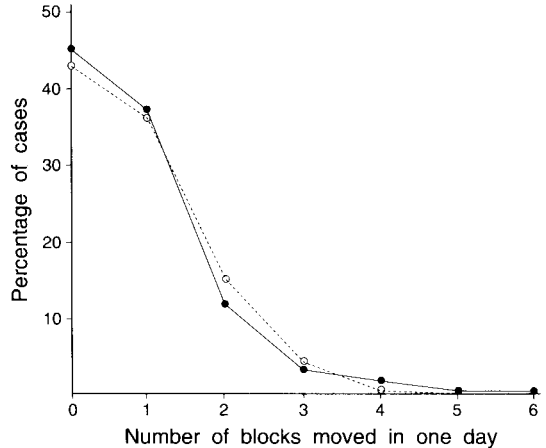
Of importance is the source of the new animals that enter the population after the early-summer burst. Indications are that the emergence of new individuals continue over a long period of the activity season. In *Anomalipus* where individual longevity is several years, adults are active only during the rainy season and spend the cold, dry season in an akinetic state in the ground. These overwintering adults emerge anew with the first rain of the new season. Thus the initial population is composed of overwintering adults, soon joined by the majority of the newly eclosed ones that can usually be recognized as such. Virtually all newcomers thereafter are attributed to new eclosures in gradually declining numbers as the season progresses. The considerable range of the larval development period observed in the laboratory (9 to 14 months), and the laying of their eggs singly over an extended period, coincides with the extended appearance of newly emerging adults in the garden population.

Activity is strongly weather dependent within the rainy season. Kramm and Kramm (1972) attributed the reduced mid-day activity of adults to increased temperature, but temperature and humidity normally covary. Saturation deficit is probably the critical variable. As expected, on humid, cloudy days a much larger proportion of

our population was surface-active than on hot and dry days, but during dry spells even cool hours did not produce similar activities. On humid and cloudy days the activity extended over the mid-day hours but not into the night. As in Tenebrionidae in general, diurnality is a characteristic of taxa higher than genera and is not an effect of weather conditions or competition. *Anomalipus mastodon* and its congeners in the sub-tribe Anomalipina are strictly diurnal, whereas species of the other subtribes of Platynotini (Platynotina, Stizopina and Gonopina) are all nocturnal or cre-puscular (personal observation). Cloudsley-Thompson (1963) tested the light response of some Sudanese Tenebrionidae in the laboratory. He found that Pimeliini are facultatively nocturnal and Adesmiini diurnal. The diurnal activity pattern in the higher categories of Tenebrionidae is similar throughout their distribution (Louw, 1983, and personal observation).

The patchy distribution of most terrestrial Tenebrionidae is a phenomenon largely unexplained. Often populations are spatially restricted within the habitat without apparent environmental reasons (e.g., *Anomalipus endroedii*). As a result, the population density within a patch may be quite high, while outside it is practically nil. In our calculations of population densities, as in those that follow the values, are averages for the whole high-density observation area irrespective of the heterogeneity within.

The estimated peak population of 350 individuals (Fig. 3) is calculated for the 147 m^2 area of the seven plots (7 × 3 m) which resulted in more than one percent of the sightings. This is equivalent to 23 800 individuals per hectare as an indicator for the localized high density area. Doyen and Tschinkel (1974) estimated a combined population of several Tenebrionid species for 5600/ha in a study in Arizona, U.S.A. Wise (1981) estimated the population in New Mexico, U.S.A. in three subsequent years as 6600, 6200 and 6000/ha. Thomas and Sleeper (1977) determined estimates in the Mojave desert in three subsequent years of 2400, 2900 and 5200/ha. Thus the population density values calculated for *A. mastodon* are much higher than those for U.S.A. populations. This could be the result of within-plot heterogeneity of their larger plots, or uniformly lower densities. Had other studies been limited to the occupied patches, their observed densities might have been higher.
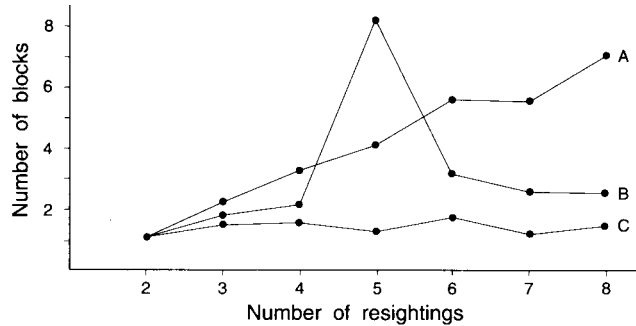

Fig. 8

Characteristics of movement. A = total movement; B = maximum displacement; C = distance between first and last sightings. Only total movement increases steadily with the number of re-sightings. Movement of individuals is random.

Considering the estimated biomass of adults as 142,8 kg/ha or 2,1 kg for the study area (live weight = 6 g per adult) the question of resource limitation arises. At our site the food source of adults, i.e., the layer of fallen leaves, was not appreciably reduced during the observation period, nor was there an apparent degradation of green vegetation due to the possible root feeding of larvae. In our study food resources do not appear to be limiting. Doyen and Tschinkel (1974) suggested that shelter, not food, limited populations at their montane site. In his study on a Mojave Desert (U.S.A.) tenebrionid community, Thomas (1979) also concluded that food resources do not limit population levels. Rickard and Haverfield (1965) estimated 142 000/ha individuals, equivalent to 32,3 kg/ha in a desert steppe population, in Washington (U.S.A.), and do not report a food shortage either. During decades of fieldwork we did not encounter a single situation where food shortage could be suspected as a limiting factor of detrivorous tenebrionid populations, including those in the Namib Desert.

Vagility and dispersal

The dispersal capacity of a population can be understood as a combined function of vagility, habitat conservatism, spatial extent of preferred habitat and level of unacceptability of the adjoining habitats.

The locomotive capacity is vastly different in terrestrial Tenebrionidae. Some of them such as the majority of the Southern African nocturnal species (e.g., Molurini, Eurychorini, Asidini) are extremely slow in their movement. At the other

extreme are the species that are active during the hottest hours of the day, for example most Zophosini and Adesmiini. Indeed, some long-legged Adesmiini such as the *Onymacris* species of the Namib Desert dunes can only be captured in a sprint. The *Anomalipus* species are somewhere in the middle. Some individuals covered a metre in 12 seconds during 'escape' after handling (marking). Even these stopped, however, at the first shelter. If undisturbed they move slowly, at a fraction of this speed.

The locomotive capacity of individuals far exceeds their vagility as measured by their daily spatial displacement. Differing vagility among North American tenebrionid species has been observed by Doyen and Tschinkel (1973) who found the lowest vagility in an Asidini species, a tribe that exhibits similar habits in South Africa. The degree of vagility seems to be a specific character. The lowest vagility in Tenebrionidae has been observed in species with brood care. For example, a *Stizopus* species in the Cederberg, southwestern Cape Province (Platynotini, Stizopina), forms brood chambers under flat stones. Both parents forage only short distances from their stones. Similarly the Namib Desert cryptochine species *Calognathus chevrolati* leave their sand tunnel only far enough to find plant debris to carry into their underground chamber. If disturbed they return to their tunnel at a speed of about 1 m/4–6 sec. Thus the locomotive capacity of these species might be considerable, but their vagility at least during the breeding period, is virtually nil (personal observation). At the opposite extreme of vagility, in *Onymacris plana* in the Namib Desert, Roer (1984, 1985) reported up to 20 km displacement of marked individuals in a season. There is no brood care in this species and the high locomotive capacity is combined with high vagility. In our *Anomalipus* population the extent of the preferred habitat (bush cover) evidently provided the spatial limits of the movements of the individuals (see below), but actual movement was considerably less than that set by habitat limits. Figure 8 shows that total movement might have been considerable during the season, but the distance between first and last sightings is very small.

Another important aspect of movement in a population is the dispersal from the area of birth. This population characteristic is influenced by the level of habitat conservatism of the species and by the spatial extent of their preferred habitat. Different habitat preferences in tenebrionid species were described by Doyen and Tschinkel (1974) in the montane Arizona, U.S.A., by Koch (1961) and Louw (1986) in the Namib Desert and in the Kalahari, and by Calkins and Kirk (1973) even within wheat fields in South Dakota, U.S.A.

Anomalipus mastodon, like most of its congeners, live under rather thick bush cover that occurs in isolated patches in Transvaal. *Anomalipus mastodon* adheres to this type of habitat to such an extent that only 17 of our 1004 sightings were made on the open lawn adjacent to the bush-covered blocks. This suggests that dispersal from one habitat to another must be quite low. The colony-like distribution of a number of *Anomalipus* species may result, in part, from such low dispersal. The most striking example is *A. endroedii* in a bush-covered 2 km ravine in the Watervalriver Pass (eastern Transvaal). Over a six-year period (1980–1986) the population was found only in the same 80 m section of the ravine, although there seemed to be no difference on either side of the site.

The natural distribution of *A. mastodon* falls between the Limpopo and Vaal Rivers, a north-south distance of almost 700 km (Endrödy-Younga, 1988). The vegetation there is a woody savanna-type with scattered and isolated clumps of bushes. Some of these clumps shelter populations of *A. mastodon*. The low vagility and dispersal capacity of this species suggest that gene flow between the extreme populations may be very low indeed.

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