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Seasonal variation in the dung of African grazing mammals, and its consequences for coprophagous insects

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Abstract. The dung of African grazing mammals varies in nutrient and moisture content according to the condition of the pasture on which the animals feed. This study investigated the effect of variation in quality of herbivore dung on the survival and reproduction of coprophagous insects. Seasonal variation was recorded in physical and chemical characteristics of zebra, wildebeest and impala dung. Dung was collected from free-ranging animals grazing in natural habitat in Mkuzi Game Reserve, a hot summer-rainfall region of South Africa. Interspecific differences in dung were related to the feeding ecology, digestive physiology and size of each species. Seasonal changes in water and nitrogen content of dung were related to patterns of rainfall and hence pasture growth. Dung moisture was significantly correlated with the amount of rain that fell in the preceding 2 weeks for wildebeest, in the preceding 4 weeks for impala and in the period 2–6 weeks before collection for zebra dung. Seasonal variability in wildebeest dung affected the reproductive rate of the dung beetle *Euoniticellus intermedius* (Reiche). Egg production at 25 °C ranged from 0·1 per female per week in winter dung to 12·1 in summer dung, and was significantly correlated with dung moisture. *Euoniticellus intermedius* and the African buffalo fly *Haematobia thirouxi potans* (Bezzi) could not breed in fresh wildebeest dung of 62% water content. However when the water content was raised to 68% and above, breeding by *Euoniticellus intermedius* increased; and at moisture contents of 73% and above, buffalo fly size increased and survival improved. Higher water content was correlated with an increase in availability of dung fluid, the component of dung used by these insects.

Key-words: African herbivores, coprophagous, dung, dung beetles, food-quality, impala, wildebeest, zebra

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Introduction

Dung is the only source of nutrition for most dung beetles (Scarabaeidae) and for larvae of several species of coprophagous flies. Adult dung beetles and coprophagous fly larvae feed on the fluid component of dung, whereas dung beetle larvae ingest whole dung, usually after it has been buried in an underground nest by the adults (Halffter & Matthews, 1966).

The suitability of dung as insect food is influenced by the species of animal that produces it. For it. For herbivores, interspecific variability in dung characteristics arises from the major dichotomies in herbivore feeding and digestion, namely grazing *vs* browsing, and rumination *vs* non-rumination. Body size of herbivores places further constraints on their nutritional requirements and feeding ecology (Demment & Van Soest, 1985). These sources of variation result in dung that differs in characteristics such as texture and size of droppings, and in water, nitrogen and fibre content.

In the study reported here, interspecific differences in the physical and chemical composition of the dung of three African herbivores grazing in their natural habitat were determined and the implications of those differences for dung-feeding insects were considered. Zebra (*Equus burchelli* (Gray)), wildebeest (*Connochaetes taurinus* (Burchell)) and impala (*Aepyceros melampus* (Lichtenstein)) were selected because they occur sympatrically yet have markedly different feeding strategies and digestive physiologies.

Impala and wildebeest are ruminants. Impala are small (approx. 40 kg) and have a higher metabolic rate per unit of body tissue than wildebeest (approx. 120 kg), and thus require a higher quality diet. They select only the green leaves of young grass plants, material that is high in protein and low in cell wall material. In the dry season they often include dicotyledonous browse in their diet (Hofmann & Stewart, 1972), since leaves of woody plants contain more protein and less fibre than grass leaves (Owen-Smith, 1982). Wildebeest mainly eat the leaves of short grass or feed near ground level in tall grasses (Hofmann & Stewart, 1972). Zebra are large (approx. 200 kg) non-ruminants that eat the leaves and stems of older long grass, material that is avoided by ruminants (Gwynne & Bell, 1968). Unlike ruminants, non-ruminants can compensate for a diet high in fibre and low in nitrogen by increasing the rate of throughput (Bell, 1971).

Seasonal change in pasture quality is a critical variable in the nutrition and feeding ecology of African grazing mammals. For instance, in the dry season the nitrogen content of tropical grasses can fall to levels that are insufficient to meet the protein requirements of many grazing species (Sinclair, 1975). Such changes in turn will affect the nutrition and population processes of insects that feed on herbivore dung. This has already been well documented for insects feeding on cattle dung, where variation in pasture condition is accompanied by marked changes in the survival and reproductive rates of coprophagous beetles and flies (Macqueen, Wallace & Doube, 1986; Ridsdill-Smith, 1986).

Seasonal variations in the dung characteristics of impala, wildebeest and zebra were monitored in the present study. Changes in the reproductive performance of a dung beetle (*Euoniticellus intermedius* (Reiche)) and the African buffalo fly (*Haematobia thirouxi potans* (Bezzi)) were correlated with seasonal changes in wildebeest dung. Seasonal variation in the water and nitrogen contents of dung from all three herbivores was compared with rainfall patterns, since it is known that the dry matter and protein production of pastures are largely governed by rainfall (Strugnell & Pigott, 1978).

The specific aims of the study therefore were:

1 To determine the interspecific differences in the dung of impala, wildebeest and zebra.

2 To relate seasonal changes in the dung of the three herbivores to rainfall patterns and hence pasture conditions.

3 To determine the effect of seasonal differences in wildebeest dung on the reproductive performance of two species of coprophagous insects.

Materials and methods

Study sites

Mkuzi Game Reserve is an area of 25 000 ha located in the hot, summer-rainfall area of the lowland in northern Zululand in Natal, South Africa (27° 36′S, 32° 13′E, at an altitude of 135 m). The vegetation is predominantly grassland and open bushland, on soil types ranging from heavy clay to deep sand (Moll, 1968). The dominant grasses are *Themeda triandra* and *Bothriochloa insculpta* (Moll, 1968), and the vegetation is classified as 'lowveld tropical bush and savanna', and the grasses as 'sweetveld' (Acocks, 1953). Large herbivores include 140 rhinoceros, 1400 wildebeest, 680 kudu, 820 zebra, 8100 impala, 3100 nyala, 180 giraffe and 480 warthog (April 1984 census; P. Goodman, personal communication). Daily rainfall and temperature data are recorded by Mkuzi Game Reserve staff.

Derdepoort Radio Station is located in a warm summer-rainfall area of the highveld, 20 km north-east of Pretoria (25° 40′S, 28° 15′E, at an altitude of 1240 m). The vegetation is unimproved native pasture in open bushland and is classified as 'sour grassveld' (Acocks, 1953). Large herbivore species include wildebeest, impala, zebra and blesbok.

Dung collection and storage

Fresh wildebeest, impala and zebra dung was collected monthly from January 1984 to June 1985 in Mkuzi Game Reserve. Up to 25 kg of wildebeest dung was collected on each occasion, to provide sufficient material for bioassays, and for physical and chemical analyses. The sample thus came from a large number of animals and was thoroughly mixed before use. Impala and zebra dung was required only for physical and chemical analyses, so only small amounts were collected, but always from several animals. These samples were also well mixed before use. Dung was placed immediately at 4 °C and returned to Pretoria where subsamples of fresh dung were dried for determination of water content. Dried subsamples of each dung type were crushed to 1-mm fragments for chemical analyses. Wildebeest dung was used in bioassays with the dung beetle *Euoniticellus intermedius*. Fresh wildebeest dung was frozen in 1-litre plastic bags until required. Bioassays were performed within 2 months of dung collection. When required for bioassay, the dung was thawed in plastic bags under infra-red lamps. Subsamples of thawed wildebeest dung were analysed for dung fluid parameters during each bioassay (see below). On one occasion, September 1985, fresh wildebeest dung was collected in Pretoria (Derdepoort) for an experiment on dung moisture levels. It was used fresh in dung fluid analyses and bioassays.

Physical and chemical analyses of dung

The water content of dung was determined by weighing subsamples (usually five) before and after drying at 100°C for 24h. Total nitrogen and crude fibre contents were determined for one subsample on each occasion, according to the methods of AOAC (1984).

The amount of dung fluid available to dung-feeding insects was assessed by pressing gauze-wrapped subsamples (usually two) with a hydraulic press set at 2 MPa for 2 min. Detailed methods are given by Aschenborn, Loughnan & Edwards (1990). Subsamples (usually three) of extracted fluid were dried at 100°C for 24h to determine their dry matter content.

Dung beetle bioassays

The reproductive rate of the dung beetle *Euoniticellus intermedius* was used to determine the suitability for the insects of wildebeest dung collected in Mkuzi, from April 1984 to June 1985. A laboratory colony of the beetle was maintained at 25°C at the Dung Beetle Research Unit (DBRU) in Pretoria. Newly emerged beetles were fed on wildebeest dung from the sample to be tested for 10 days before being used in an experiment. Each replicate in a bioassay comprised a pair (male and female) of 10-day-old beetles in a container (12 × 12 × 15 cm high) two-thirds full of compacted moist loamy soil. Beetles were fed with 125 g of dung twice a week, and held at 25°C, 70% r.h. The contents of containers were tipped out after 7 days and the number of brood balls in the soil counted. Each brood ball contained one egg. Beetles were re-set in fresh containers and the procedure repeated for a further 2 weeks. The number of replicates varied each month, depending on the amount of dung that had been collected. Insect performance was taken to be the rate of brood-ball production in the third week of each trial (when the rate was usually at a maximum), and the number of females still alive during this week is given with the results.

Dung moisture experiment

The African buffalo fly *Haematobia thirouxi potans* and the dung beetle *Euoniticellus intermedius* were used in an experiment to investigate the relationship between water content of dung and insect performance. Wildebeest dung was collected at Derdepoort in Pretoria in September 1985 before the spring rains, at a time when the dung was still very dry. The dung was divided into eight aliquots which were diluted with multiples of 100 ml of water (from 0 to 700 ml) per 1 kg of dung. The fluid availability, fluid quality and total dung moisture were measured for each of the eight samples used in bioassays. A colony of *Haematobia thirouxi potans* was maintained at DBRU on a live steer in the laboratory (Doube, Fay & Aschenborn, 1982). Three replicates of 50 buffalo fly eggs were used for each of the eight treatments. Freshly laid eggs were brushed onto 150 g of dung, in a 9-cm petri dish. The petri dish was placed on 2 cm of fine sand in a clear plastic container (12 × 12 × 15 cm high). Ventilation holes near the base of the container and in the lid were covered with fine 250-μm gauze to exclude mites. Containers were placed on a moist sponge in a large tub with a loose-fitting lid to maintain high humidity. Prepupae left the dung after about 6 days at 25°C and crawled into the sand to pupate. The sand was sieved and pupae were counted and weighed. *Euoniticellus intermedius* was bioassayed as described above, with 10 pairs of beetles used in each treatment. The rate of brood-ball production was recorded in the second week of the experiment, since there was insufficient dung for a third week.

Statistical treatment of data

Relationships between dung parameters and rate of dung beetle egg production, and between rainfall and dung parameters were analysed by linear regression techniques (GLIM; Nelder & Wedderburn, 1972). Measurements made as percentages were not transformed, because in the former set of analyses the percentages were the *x*-variates, which do not require transformation (R. Morton, personal communication). In the latter analyses, although the percentage measurement was the *y*-variate, inspection of the data showed that the analysis was not distorted by any large residuals, indicating that there was no evidence of gross non-normality.

Results

Characteristics of zebra, wildebeest and impala dung

Seasonal changes in the water, nitrogen and crude fibre content of zebra, wildebeest and impala dung from Mkuzi Game Reserve are presented in Table 1. Temperature and rainfall data for the 18-month period of dung collection are plotted in Fig. 1a.

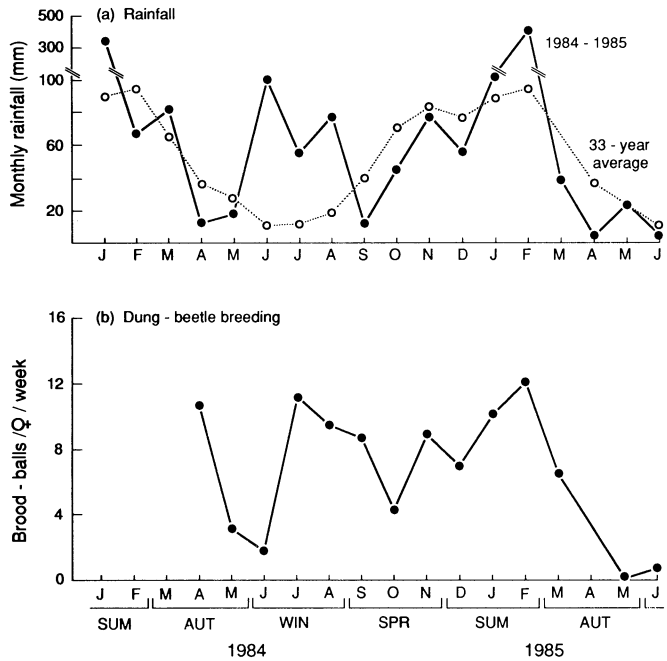

Fig. 1. (a) Monthly rainfall in Mkuzi Game Reserve for period January 1984 to June 1985. Dotted line represents mean rainfall 1951–1983; (b) Brood-ball production by *Euoniticellus intermedius* in wildebeest dung collected in Mkuzi Game Reserve between April 1984 and June 1985.

Winter is normally the driest part of the year in Mkuzi (dotted line on Fig. 1a), however the 1984 winter (June–August) was significantly wetter than average (232 mm cf. 33-year mean of 41 mm). Rainfall in both summers was also abnormally high due to cyclonic rains in January 1984 and February 1985.

Impala dung was considerably drier than that of the other two species, and contained more nitrogen on a dry weight basis (Table 1). Zebra dung was low in nitrogen and contained more fibre than the dung of impala or wildebeest. Considerable seasonal variation occurred in the water content of dung, ranging from 70·7 to 80·3% for zebra, from 71·1 to 78·1% for wildebeest, and from 50·9 to 71·5% for impala (Table 1). Impala dung was the most variable in moisture content, with extremely low values recorded during three dry periods in autumn 1984, spring 1984 and winter 1985. During autumn and spring of 1984 impala were observed browsing on woody shrubs. In May and June 1985 it was noted that the grass was very dry, so it is probable that browsing also occurred at these times.

The effect of previous rainfall on dung moisture was tested by considering the amount and pattern of rainfall recorded during the 8 weeks preceding dung collection. Rainfall totals in mm for the four 2-week periods prior to each dung collection date were transformed to $\log_e(x + 1)$. The effect of rain on dung moisture was calculated for the entire 8-week period, for each 2-week period considered separately, and for all possible 4- and 6-week periods within the 8 weeks (Table 2). For zebra dung, none of the 2-week periods of rainfall considered separately affected dung moisture. The 4-week total from 2 to 6 weeks before collection provided the most significant correlation with dung moisture and all rainfall regressors that included this 4-week period were also significantly correlated with dung moisture (Table 2).

For wildebeest dung, the most significant regressor on dung moisture was rainfall in the 2-week period prior to collection. All combinations that included this 2-week period were also positively correlated with dung moisture (Table 2).

For impala dung, rainfall in the 0–2- and 2–4-week periods both significantly affected dung moisture, and the greatest proportion of the variance was explained when both periods were combined (Table 2).

The above analyses were repeated to determine the effect of rainfall on the nitrogen content of dung (Table 2). For zebra, rainfall in the 2 weeks and 4 weeks prior to dung collection was signifi-

Table 1. Seasonal changes in the composition of zebra, wildebeest and impala dung collected in Mkuzi Game Reserve, January 1984 to June 1985. Mean water composition ± SD calculated from five subsamples unless stated otherwise (*n*). (Nitrogen and crude fibre expressed as percentage of dry dung.)

	Zebra			Wildebeest			Impala		
	Water (%)	Nitrogen (%)	Fibre (%)	Water (%)	Nitrogen (%)	Fibre (%)	Water (%)	Nitrogen (%)	Fibre (%)
20 January 1984	75·2 ± 0·2 (4)	1·32	32·0	75·9 ± 0·1 (4)	1·68	23·5	68·0 ± 0·6 (4)	2·13	20·7
12 February 1984	76·8 ± 0·3	1·32	30·6	76·0 ± 0·1	1·61	21·9	67·1 ± 0·6	2·43	21·9
26 February 1984	78·0 ± 0·2	1·48	30·4	74·1 ± 0·0 (4)	1·50	26·2	69·0 ± 0·1 (3)	2·43	29·5
9 March 1984	78·9 ± 0·2 (4)	1·07	38·6	76·6 ± 0·3 (4)	1·70	25·6	66·2 ± 0·4 (4)	2·17	28·9
24 March 1984	–	–	–	73·8 ± 0·7 (4)	1·36	25·3	65·9 ± 0·6	1·96	27·0
19 April 1984	75·3 ± 0·2	1·50	28·5	73·6 ± 0·3	1·50	23·4	68·2 ± 0·3	1·79	25·9
17 May 1984	73·4 ± 0·3	1·06	32·9	74·1 ± 0·2	1·23	24·8	56·1 ± 0·3	1·85	23·8
8 June 1984	75·2 ± 0·1	0·85	36·7	73·1 ± 0·2 (4)	1·27	25·3	69·2 ± 0·4 (3)	1·89	23·5
21 July 1984	78·2 ± 0·2	1·14	35·9	74·7 ± 0·1	1·39	23·1	67·1 ± 0·6	2·00	19·5
10 August 1984	74·5 ± 0·1	1·26	31·3	74·9 ± 0·1	1·39	24·1	68·6 ± 0·8	2·16	23·8
15 September 1984	78·2 ± 0·1	1·26	29·5	75·4 ± 0·2	1·31	24·4	71·5 ± 0·2 (3)	1·89	24·9
7 October 1984	77·0 ± 0·9	1·19	28·6	72·6 ± 0·4	1·43	24·2	61·1 ± 0·5	2·04	26·5
2 November 1984	70·7 ± 0·3	1·09	32·5	74·3 ± 0·2	1·55	21·4	62·2 ± 0·4	3·45*	24·1
25 November 1984	77·3 ± 0·5	1·34	27·1	76·4 ± 1·8	1·89	20·5	71·0 ± 1·0	2·59	21·5
21 December 1984	80·3 ± 0·3	1·55	29·3	74·3 ± 0·3	1·44	23·0	67·4 ± 1·5	1·62	28·8
18 January 1985	77·5 ± 0·2	1·23	31·6	76·8 ± 0·1 (3)	1·97	18·9	67·6 ± 0·2	1·88	21·9
23 February 1985	77·2 ± 0·5	1·52	31·9	78·1 ± 0·3	2·18	18·5	67·7 ± 0·5	2·67	24·2
15 March 1985	79·1 ± 0·6	1·26	31·9	74·9 ± 0·2	1·79	23·8	65·3 ± 0·2	2·25	24·8
3 May 1985	75·8 ± 0·2	1·41	33·7	71·1 ± 1·1	1·60	23·0	50·9 ± 1·6 (2)	2·31	25·1
13 June 1985	–	–	–	72·4 ± 0·3 (4)	1·91	24·0	56·1 ± 0·8	1·48	26·5
Mean ± SD	76·6 ± 2·3	1·27 ± 0·19	32·3 ± 3·5	74·7 ± 1·7	1·59 ± 0·26	23·2 ± 2·1	65·3 ± 5·4	2·13 ± 0·29	24·6 ± 2·8

* High nitrogen level probably caused by contamination from urine. Sample excluded from all calculations.

Table 2. Effect of rainfall on moisture and nitrogen levels in zebra, wildebeest and impala dung collected monthly in Mkuzi Game Reserve, January 1984 to June 1985 ($x = \log_e$[rainfall in mm + 1]); y[dung moisture] = % water in fresh dung; y[dung nitrogen] = % nitrogen in dry dung).

Rainfall period (weeks before dung collection) (x)	Effect of rainfall on dung moisture (y)			Effect of rainfall on dung nitrogen (y)		
	Zebra dung ($n = 18$)	Wildebeest dung ($n = 20$)	Impala dung ($n = 20$)	Zebra dung ($n = 18$)	Wildebeest dung ($n = 20$)	Impala dung ($n = 19$)
0–2	NS	$y = 73{\cdot}01 + 0{\cdot}66x$ ($r^2 = 0{\cdot}48^{***}$)	$y = 60{\cdot}90 + 1{\cdot}74x$ ($r^2 = 0{\cdot}33^{**}$)	$y = 1{\cdot}139 \pm 0{\cdot}050x$ ($r^2 = 0{\cdot}23^{*}$)	NS	NS
2–4	NS	NS	$y = 57{\cdot}47 + 2{\cdot}72x$ ($r^2 = 0{\cdot}46^{***}$)	NS	NS	NS
4–6	NS	NS	NS	NS	$y = 1{\cdot}331 + 0{\cdot}081x$ ($r^2 = 0{\cdot}24^{*}$)	NS
6–8	NS	NS	NS	NS	NS	NS
0–4	NS	$y = 71{\cdot}90 + 0{\cdot}74x$ ($r^2 = 0{\cdot}41^{***}$)	$y = 54{\cdot}78 + 2{\cdot}34x$ ($r^2 = 0{\cdot}56^{***}$)	$y = 1{\cdot}014 + 0{\cdot}066x$ ($r^2 = 0{\cdot}22^{*}$)	NS	NS
0–6	$y = 70{\cdot}68 + 1{\cdot}27x$ ($r^2 = 0{\cdot}36^{**}$)	$y = 69{\cdot}97 + 1{\cdot}03x$ ($r^2 = 0{\cdot}43^{***}$)	$y = 52{\cdot}73 \pm 2{\cdot}75x$ ($r^2 = 0{\cdot}29^{*}$)	NS	NS	NS
0–8	$y = 69{\cdot}71 + 1{\cdot}39x$ ($r^2 = 0{\cdot}28^{*}$)	$y = 69{\cdot}10 + 1{\cdot}13x$ ($r^2 = 0{\cdot}39^{**}$)	NS	NS	NS	NS
2–6	$y = 70{\cdot}44 + 1{\cdot}46x$ ($r^2 = 0{\cdot}43^{***}$)	NS	NS	NS	NS	NS
2–8	$y = 69{\cdot}51 + 1{\cdot}54x$ ($r^2 = 0{\cdot}31^{*}$)	NS	NS	NS	NS	NS
4–8	NS	NS	NS	NS	NS	NS

Significance levels: * $P < 0{\cdot}05$, ** $P < 0{\cdot}01$, *** $P < 0{\cdot}005$.

Table 3. Characteristics of dung fluid extracted from wildebeest dung collected in Mkuzi Game Reserve, and weekly rate of brood-ball production by female *Euoniticellus intermedius* dung beetles.

Collection date	Availability of dung fluid (%)* (n = 2)	Dry matter in dung fluid (%)† (n)	Number of brood balls $\bar{x} \pm$ SD (n)‡
April 1984	13·3 ± 0·28	5·22 ± 0·02 (3)	10·7 ± 5·1 (21)
May 1984	21·8 (n = 1)	4·10 ± 0·08 (3)	3·1 ± 1·8 (10)
June 1984	16·3 ± 2·12	3·72 ± 0·02 (2)	1·8 ± 1·6 (8)
July 1984	15·4 ± 0·28	4·52 ± 0·02 (4)	11·2 ± 3·8 (16)
August 1984	15·8 ± 0·35	4·27 ± 0·06 (3)	9·5 ± 3·6 (16)
September 1984	15·3 ± 0·85	4·62 ± 0·41 (3)	8·7 ± 3·9 (17)
October 1984	12·4 ± 0·57	4·34 ± 0·02 (3)	4·2 ± 3·2 (11)
November 1984	13·4 ± 0·35	5·45 ± 0·12 (3)	9·0 ± 3·1 (11)
December 1984	15·7 ± 0·78	5·77 ± 0·05 (4)	7·0 ± 3·5 (8)
January 1985	19·7 ± 0·35	5·16 ± 0·03 (3)	10·2 ± 1·5 (5)
February 1985	17·4 ± 0·92	5·52 ± 0·06 (3)	12·1 ± 3·2 (10)
March 1985	16·5 ± 0·57	4·48 ± 0·05 (3)	6·5 ± 3·3 (8)
May 1985	12·9 ± 0·57	5·39 ± 0·19 (3)	0·1 ± 0·4 (15)
June 1985	11·4 ± 0·85	5·43 ± 0·22 (2)	0·7 ± 0·8 (15)

* Proportion of total dung weight removed by pressing with hydraulic press for 2 min at 2 MPa.
† Proportion of dry matter in dung fluid extracted in 2 min at 2 MPa.
‡ Mean calculated from brood production during third week of experiment; n = number of females alive at end of third week.

cantly correlated with dung nitrogen. For wildebeest, the only significant positive relationship was with rainfall in the 4–6 weeks prior to collection. For impala there were no significant regressions.

Bioassay of dung beetles on wildebeest dung

The mean number of brood balls (= eggs) produced by female *Euoniticellus intermedius* in the third week of each rearing trial provided an index of the effect of seasonal changes in wildebeest dung characteristics on insect performance (Table 3). Brood-ball production (y_B = brood balls per female per week) showed a significant linear response to the water content (x_W = % water in fresh dung) and crude fibre content (x_F = % fibre in dry dung), but no response to the nitrogen content of dung. Water content and crude fibre levels of wildebeest dung were strongly correlated, and the inclusion of both in a single expression did not significantly increase the explained variance. The two relationships are therefore presented separately:

$$y_B = -123{\cdot}30 + 1{\cdot}82x_W \qquad (r^2 = 0{\cdot}63, P < 0{\cdot}005)$$
$$y_B = 32{\cdot}20 - 1{\cdot}11x_F \qquad (r^2 = 0{\cdot}31, P < 0{\cdot}05)$$

Since water content of wildebeest dung was significantly correlated with rainfall in the 2-week period prior to collection (see above), the regression between rainfall in the 2-week period before dung collection ($x = \log_e$[rain in mm + 1]) and dung beetle brood-ball production (y_B = brood balls per female per week) was calculated:

$$y_B = 3{\cdot}06 + 1{\cdot}80x \qquad (r^2 = 0{\cdot}63, P < 0{\cdot}005)$$

The observed levels of brood-ball production are plotted in Fig. 1b. On five occasions the rate fell below five per week, which was markedly fewer than the mean of 9·7 for all other occasions. While this decrease can be accounted for by changes in the total water content of the dung, the cause of the decline becomes more apparent from a physical analysis of the dung.

The amount of dung fluid expressed by a hydraulic press provided an index of fluid 'availability', and the amount of dry matter in the fluid provided an index of fluid 'quality' (details in Aschenborn *et al.*, 1990). Results of these analyses are given in Table 3. On three of the five occasions of low brood-ball production, fluid availability was at its lowest levels, less than 13% of fresh dung weight. On the other two occasions, fluid quality was at its lowest levels, with less than 4·2% dry matter. On the former three occasions it appears that the quality of the dung fluid was adequate but the fluid was largely unavailable to the beetles, whereas on the latter two occasions the fluid was available but was of low quality.

A curvilinear regression line was fitted to define the effect of percentage dry matter in dung fluid (x) (i.e. fluid quality) on the number of brood balls produced per female *Euoniticellus intermedius* per week (y) (Fig. 2). The three samples in which

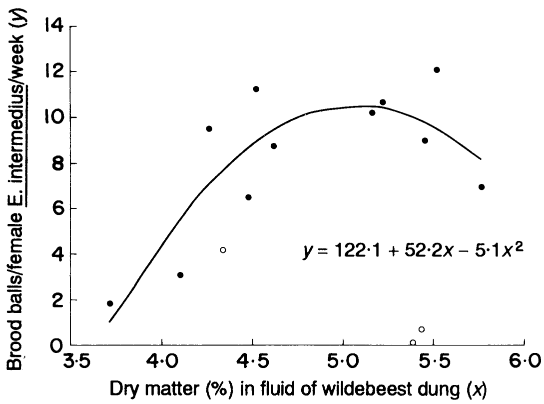

Fig. 2. Effect of the amount of dry matter in fluid of wildebeest dung on rate of brood-ball production by the dung beetle *Euoniticellus intermedius.* Dung fluid was extracted by an hydraulic press set at 2 MPa for 2 min. Open circles were not included in equation, since in these samples fluid availability was less than 13%, which confounded results.

fluid levels were less than 13% of the whole dung weight were omitted from the regression, since in these samples fluid quality was comfounded by the effect of fluid availability. The fitted regression accounted for 71·0% of the observed variability in brood-ball production ($F_{2,8} = 9{\cdot}81$, $P < 0{\cdot}01$).

Effect of dung moisture on dung beetle and buffalo fly reproduction

The above analyses indicate the importance of the water content of dung in determining the breeding rate of the dung beetle *Euoniticellus intermedius.* The results also suggest that on some occasions nutrients in the dung may become unavailable to the beetles due to reduced amounts of fluid in the dung. This was tested experimentally by increasing the fluid content of wildebeest dung collected in the dry season, and performing bioassays with *Euoniticellus intermedius* and the African buffalo fly *Haematobia thirouxi potans.*

No brood balls were produced by *Euoniticellus intermedius* in the natural dung, which had a moisture content of 61·9%. The number of brood balls produced increased almost linearly in dung of water content of 68% and above (Fig. 3a). This was due to an increased proportion of females breeding and an increased rate of brood-ball production per breeding female (Fig. 3b). The increase in water content of dung was associated with an increase in fluid availability (Table 4). Fluid quality decreased slightly due to dilution as the water content increased.

No buffalo fly larvae survived to pupation in natural dung or dung below 73% water content (Fig. 4). At 73% and above, there was a linear increase in survival rate until a maximum was attained at 76% water content. Pupal weights followed the same trend as larval survival, with heaviest pupae reared in dung of 76–78% water content (Fig. 4). At these moisture levels fluid availability was 17–22% (Table 4).

Discussion

Differences in the characteristics of dung of zebra, wildebeest and impala reflected differences in the feeding ecology of the three herbivores. Zebra dung was coarse textured and contained more fibre and less nitrogen than dung of the other species; a reflection of zebras' preference for older grass and the less thorough digestive processes of non-ruminants. Certain species of dung beetles feed almost exclusively on the dung of non-ruminants. For

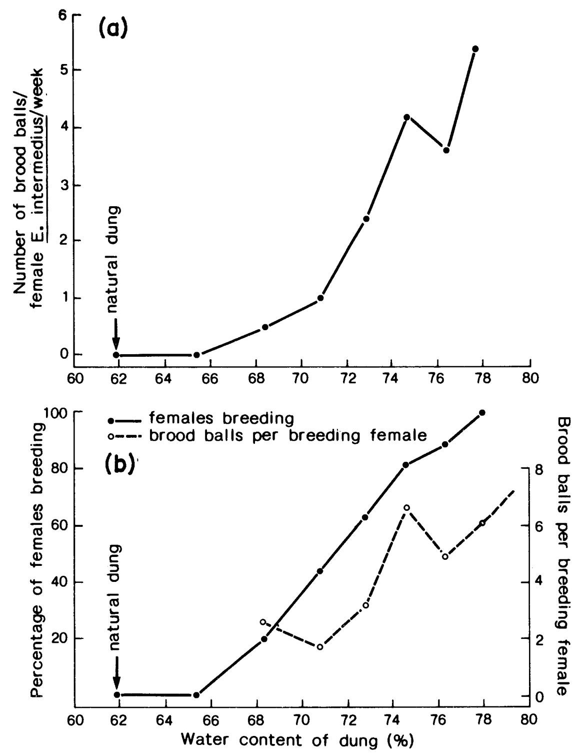

Fig. 3. (a) Effect of the water content of wildebeest dung on brood-ball production by the dung beetle *Euoniticellus intermedius.* Natural dung of 62% moisture was diluted with different amounts of water to obtain dungs between 65 and 78% moisture. (b) Results of (a) separated into proportion of females breeding, and brood-ball production by breeding females, i.e. excluding those females that did not breed.

Table 4. Characteristics of fresh and diluted wildebeest dung collected in Pretoria in September 1985.

	Total water content (%)	Availability of dung fluid (%)*	Dry matter in dung fluid (%)[†]
Natural dung	61·9	5·2	NM
Dilution 1 (100 ml water per 1 kg dung)	65·4	4·7	9·5
Dilution 2 (200 ml water per 1 kg dung)	68·3	4·7	10·1
Dilution 3 (300 ml water per 1 kg dung)	70·7	7·9	9·0
Dilution 4 (400 ml water per 1 kg dung)	72·9	9·9	9·1
Dilution 5 (500 ml water per 1 kg dung)	74·6	11·6	8·8
Dilution 6 (600 ml water per 1 kg dung)	76·2	17·3	8·3
Dilution 7 (700 ml water per 1 kg dung)	77·6	21·5	7·8

* Proportion of total dung weight removed by pressing with hydraulic press for 2 min at 2 MPa.
[†] Proportion of dry matter in dung fluid extracted in 2 min at 2 MPa.
NM, not measured because dung too dry to extract sufficient fluid.

instance *Heliocopris dilloni* is found only in elephant dung (Kingston & Coe, 1977), *Kheper platynotus* uses elephant and zebra dung (Sato & Imamori, 1987) and *K. subaeneus* and *K. lamarcki* are normally found in rhinocerus or zebra dung (P. B. Edwards, unpublished observations). These dung beetles are all large, and their association with coarse-fibred non-ruminant dung may indicate either that larger beetles can cope better than small beetles with the low nutrient content of non-ruminant dung, that they are better able to manipulate the large coarse fibres found in such dung, and/or that they need the large dung pads of non-ruminants to provision their multibrood-ball nests. However, some smaller species also prefer coarse dung. For instance *Oniticellus egregius* has been recorded mainly from elephant, rhinocerus and zebra dung (Davis, 1989).

The dung of the two ruminants, wildebeest and impala, was much smoother and more finely textured than that of zebra. Wildebeest dung was moist, and, at least during the wet season, was dropped in the form of pads. In Mkuzi Game Reserve it is used by a large variety of dung beetles (P. B. Edwards, unpublished observations). Impala dung, on the other hand, although having a much higher nitrogen content, was considerably drier than wildebeest dung. This latter feature is accentuated under field conditions where the small pellets of impala dung dry out much faster than the solid pads of wildebeest. The dung beetle *Euoniticellus intermedius* could not breed in wildebeest dung when the water content was lower than about 68%, even though it was shown in the dilution experiment that this dung contained sufficient nutrients to support adult reproduction. This would indicate that *Euoniticellus intermedius*, and probably many other species, may not be able to use impala dung, which often had less than 68% water content. However at least one species is particularly efficient at utilizing impala dung in Mkuzi. *K. nigroaeneus* is a large beetle that rapidly mashes fresh impala pellets into a ball which it then buries (Edwards & Aschenborn, 1988). Unlike the other large species mentioned above, it constructs just a single brood ball in each nest (Edwards & Aschenborn, 1989), and there is sufficient dung in one impala dropping to provision a nest. Additionally, the female coats the brood ball

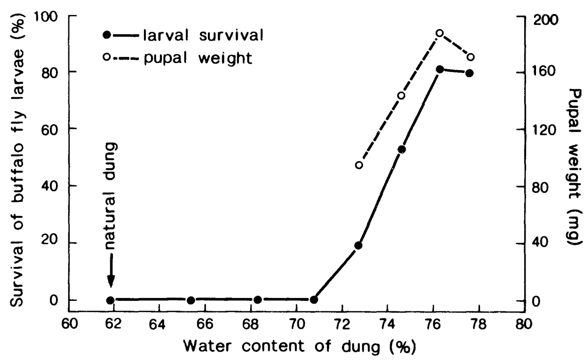

Fig. 4. Effect of the water content of wildebeest dung on larval survival and pupal weight of the African buffalo fly *Haematobia thirouxi potans* (see Fig. 3).

with a mixture of faeces and soil (Edwards & Aschenborn, 1989), thus further reducing the rate of desiccation.

The moisture content of dung is probably its most important attribute for coprophagous insects. Indeed the need to conserve dung moisture is thought to be one of the main selective pressures that led to the evolution of dung beetle nesting behaviour (Halffter & Matthews, 1966), since buried dung loses moisture much more slowly than unburied dung. Dung of low moisture content is unsuitable for dung beetles since the adults cannot extract the dung fluid from the whole dung. This results from the fact that the mouthparts of adult dung beetles are adapted to squeeze the fluid from dung (Hata & Edmonds, 1983). They cannot cut or chew whole dung (Halffter & Matthews, 1966). In wildebeest dung, brood-ball production by *Euoniticellus intermedius* decreased linearly as fluid availability (*sensu* Aschenborn *et al.*, 1990) declined from 22 to 5%, and below 5% the dung was unusable. For the African buffalo fly, wildebeest dung was unusable when fluid availability was less than 10%. Some dung beetle species are able to overcome the problems of dry dung. For instance *Pachysoma striatus* makes use of dry rodent pellets by burying them below the soil moisture line where they absorb water (Scholtz, 1989), and *Onthophagus emarginatus* uses sheep dung that has been dry for months, but only after it has been rewetted by rain (Lumaret & Kirk, 1987).

Seasonal changes occurred in the dung of wildebeest, impala and zebra. For all species the dung moisture content was positively correlated with recent rainfall and hence presumably with the water content and digestibility of grass. Low rainfall may also have restricted the availability of drinking water, which can cause impala, hartebeest and probably other herbivores, to desiccate their dung (Maloiy & Hopcraft, 1971). Rainfall during the 2 weeks before the date of dung collection had the greatest influence on the moisture content of wildebeest dung, and rainfall during the 4 weeks before collection for impala dung. Impala have small mobile mouths (Skinner, Monro & Zimmerman, 1984), so may be able to select new growth from amongst the maturing grass for a longer period than can wildebeest. For zebra, rainfall 2–6 weeks before dung collection had most effect on dung moisture. Zebra eat older grass, which may account for the 2–6-week lag between the time of rainfall and the increase in dung moisture. Stanley Price (1977) found a positive correlation between the water content in the diet of hartebeest and effective rainfall over the previous 3 months. The nitrogen content of wildebeest and zebra dung showed some correlation with recent rainfall, but the nitrogen content of impala dung did not. This non-correlation was probably a consequence of impala including browse with a high nitrogen content in their diet during dry periods.

Winter in Mkuzi Game Reserve is normally a very dry period when the grasses decline and hay off. It was interesting that during the wet winter of 1984 fresh grass growth occurred in response to the rainfall, a response that was reflected in the increased water content and 'quality' of the herbivore dung. Winter temperatures in the lowveld are quite mild, the mean in Mkuzi for June, July and August 1984 was 18·6 °C. Grasses would be unlikely to grow after winter rain in highveld regions, where frosts are quite common. The winter fall-off with development in the quality of 'sourveld' grasses of the highveld is much greater than in the 'sweetveld' grasses of the lowveld (Barnes, 1969).

Seasonal changes in the characteristics of wildebeest dung had a marked effect on the reproductive rate of the dung beetle *Euoniticellus intermedius*. The positive relationship between rainfall and rate of brood-ball production can be clearly seen in Fig. 1. Although the rainfall figures in Fig. 1 are based on monthly totals (and therefore are not as sensitive as the 2-week totals used in the regression analyses), there is still evidence in Fig. 1 of the lag between rainfall and dung beetle reproductive rate. The weekly rate of brood-ball production at a constant temperature of 25 °C ranged from 0·1 per female in May to 12·1 in February, and was strongly correlated with the moisture content of the dung, and hence recent rainfall and pasture condition. Strikingly similar results were obtained by Macqueen *et al.* (1986) for *Euoniticellus intermedius* reared in cattle dung collected in central Queensland. Brood-ball production ranged from 0·9 per female in July to 11·7 in December, and was also significantly correlated with dung moisture.

The suitability of wildebeest dung for *Euoniticellus intermedius* could also be predicted from the amount of dry matter in the dung fluid extracted at 2 MPa. Similarly, Aschenborn *et al.* (1990) found a significant positive correlation between the amount of dry matter in the fluid extracted from cattle dung at 2 MPa and brood-ball production by *Euoniticellus intermedius*. It is the fluid component of dung that adult dung beetles ingest, and the 'dry matter' content of dung fluid consists predominantly of organic matter (P. B. Edwards & M. L. Loughnan, unpublished observations). Thus the dry matter content of dung fluid probably provides a more biologically 'accurate' measure of dung suitability for *Euoniticellus intermedius* than does dung moisture, even though both indices yield significant correlations.

That dung quality can produce a 100-fold change in the reproductive rate of dung beetles indicates that it is potentially a major variable in the population dynamics of species. However, in summer rainfall regions such as Mkuzi, most dung beetle activity is restricted to the warm wet summer months (P. B. Edwards, unpublished observations). Beetles usually emerge in response to rainfall (e.g. *K. nigroaeneus* [Edwards, 1988]), and their activity can continue for as long as the ground remains soft enough for dung burial. This study has shown that it is in the weeks following rainfall that dung quality is at its highest. Thus the periods following rain provide not only the best physical conditions for dung beetle activity, but also the highest quality dung, allowing the maximum rate of egg production as well as ensuring that offspring are provisioned with a high-quality resource.

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