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SHORT NOTE

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Daily patterns of behaviour compared between two sand-grouse species (Aves: Pteroclididae) in captivity

by

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ABSTRACT

Captive Pterocles namacoa and P. leucopus showed behavioural adaptations for thermoregulation and water conservation. Reduction of environmental and metabolic heat loads by day, and conservation of metabolic heat at night, were achieved by altering activity levels and by exploiting or creating appropriate microclimatic conditions. Experimental dehydration and field observations indicate that P. namacoa drinks only every 3–5 days normally, and that both species can easily withstand such water deprivation by augmenting water conservation measures. Birds were gregarious, but social interactions were pacific, undemonstrative and egalitarian.

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1 INTRODUCTION

Sand-grouse of various species are characteristic occupants of the arid and semi-arid zones of Africa, the Middle East and central-southern Asia. They have diversified into several groups of sympatric species and may become extremely abundant in environments of generally low biological productivity and of thermal extremes. Therefore, they must be judged as successful inhabitants of these difficult habitats, and knowledge of their biology is important if one is to understand the spectrum of adaptations amongst animals living in such extreme environments.

Interest in sand-grouse biology has quickened in the last two decades, with substantial publications by Christensen, Bohl & Bump (1964), Maclean and his associates (see Maclean, 1968, 1976), George (1969, 1970), Thomas & Robin (1977), Dixon & Louw (1978), and several other articles. Naturally, much of the work reported centres on observations at water-holes and at nests, where the birds are most easily seen, and there is much less information on their behaviour elsewhere and under other circumstances. In our experience, reliable prolonged field observations of non-breeding birds are extremely difficult to obtain because of the bird's crysis, elusiveness and wary disposition. Therefore, we kept a group of wild-caught adult birds in a large aviary where they could be studied with minimum disturbance at any chosen time. The results of these observations are
reported here, and are used to interpret behaviour of birds seen in the field.

2 MATERIALS AND METHODS

The study was performed in Namibia in January—February 1980, based mainly at the Namib Desert Research Station, Gobabeb (23°34'S, 15°03'E) with supplementary field observations in the Namib Desert around Ganab (23°06'S, 15°33'E) and Zebra Pan (23°31'S, 15°28'E) and in the Etosha National Park in the vicinity of Okaukeujo (19°10'S, 15°55'E). In both the Namib and Etosha areasNamaqua sand-grouse (Pterocles namaqua (Gmelin)) and double-banded sand-grouse (P. bicinctus Temminck) were the common sand-grouse species. Specimens of both species were caught under licence by mist-netting beside artificial waterholes in the Namib Desert. Three male and four female P. namaqua were caught during morning drinking flights at Zebra Pan and transferred to the aviary at Gobabeb the same morning. Four P. bicinctus (two of each sex) were caught during their evening drinking flights at Ganab and transferred to the aviary the following morning. On arrival at Gobabeb, all birds were weighed and marked individually with different colours of nail varnish on bill and feet before release into the aviary; these marks allowed individual recognition in daylight without recapture.

Aviary dimensions were 6.3 x 3.2 x 8 m (L x W x H); it was made of chicken wire on a pipework frame, built on the natural substrate of sandy gravel. The availability of shade depended on the time of the day: complete shade from adjacent buildings lasted until 09h45 (local solar time, LST: see below); wooden slats over one quarter of the roof provided 35% shade until 14h30 LST; after 14h30 LST partial shade was still available from the cage framework and from the chicken wire where it was at an oblique angle to the sunlight. In the absence of early morning fog, some direct sunlight was available at all times from somewhat before 07h00 LST.

Air temperatures 5 cm above the ground at three chosen points in the aviary were measured with thermistors, shaded from direct sunlight using expanded polystyrene cups lying on their sides to allow circulation of air. Thermistors were connected via long leads to a YSI thermometer in a building immediately beside the aviary, whence all observations of bird behaviour were made. By noting whether thermistors were in complete, partial or no shade, estimates of air temperature differences between these conditions could be made. In addition, a selection of weather data for the relevant period was abstracted from the records of a first order weather station and a recording solarmeter, both sited within 100 m of the aviary. All weather and behaviour records were made at local civil time (S. African Standard Time = GMT + 2h) but converted to local solar time (LST = GMT + 1h) for publication, since solar time is biologically the more relevant measure; thus sunrise and sunset are symmetrically disposed about 12h00 LST, the time of the solar zenith when maximum potential solar irradiance will occur.

Birds were fed a commercial cage bird (budgerigar) seed mixture ad libitum, which they foraged from the ground. Tap water was available ad libitum from plastic bowls sunk in the ground, except for a 3-day experimental dehydration period. Observations were made on birds with free access to water during 31 January to 7 February. At 16h00 – 17h00 LST on 7 February birds were caught and held overnight in darkened boxes without water, weighed the following morning in a post-absorptive state and returned to the aviary (whence water had been removed) between 09h30 and 11h30 LST. Birds then had no water from 8–10 February inclusive; on 11 February they were recaptured at 05h30 – 05h50 (i.e. before they had started to feed) and held in darkened boxes. One at a time, the birds were then weighed, returned to the aviary, watched until they drank at the restored water supply (when the number of sips was counted) and then recaptured and reweighed. Weight losses and gains were calculated for dehydration and rehydration phases. This protocol exposed birds to dehydration for not less than 96–99h (depending on the individuals), of which 2.5 days were spent exposed to full sunlight.

From an immediately adjacent building, windows (covered except for observation slits, to minimise disturbance) gave an uninterrupted view of birds in the aviary. In addition to descriptive notes made as behaviour occurred, the following numerical data were recorded at intervals (15 – 30 – 60 min) through the day time; thermistor temperatures; the number of birds (separately by species) involved in each of the following activities: sitting, standing, walking, preening, being in shady as opposed to sunny positions, feeding, drinking, huddling (i.e. being stationary and in contact with at least one neighbouring bird), having dorsal (mantle) feathers erect, guil fluttering, and holding wings drooped and away from the sides (wing drooping) (cf. Dixon & Louw's (1978) Fig. 4).

In order to make these data comparable between species, the number of birds of each species carrying out an activity on a given occasion was expressed as a proportion of the birds so involved, by dividing the number by the total number of individuals of the same species. Mean proportions were calculated for each hour of the day (i.e. from 00 to 59 minutes past each hour), using observations on all relevant days to build up a generalised picture of daily activity patterns, but keeping data separate between species and between periods when water was and was not available to enable estimation of interspecific differences and of the effects of dehydration within species.

The statistical validity of dehydration effects and of interspecific differences was tested by means of paired t-tests, using serial contemporaneous pairs of mean proportions. Where no significant difference was found
between two series of means, the data were combined and a joint mean for each hour was calculated and plotted. All means are given ± their standard errors, with the number of observations in parenthesis. The number of degrees of freedom (d.f.) are shown as t(d.f.) for t-tests.

3 RESULTS

3.1 Weather and the aviary microclimate

Relevant weather station data are shown in Table 1; the weather during periods of observation of hydrated and dehydrated birds was essentially similar, except that the former period experienced higher air temperatures and lower solar irradiance than the latter. This difference in air temperatures between periods was also found in the aviary: Figure 1 shows air temperatures under conditions (sun or shade) chosen by most birds at any given time through the day. In the aviary, average air temperature differences measured between thermistors in sun and full or partial shade were 5.2 ± 0.4°C (9) and 3.8 ± 0.2°C (47) respectively. Inspection of traces from the solarimeter and screen thermograph showed that insolation peaked almost symmetrically at 12h00 LST (consistent with generally cloudless conditions, at least after mid-morning, on most days) while air temperatures reached maxima between 14 and 15h LST, as is commonly observed and is shown in Figure 1.

At capture, the mean body weight of *P. namaqua* (168.0 ± 3.5 g (7)) was significantly lighter (t(10) = 2.86; P < 0.02) than that of *P. bicinctus* (189.1 ± 6.5 g (4)). During the observation period following capture (when the birds were hydrated), many lost but some gained weight,

![Figure 1: Air temperature 5 cm above the ground in the aviary, in conditions of sun, full or partial shade occupied by most birds at the time. Points show mean air temperatures in each hour at the mean local solar time of observations. Filled and open symbols represent means during periods when birds were hydrated (n=2–5) and dehydrated (n=1–7) respectively, and bars represent standard errors of the means. For all times and some temperatures, the plotting symbol is larger than the SPM bar would be.](image)

**TABLE 1:** Selected data from the Gobabeb weather station (mean ± SEM (range)) for the periods 31 January – 7 February and 8–10 February 1980, corresponding to periods of observations of behaviour of hydrated and dehydrated sand-grouse respectively. Comparisons between periods by t-test.

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>31 JAN. – 7 FEB. (HYDRATED BIRDS)</th>
<th>8–10 FEB. (DEHYDRATED BIRDS)</th>
<th>P &lt; (df = 9)</th>
</tr>
</thead>
<tbody>
<tr>
<td>TEMPERATURE, °C:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Screen, minimum</td>
<td>16.7±0.9 (14.3 – 20.8)</td>
<td>11.8±0.7 (10.7 – 13.1)</td>
<td>0.002</td>
</tr>
<tr>
<td>Screen, maximum</td>
<td>32.0±1.1 (27.4 – 36.1)</td>
<td>28.5±0.7 (27.4 – 29.9)</td>
<td>0.05</td>
</tr>
<tr>
<td>Screen, 13h00 LST</td>
<td>30.5±1.3 (24.5 – 34.6)</td>
<td>26.6±0.6 (25.3 – 27.2)</td>
<td>0.02</td>
</tr>
<tr>
<td>Soil surface, 07h00 LST</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil surface, 13h00 LST</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RELATIVE HUMIDITY, %:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Screen, 07h00 LST</td>
<td>80±5 (43–95)*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>13h00 LST</td>
<td>35±2 (27–46)*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>19h00 LST</td>
<td>37±3 (25–61)*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>WIND RUN, km/day:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>153±5 (126–177)*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SOLAR IRRADIANCE:**</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total, m²/day, mean range</td>
<td>(2.36±0.04) × 10⁷</td>
<td>(2.51±0.03) × 10⁷</td>
<td>0.02</td>
</tr>
<tr>
<td>Maximum, W/m²</td>
<td>(2.19–2.47) × 10⁷</td>
<td>(2.45–2.56) × 10⁷</td>
<td>0.02</td>
</tr>
<tr>
<td>Time of maximum</td>
<td>906±8 (872–956)*</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*A combined mean (n=11) etc. is shown in the absence of a significant difference between periods.

**Short-wave = visible + near infra-red.
and the mean weight changes ($P. namaqua$: $-0.62 \pm 0.29$ (7); $P. biceinctus$: $-0.41 \pm 0.36$ g/100 g body weight/day (4)) were not significantly different from zero. This is consistent with observations that birds learnt quickly to feed and drink in the aviary, and that they appeared to be able to find and would eat all types of seeds in the mixture provided. Weight losses on dehydration were not significantly different between species ($P. namaqua$: $3.4 \pm 0.4$ (7); $P. biceinctus$: $4.4 \pm 0.2$ (4) g/100 g BW/day (4)).

3.3 Stance and ambulatory activity

The daily patterns of sitting, standing and walking (mutually exclusive activities) are shown in Figures 2, 3 and 4 respectively. All birds sat in tight huddles overnight (see section 3.4.2); thus birds were usually found at or before sunrise sitting in the same place as they had been seen last, 1–2 h after the previous sunset. By day, activity patterns were polymodal: in general, proportions of birds sitting peaked early and late in the day and about the solar zenith, while proportions of birds standing and walking peaked mid-morning and mid-afternoon. However, midday peaks or troughs were not marked in hydrated $P. namaqua$.

Interspecific differences and effects of dehydration were apparent only during the main part of the day. In general, $P. biceinctus$ were less active than $P. namaqua$ (i.e. greater proportions sitting and lesser standing). Although proportions of the two species walking were similar at any time, $P. biceinctus$ walked slowly and circumspectly, while $P. namaqua$ walked more quickly and with a "busy" manner. Dehydration increased general inactivity in both species: lesser proportions stood or walked and greater proportions sat than when hydrated. In addition, dehydrated birds seemed to spend more time asleep during the day, but quantitative data are lacking.

3.4 Thermoregulatory behaviour

This section deals with certain aspects of behaviour (illustrated in Figure 5) which can be related primarily to
the control of heat exchange between the birds and their environment. Using the proportions of birds involved as an indicator of relative importance, choice of shade (Figure 6), huddling with other birds (Figure 7), and erection of dorsal feathers (Figure 8) are apparently the principal mechanisms used by non-incubating birds, while wing drooping and forced evaporation by gular fluttering (Figure 9) seem less important in maintaining heat balance. The birds' state of hydration had significant effects on all these behavioural mechanisms, but differential response between species could be detected only for feather erection.

Evidence to be presented elsewhere (Thomas & Maclean, in preparation) suggests that *P. namaqua* and *P. bicinctus* maintained rather constant daytime deep body (colon) temperatures in the range 40–42°C even at ambient air temperatures of 45–50°C. Night-time deep body temperatures were somewhat lower.

### 3.4.1 Choice of shade vs. sun

Captive birds chose to sit in the sun (if available) early in the morning, but would almost all be in shade from solar zenith and through the afternoon period of maximum air temperatures (Figure 6). Dehydration accentuated these effects. Birds backing in the morning tended to stand broadside on to sunlight, while birds in partial shade during the heat of the day tended to face towards (or occasionally directly away from) the sun (Figure 5). Evidence for active selection involved derives from frequent observations that birds would congregate in a disproportionately small area of sun or shade (depending on circumstances), and would move with this patch of sunlight or shadow.

We obtained corresponding field observations of *P. namaqua* foraging in sunlight in the morning, and sitting in shade during the early afternoon period of maximum air temperatures.

#### 3.4.2 Huddling behaviour

Huddling in groups of up to seven birds was the normal situation overnight, and occurred during the heat of the day, especially amongst dehydrated birds (Figure 7). Such behaviour would be extremely difficult to see in the wild, because the immediate response to disturbance was for individuals to leave the huddle and crouch again having separated by a few metres from one another. There were differences between day and night-time huddles. At night birds sat invariably with bellies on the ground and tightly packed against one another. Nocturnal huddles were often beside a small bush or large stone, and were started by a single bird forming a scrape, rocking from side to side on its belly, rotating and wriggling, and kicking material out behind. Second and subsequent birds snuggled up to the others or interpolated themselves between birds already huddled side by side, during a period of fidgeting and rearrangement lasting 10–15 min, when middle positions appeared to be preferred over end ones. Namaqua sand-grouse had a strong preference for having adjacent birds facing alternate ways at night: the ratio of numbers of adjacent pairs of birds sitting in parallel to the numbers sitting in antiparallel arrangement was 11:30. The probability (P) of such an arrangement occurring by chance is 0.0014 (Binomial equation). In contrast, *P. bicinctus* showed no apparent preference, with a ratio of parallel: antiparallel arrangement of 10:11 and P=0.168.
Daytime huddles differed in having birds both standing and sitting, in the absence of scrape formation, and in being less tightly packed together, although middle positions still seemed at a premium. There was still no preference for parallel or antiparallel arrangement by *P. bicinctus*, but in *P. namaqua* the night-time preference was reversed and now they showed a strong preference for parallel orientation (parallel : antiparallel = 44:26; $P=0.0095$), which may have arisen from the birds' strong tendency to face the sun.

3.4.3 Feather erection

Feather erection was comparatively unimportant during the heat of the day, but was more so in the mornings and evenings, when feather posture was differentially affected both by dehydration and between species (Figure 8).

3.4.4 Gular fluttering and drooping wings

Gular fluttering was not used much by captive sandgrouse when hydrated and not at all when dehydrated (Figure 9). In comparison, an incubating female *namaqua* watched one day near Ganub spent 28±6% (5) of her time gular fluttering between 11h30 and 14h30 (LST), at ambient temperatures of 40.9 ± 0.2°C (5 cm above the ground).

Wing drooping was not common amongst hydrated birds, and was not recorded systematically until it became obvious after birds were dehydrated. In such birds, it was clearly associated with times of high ambient temperature (Figure 9).

3.5 Feeding and drinking

Feeding and drinking by captive birds occurred mainly morning and afternoon with minimal activity around solar zenith, although this pattern was not very marked (Figure 10). Feeding bouts for any individual were typic-
ally short, interspersed between relatively prolonged periods of other activities. Foraging behaviour was distinctly different between species: *P. namaqua* usually fed while walking along, with only brief halts, whereas *P. bicinctus* had longer pauses and apparently made a more thorough search with more pecks at each halt. The extra time (i.e. higher proportion of birds at any time: see Figure 10) spent feeding by hydrated *P. bicinctus* compared to *P. namaqua* may be correlated with the slower movements of the former species (see section 3.3).

Individual birds took only 1–4 sips at a time, but might return to drink at several times during the day. Both species therefore took advantage of the constant proximity of water to drink at atypical times of day. Despite the possible stimulus and synchronising effects of flocks of wild *P. namaqua* flying over the aviary to drink at a pool nearby, captive *P. namaqua* failed to show sharp peaks of drinking in early morning and late afternoon. On the other hand, despite drinking during the day (which wild *P. bicinctus* never do) this species showed a remarkable conservation of their normal evening drinking behaviour (Figure 10) without any synchronising effect from wild *P. bicinctus*, which did not occur around Gobabeb at the time of these studies. Captive *P. bicinctus* formed typical night-time huddles at or soon after sunset (about 18h30 LST), but dispersed again about 19h00 and made their way to the water bowls by 19h15, precisely when the main drinking flocks of wild *P. bicinctus* arrived at the Ganab water-hole (about 70 km away) where captive birds had been netted. This behaviour was repeated night after night (even when bowls were empty during the dehydration experiment), but *P. namaqua* were not stimulated to follow. Having visited the water bowls, *P. bicinctus* reformed their huddle.

Dehydration for 3 days was survived easily. On regaining access to water, *P. namaqua* drank 8.0 ± 0.5 (7) g H₂O/100 g BW (77% of mean total weight loss during the dehydration period) which was significantly less (t(10) = 4.45; P < 0.002) than the 12.0 ± 1.0 (4) g/100 g BW drank by *P. bicinctus* (98% of mean total weight loss). The water intake per sip was not significantly different between species, and the mean for all birds was 2.34 ± 0.24 (11) g water/sip. Wild *P. namaqua* drank 8–10 sips before leaving the water-hole, equivalent to 18.7 – 23.4 g H₂O or 11.1 – 13.9% body weight. Dehydration depressed feeding activity in *P. bicinctus* but not in *P. namaqua*.

3.6 Comfort movements

Birds preened at all times of day, although significantly more commonly in the forehead (mean proportion of birds = 0.105 ± 0.017 (95)) than in the afternoon (0.050 ± 0.010 (140); t = 2.80; P < 0.01).

Stretching was also common. The two most usual movements maintained low silhouettes and presumably aid

![FIGURE 10: The proportions of *Pterocles namaqua* (squares) and *P. bicinctus* (triangles) drinking (above; n=3–23) and feeding (below; n=3–20) at different times of day (local solar time). Birds were hydrated (filled symbols) or dehydrated (open symbols). Points representing combinations of species or treatments are shown by circles or partially filled symbols respectively; see Fig. 2 for other details. No significant interspecific differences in drinking behaviour were demonstrable except at 19h15. No significant differences in feeding behaviour were demonstrable between hydrated and dehydrated *P. namaqua*, or between dehydrated *P. namaqua* and *P. bicinctus*, and these data were combined (part-filled circles, lower graph). Effect of dehydration on *P. bicinctus*: t (8) = 4.26; P < 0.01.](image-url)
individuals, nor were positive or negative associations apparent between particular birds.

Movements and behaviour patterns appeared strictly functional and lacked ritualisation or signalling value as such, with the single exception of flight intention movements.

4 DISCUSSION

The relevance of observations on captive birds to their behaviour in the wild must be an important consideration when assessing the present results. Certainly the permanent proximity of water was an artificial aspect of the captive environment, and the relatively high density of seeds may also have been so, although patchy plant distribution and particle assortment by the wind can result naturally in local concentrations of seeds. Disturbance due to human activities was presumably unnaturally high: although people were normally out of sight, background noises were sometimes obtrusive. These intermittent disturbances can be considered equivalent (in some respects) to disturbance by predators in the wild (which is not infrequent as shown by field observations), and there were certainly times and days when human disturbance was slight.

Several points favour the view that the present observations may be a reasonable approximation to a knowledge of natural behaviour. Firstly, birds settled well in captivity, feeding and drinking readily so that weight losses were small, and apparently habituating soon to many of the unnatural disturbances. Secondly, since observations were on wild-caught birds within 2 weeks of capture, there was no opportunity for selection of traits for captivity, and little opportunity for learnt abnormalities of behaviour. Thirdly, many behavioural patterns seen in captivity may be matched with similar observations in the wild, or can be shown to be adaptive to the natural environment (see below).

A major feature in favour of this study is that it is difficult or impossible (because of the open nature of the habitat) to obtain a regular series of co-ordinated observations on free sand-grouse away from water-holes or nests without their being aware of the observer's presence. By contrast it is reasonably sure that our captive birds were usually unaware of surveillance, in that periods of observations could be started without the birds showing signs of special alertness or anxiety such as characterised responses to disturbance.

4.1 Behavioural responses to the thermal environment

Many of the behavioural patterns reported may be rationalised in terms of their thermoregulatory significance. This is not surprising, since the natural environment of sand-grouse is a rather extreme one in thermal terms.

Calculation of heat exchange between real animals and their environment is complicated by geometrical considerations. However, it is illuminating to consider heat fluxes near the ground quantitatively as far as possible, to indicate the relative importance of different components which determine the heat balance of an animal.

It is convenient to consider short-wave (visible and near infra-red) and long-wave (far-IR) radiation separately. Potentially, solar radiation comprises the biggest radiative component: mean downward short-wave radiation varied between zero and 906 W/m² (Table 1), to which must be added a downward solar long-wave component (approximately 30% of short-wave = 0 to 272 W/m²: (Gates, 1962)) and (for purposes of an animal's heat load) an upward component of short-wave radiation reflected from the ground. Since the reflectivity to short-wave radiation (0.35 — 0.60 for dry sand: (Lowry, 1969) decreases with increasing solar altitude, the reflected solar short-wave component may be quite high for large parts of the day (e.g. 0.35 x 906 = 317 W/m² at 12h00 LST; 0.6 x 300 = 180 W/m² at about 07h00 and 17h00). Reflected long-wave fluxes can be neglected generally, because most materials have very low reflectivities (0.05) at these wave-lengths (Birkebak, 1966).

Emission of long-wave radiation occurs from all matter at temperatures above zero K as described by the Stefan-Boltzmann (fourth power) law. Thus, there is an exchange of long-wave radiation between an animal, its solid (and liquid) surroundings and the atmosphere. The net value and direction of any exchange depends on the relative temperatures and emissivities (= (1 — reflectivity), usually 0.95 in the far-IR) of the radiant surfaces. The mean radiant temperatures of a clear atmosphere is 263K, but only about 60% of far-IR reaches the ground because of absorption by CO₂ and water vapour (Gates, 1962): near sea level, this downward component is approximately 160 W/m². The range of radiant surface temperatures experienced by our sand-grouse can be taken as of the same order as the soil surface temperatures in Table 1, although there are several reasons for supposing that values for radiant temperatures would have varied beyond the range by some degrees in both directions. At these temperatures there could be net long-wave radiant losses from solids to the atmosphere of the order of 200 to 500 W/m², and net exchanges between solids of ±5 to 7 W/m². °C depending on the absolute temperature and temperature differences. Thus, radiant energy exchange is dominated by the solar components during the day and by losses to the atmosphere (especially if clear) at night.

Conductive and convective heat exchanges are highly dependent on the geometry of the body concerned, and order-of-magnitude calculations have been done for a cylinder of approximately sand-grouse dimensions (0.15 m long x 0.07 m diameter). For forced convection parallel to the cylinder's long axis at the average wind speed experienced (1.77 m/s: Table 1), calculated heat exchange would have been 15.7 W/m². °C for each
degree difference between surface and air temperatures (Calder and King, 1974). The thermal conductivity coefficient of feathers was assumed to be similar to fur, and as calculated as $4.43 \times 10^{-2}$ W/m² °C from data in Birkebak's (1966, Figure 19). Conductive heat transfer per degree Celsius temperature difference across the feather layer was calculated as about $8.2 \times 10^{-3}$ W/m² (0.5 cm insulative thickness) or $3.9 \times 10^{-3}$ W/m² (1.0 cm insulative thickness).

The metabolic rate for *P. namaqua* and *P. bicinctus* at rest (calculated from body weights, using standard allometric equations for non-passerines: Calder and King, 1974) comes to 1.2 to 1.3 W/bird or about 49 W/m² external surface (Walsberg and King, 1978). It is known that many desert animals have metabolic rates less than expected on the basis of standard allometric equations, but nothing is known about sand-grouse in this respect. Various activities augment metabolic rates above basal levels (Wunder, 1975): for example, Redshanks (*Tringa totanus*) standing alert or foraging increase their metabolic rates by about 30% or 100% respectively over rates when asleep (Ferns, Macalpine-Leney and Goss-Custard, 1979). Approximately 75% of metabolic energy is released as heat, while 15–35% of metabolic heat production may be dispersed as latent heat of evaporation of body water ($2.43 \text{ kJ/gH}_2\text{O}$) depending on species and ambient temperatures (Calder and King, 1974).

The geometry of the system is the main difficulty in integrating the effects of all these potential exchanges of heat on an animal's heat balance: different surface areas and orientations are involved for the different components. However, one can see from the foregoing data that, for sand-grouse in their natural environment, heat loads during the day could be minimised by avoiding direct and reflected sunlight while maintaining exposure to a clear sky (for radiant heat loss), by having solid surroundings at or below (rather than above) body temperatures, and by reducing metabolic heat production. Forced convection can be a potent means of dispersing heat if bare skin can be exposed to a cool wind, since skin temperatures can be raised to near deep body temperatures by increasing cutaneous blood flow. At night, heat losses can be minimised by reducing surface areas exposed to the sky (especially if clear) and by having solid surroundings as near as possible to body temperatures. At all times, insulation is a potent mechanism for retarding heat transfer when temperature gradients would otherwise lead to unfavourable heat gain or loss by the animal. In fact, our observations show that both *P. namaqua* and *P. bicinctus* behaved much as expected if they were to minimise heat loss during the colder periods and heat gain during the hotter periods of the 24-hour cycle.

Many daytime behaviour patterns can be interpreted as mechanisms likely to reduce or disperse the total heat load during the hottest period: relative inactivity to reduce metabolic heat production; choice of shade to minimise solar radiant heat load and to experience lower air temperatures; huddling to provide an immediate environment with more equable surface and deep temperatures than those of the general environment; gular fluttering by hydrated birds to disperse heat; erection of dorsal feathers to insulate the skin mainly from high outer surface temperatures (not so much from high air temperatures since generally these did not exceed deep body temperatures: Figure 1). These activity patterns were clearly in register with either the pattern of solar radiation (i.e. peaks or troughs about noon: sitting, standing, walking, feeding, drinking, and choice of shade by hydrated birds) or that of ambient temperatures (i.e. peaks at 14–15h LST: huddling by hydrated birds, wing drooping) or had peaks spanning both insolation and temperature maxima (choice of shade and huddling by dehydrated birds, feather erection and gular fluttering).

Individual birds adopted a mixture of these thermoregulatory mechanisms which was not necessarily consistent within the group at the time nor from time to time, nor was any individual seen to use all available mechanisms at once. The latter suggests that *P. namaqua* and *P. bicinctus* had thermoregulatory reserves and could readily withstand larger heat loads than obtained during our observations.

Since wing drooping occurred characteristically during the heat of the day, one may assume that it is mainly a means of heat dispersal, although it is not obvious a priori whether it would result in net gain or loss of heat, because the lightly insulated axillary region might experience increased radiant heat gain (reflected short-wave + long-wave if soil surface temperature exceeds skin temperature), or it might experience increased convective heat loss if skin temperature exceeds air temperature. It seems likely that the relatively narrow gap between body and wings (which we never saw as wide in non-incubating birds as indicated in Dixon and Louw's (1978) figure 4 of an incubating bird) results in the axilla being shaded from much of the potential radiant heat load but allows passage of wind through the gap and hence heat loss by forced convection. Indeed, since fluid flowing through a constriction accelerates (the Venturi principle) and since forced convective heat exchange is proportional to (wind velocity)$^6$, wing drooping may actually enhance convective heat loss above the level expected for the mean wind velocity. It is possible that the prevalence of wing drooping during the period of dehydration may have been only coincidental, and that the significant factor over this period was the lower air temperatures (associated with cooler westerly winds from the Atlantic; Table 1) which would have made convective heat loss more effective. It is probably significant that wing drooping by several N. African sand-grouse species (*P. coronatus*, *P. senegallus*, *P. lichiensterni*, *P. alicata* or *P. orientalis*) was never observed (Thomas and Robin, 1977); these species were exposed to air temperatures above likely body temperatures ($40^\circ$C) for several hours per day, which would result in convective heat gain by the birds.
There seems little doubt that these apparently thermoregulatory behaviour patterns are available to and are used by sand-grouse in the wild. Even in the Namib Desert small bushes, grass tussocks and large stones provide shade; vegetation is much more readily available over much of the range of both *P. namaqua* and *P. bicinctus* (Snow 1978), and shade is used by these and other species (this study; George, 1969). However, some mechanisms (such as choice of shade and huddling) which seem important to birds without nests are not available to incubating birds. Thomas and Robin (1977) and Dixon and Louw (1978) emphasised the importance of feather erection, gular fluttering and (in *P. namaqua* but not *P. australis, P. coronatus* or *P. senegallus*) wing drooping and orientation by incubating females, and it may be that these mechanisms become relatively more important while birds are necessarily solitary and exposed on a nest.

Although hitherto unreported in sand-grouse, nocturnal huddling is well-known in many bird species, providing a local environment close to body temperatures, and reducing the surface area exposed to the night sky, the major heat sink. Radiant heat loss to the sky would also have been reduced by the habit *P. namaqua* and *P. bicinctus* had of huddling close to a bush or stone, with the additional advantage of camouflage by breaking the birds' silhouettes. Ward (1972) and Ward and Zahavi (1973) state that sand-grouse roost solitarily, rationalising that communal roosts would be vulnerable to predators. Our observations suggest that both these statements are incorrect with respect to *P. namaqua* and *P. bicinctus*; moreover the absence of field observations of huddling (night or day) by these or other sand-grouse species cannot be taken as evidence that huddling does not occur, since our observations show that huddles break apart on disturbance and so would be unlikely to be seen in the wild. It seems likely that, in addition to heat conservation, an advantage of roosting in a huddle would be to reduce vulnerability by group vigilance, enhanced by the possibility of communicating alertness within the group by tactile (silent) means.

Thus, behavioural mechanisms of thermoregulation by *P. namaqua* and *P. bicinctus* seem very important, often bringing to mind similar behaviour by heterothermic reptiles. One benefit of such an astute use of small scale variations in microclimate would be conservation of energy (and water), which would help to explain the relative success of sand-grouse in biologically unproductive environments.

### 4.2 Responses to dehydration

Namaqua and double-banded sand-grouse are evidently well adapted to dehydration, easily surviving 3 days’ exposure to a normal environment without water. Willoughby and Cade (1967) kept *P. namaqua* “up to a month without water in the absence of heat stress, being fed on dry bird seed only”, and noted a “slow steady weight loss” during dehydration. By losing weight somewhat more slowly during dehydration, and by seeming content to drink proportionately less when given water afterwards, *P. namaqua* showed evidence of being somewhat better adapted to water deprivation than *P. bicinctus*. This is consistent with the geographical ranges of the two species: despite a wide overlap in their occurrence, *P. namaqua* extends further into drier regions while *P. bicinctus* extends further into moister regions (Snow, 1978).

Responses to dehydration involved direct saving of body water by abolition of gular fluttering (i.e. evaporative water loss) together with other mechanisms (reduced ambulatory activity, longer periods spent sitting in the shade, increased feather erection, and, in *P. bicinctus*, reduced feeding) which would have reduced the metabolic and environmental heat load, and hence reduced the demands on body water reserves. McFarland and co-workers have described and discussed similar behavioural responses to dehydration in the Barley Dove (*Streptopelia rioria*, probably a domesticated strain of *S. roseogrisea*: Parkes, 1971) (McFarland and Baher, 1968; McFarland and Budgell, 1970; McFarland and Wright, 1969).

The existence of well-developed responses allowing tolerance of water deprivation for a number of days makes it questionable whether individual sand-grouse drink daily. There is no direct evidence of drinking frequency by wild sand-grouse, but there is quantitative indirect evidence that they do indeed forego daily drinking. Willoughby and Cade (1967) (who also queried whether sand-grouse needed water daily) recorded crop water contents of *P. namaqua* shot at after drinking at one of the Namib Desert water-holes (Hotssas) as 16.4, 16.1 and 13.7% of body weight. If this represented replacement of weight loss of 3.4 g/100 g BW day due to dehydration (section 3.2), it would indicate a self-imposed water deprivation of 4.8, 4.7 and 4.0 days respectively in wild birds. A similar calculation indicates that wild *P. namaqua* observed drinking the normal 8–10 ships may have been without water for 3.3 to 4.1 days respectively. Thomas and Robin (1977) found fewer *P. australis* and *P. orientalis* drinking on misty overcast mornings than on clear ones, and suggested that many individuals did not fly to water on days which were relatively cool. The advantages of not drinking daily would include energy saved for the round trip between feeding areas and drinking points, and avoidance of the predators (especially *Falco spp.*) which exploit sand-grouse flocks at water.

A corollary of the conclusion that sand-grouse may normally go several days between drinks is that the flocks attending a watering point on any day represent a correspondingly smaller fraction (perhaps 0.2 to 0.3) of the regional population and not the majority of birds as has usually been assumed. Total populations and population densities of sand-grouse may be several-fold higher, therefore, than the impression created by watching the sometimes enormous drinking flocks, and the success of
sand-grouse at exploiting a difficult unproductive habitat becomes all the more remarkable.

4.3 Foraging behaviour

There were pronouncedly different foraging techniques between *P. namaqua* and *P. bicinctus*, which are perhaps effective alternatives reducing competition and promoting coexistence between species. The technique of searching a limited area thoroughly (*P. bicinctus*) seems to trade off the disadvantage of risking a smaller total available food stock within the foraging path for the advantage of relatively low energy costs harvesting the food requirement. On the other hand, making a cursory search of a large area (*P. namaqua*) seems to increase the chance of finding a sparsely distributed food supply, but at the expense of a higher energy cost obtaining it. A comparable pair of foraging techniques appears to occur in two coexisting species of North American desert rodents: *Perognathus* adopts a cursory extensive foraging pattern, while *Dipodomys* uses a locally intensive one, which results in the two species exploiting large and small seeds respectively, because of the differential effects of wind assortment on seeds of different sizes (Reichmann, 1979).

4.4 Social behaviour

Intraspecific competition for scarce food resources might be expected to lead to aggressive interactions or a hierarchical social structure amongst sand-grouse. However, food particles are generally very cryptic (see Dixon and Louw's (1978) Plate I), so that the first bird to see an item will eat it promptly (in all probability), making the item not worth a contest either on that account or on account of its relatively small size. Moreover, fighting (either actual or ritualised) in a hot open habitat has the multiple disadvantages of increased metabolic heat production, increased conspicuousness as a result of movement, and the danger of injury by a conspecific or predator. Thus, mutual yielding and a continued search for the means of existence may be a better investment of time and energy than aggressive or formalised competition between individuals.

It is not surprising, then, to find that social interactions within and between species could be summarised as pacific, undemonstrative, egalitarian gregariousness. The *P. namaqua* were caught as a single flock and so might conceivably have been a pre-existing social unit, but the *P. bicinctus* were caught piecemeal and so were probably not. If these species had a hierarchical social structure one might expect to see this directly in an established group, or else expect to see aggressive interactions until a hierarchy was established within a newly formed group. Since neither aggression nor hierarchy was observed, a pacific egalitarian social structure can be concluded to exist within non-breeding mixed-sex groups of *P. namaqua* and *P. bicinctus*. In the absence of aggression, many intention movements, and threat and appeasement displays become irrelevant.

5 SUMMARY

Observations were made on captive Namaqua sand-grouse (*Pterocles namaqua*) and double-banded sand-grouse (*P. bicinctus*) at the Namib Desert Research Station and on wild birds.

Both species had well-developed behaviour patterns tending to reduce and disperse environmental and metabolic heat loads during the heat of the day and reduce heat loss by night. When air temperatures and solar irradiance were high, birds became relatively inactive, sought shade, insulated themselves by piloerection and forming huddles with other individuals, and sometimes dispersed heat by forced evaporative water loss (gular fluttering) and forced convection (wing drooping). Some of these responses were observed in wild birds also. At night, birds formed close huddles, which would have conserved metabolic heat by mutual insulation and piloerection, and by reduction of the radiant surface exposed to the sky (the major heat sink). Nocturnal huddling is also likely to reduce vulnerability to predators by promoting effective group vigilance.

Birds easily tolerated 3 days of water deprivation while exposed to the normal environmental heat load, losing weight by 3.4 - 4.4 g/100 g weight daily. This weight loss was made up partially (*P. namaqua*) or wholly (*P. bicinctus*) in one drinking session. Evidence is presented to suggest that wild *P. namaqua* may drink normally only every 3 - 5 days. Behavioural responses to dehydration can be interpreted as reducing water expenditure directly (abolition of gular fluttering) and indirectly (by further reduction of environmental and metabolic heat loads).

Interspecific differences in foraging behaviour suggest that this may promote ecological isolation between the species. Social behaviour was pacific and lacked hierarchical relationships between individuals. There was a corresponding lack of agonistic and signalling behaviour.

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7 REFERENCES


The distribution of the genus *Rhoptropus* (Reptilia, Gekkonidae) in the central Namib Desert

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1 INTRODUCTION

The gekkonid genus *Rhoptropus* (Peters) occurs over the western parts of Namibia and Angola from 24°S northwards to about 11°S. The latest check-list (Wermuth, 1965) recognises seven species, three of which extend as far as and reach their southern range limits in the area of the Namib-Naukluft Park. Although an impression of the general distribution of these three species may be obtained from the literature (FitzSimons, 1943; Haacke, 1965; Loveridge, 1947; Mertens, 1955 and 1971; Wermuth, 1963), published information is rather scanty.

A more detailed survey of the entire range of this genus has been in progress for some time by the senior author and has produced a clearer overall picture. *R. afer* (Plate 1) occurs in a coastal strip, closely coinciding with the fog-belt rarely extending inland further than about 60 km, ranging from just south of the Kuiseb River at Gobabeb to just north of the mouth of the Kunene River. *R. bradfieldi* (Plate 3) has a relatively limited range, namely from the south bank of the Kuiseb River near Honeb to western Damaraland just north of Twyelfontein and although it occurs on the coast as far south as Swakopmund it swings inland and seems to be absent from the western part of the Namib-Naukluft Park. *R. barnardi* (Plate 2) is by far the most widely distributed member of the genus and the least specific with regard to habitat preference. It occurs from coastal desert through the pro-Namib into tropical savanna woodland in the Otavi Mountains and even miombo woodland in the Angolan highlands, and ranges from Rohoboth-Solitaire (24°S) to the latitude of Novo Redondo in Angola (11°S) (Transvaal Museum records).

On a microgeographic level FitzSimons (1943) pointed out that *R. afer* is “usually confined to the dry open flats of gravelly sand and stones ...” while *R. barnardi* is “found living both on rocky kopjes (hills) and among small outcrops on the flats”. Loveridge (1947) stated
that the habitat of *R. bradfieldi* consists of "black rocky outcrops in the Namib Desert". Mertens (1955) also noted that *R. barnardi* occurs on large as well as small boulders and reported that he had seen them on the same rocks as *R. bradfieldi* as well as having seen *R. bradfieldi* and *R. afer* 1 m from one another. Odendaal (1979) also pointed out that *R. afer* may generally be regarded as an inhabitant of the gravel plains while the other two species generally inhabit rock outcrops or ridges. *R. afer* utilises a habitat which one usually would associate with fast-moving lacertids rather than a climbing gecko since it almost exclusively occupies the horizontal or slightly sloping aspects of a site. *R. bradfieldi* and *R. barnardi* are good climbers exploiting all angles of the rock face.

The above-mentioned observations were largely confirmed during the major survey and as a consequence it was suggested to the second author to investigate ecological aspects such as niche separation in areas of sympatry. Due to the accessibility of the central Namib Desert within the limits of the Namib-Naukluft Park this area was found to be the most convenient for this study. During this investigation, which included a combined field trip of both authors, extensive additional distributional information was gathered. Since the detail available for the central Namib is bulky, and exceeds the data available for the rest of the generic range, it was considered useful to present this information in this paper prior to a discussion of the entire range (Haacke, in prep.) and ecological investigations (Odendaal, in prep.).

2 METHODS

The distribution of the three species in the central Namib (Fig. 1–3) was investigated by extensive travelling over as much of the area as was practical. It was documented by collected voucher specimens which are deposited in the Transvaal Museum, Pretoria, and the State Museum, Windhoek. Material was also contributed by a number of other collectors. Published records and specimens in a number of other institutions were also incorporated. Of the various sites which were visited on one or more occasions, seven were studied more intensively by the second author and are described elsewhere in this paper. They are referred to by the following names: Gobabeb Site A, Gobabeb Site B, Mirabib Site, New Road Site, Bad Earth Site, Bakenkoppie Site and Bloodkoppie Site.

Two methods were used to derive relative density estimates for the three species at some of the main study sites, although in some cases time did not allow more than one method per site. The first method is the recording of individuals by means of a thumb counter while walking random transects across the study site for 45-minute periods during the peak activity period in the late morning (cf. Odendaal, 1978). The second method involved the recording of all individuals on four randomly established quadrangular areas of 40 x 60 m, which equals 960 m² per site. Six metres is a convenient width for observing the number of individuals on the demarcated area while walking down the middle of it. To minimise disturbance and the possibility of lizards staying under cover, these transects were only done once a day during the morning peak activity period. The counts obtained for 960 m² were converted to values of 1 000 m². The results obtained in this way do not necessarily reflect absolute densities and probably underestimate the population size, but may be used to compare sites. For various reasons marking/recapture was impractical.

Co-occurring species were recorded at the seven main study sites in order to establish whether a correlation existed between the distribution of *Rhoptropus* species and the presence or absence of other lizard species. Substrate types were investigated in an attempt to establish their effect on the distribution of the three species.

3 RESULTS

3.1 Recorded localities

The known distribution of the three *Rhoptropus* species in the central Namib is shown in Figures 1, 2 and 3. The localities from where material is available and the institutions in which the specimens are housed are listed below:

**AM** = Albany Museum, Grahamstown  
**CAS** = California Academy of Science, San Francisco  
**DERU** = Desert Ecological Research Unit, Gobabeb  
**HM** = Zoologisches Institut und Museum, Hamburg  
**LACM** = Los Angeles County Museum  
**NMP** = Natal Museum, Pietermaritzburg  
**PEM** = Port Elizabeth Museum  
**SMF** = Senckenberg Museum, Frankfurt/Main  
**SMW** = State Museum, Windhoek  
**TM** = Transvaal Museum, Pretoria  
**UZM** = Zoological Museum of the University, Copenhagen  
**ZMB** = Zoologisches Museum der Humboldt Universität, Berlin

*Rhoptropus afer* (Plate 1): Arandis (SMF); Bakenkoppie (SMW), 5 km, 6 km and 13 km E, 13 km ESE, 14 km SE, 8 km SSE and 8 km S of Bakenkoppie (TM); Bloodkoppie (TM, SMW); Carp Rock, 4 km E and 8 km NE of Carp Rock (TM); Goanikontes (AM, SMF); Gobabeb (TM, DERU, NMP, CAS, AM); Gobabeb, S of Kuiseb River (TM, DERU, UZM); Gobabeb nr. Airstrip (DERU), 10 km and 12 km from Gobabeb-Mirabib, 30 km NW of Gobabeb, 19 km NNW of
Gobabeb (TM); 20 km NNW of Gobabeb, 4 km NE of Gobabeb (SMW); N and S end of Gungochoab Mtn., 2.5 km and 3 km SE and 5 km NW of Gungochoab Mtn., Hamilton Mtn., 1 km SE of Homeb turn-off, Husab Drift, 3 km and 5 km SE and 9 km E of Klein Klipneus (TM); Kuitse River nr. Rooibank (AM); Namib Station (SMF); btw. Natab-Rooibank, “New Road Site”, btw. Nonidas-Namib, nr. Nonidas Station (TM); Otjimbingwe? (SMF); Palmehorst (TM); Rooibank (TM, SMF, ZMB); ±40 km SE of Rooibank (TM); Rooikop (SMF); Rössing Mine (TM); Rössing (TM, AM, AMF); 5 km NW of Schieferberg Pass, Schierlitz (TM); btw. Sphinx-Pforte (AM); Swakopmund (TM, AM, SMF, LACM); 5 km E of Swakopmund (UZM); 10 km E of Swakopmund (NMP); 13 km and 40 km E of Swakopmund (TM); 16 km E of Swakopmund (NMP); 3 km E of Swakop River bridge (CAS); 30 km and 42 km SE of Swakopmund (TM); 38 km SE of Swakopmund on Khomas Hochland Road, 11 km and 16 km from Swakopmund—Usakos (CAS); 20 km N of Swakopmund (SMF); 22 km N of Swakopmund (TM); Swartbankberg (TM, NMP); Swartbank S of Kuitse River, 3.5 km and 8 km E of Swartbank Village (TM); Swartkoppies (SAM); Ubib, 3 km W and 5 km NNE of Ubib, nr. Vogelfederberg, Von Stryk Mine (TM); Walvis Bay area (SMF), 80 km E of Walvis Bay on Gamsberg Road, Welwitschia flats, Welwitschia Station, 5 km SSW of Witpoortberg (TM).
Rhoptropus barnardi (Plate 2): Anigab (TM); nr. Arandis (SMF); Bakenkop (TM); Bloedkoppie (TM, SMW); Gross Tinkas (TM); Hebron (TM, DERU); 16 km SW of Hebron (TM); 30 km W of Kahn Pforte (SMF); Langer Heinrich (TM); Onanisberg (DERU); farm Rostock, Schieferberg Pass, 11 km and 16 km NNE of Uibib, Zebra Pan, 2 km and 14 km SSE of Zebra Pan (TM); 2215 DAd (DERU).

Rhoptropus b. bradfieldii (Plate 3): Bakenkop (TM); Bakenkoppie (SMW); 13 km E, 13 km ESE, 14 km SE and 8 km S of Bakenkoppie, nr. Barrowberg (TM); Bloedkoppie (TM, SMW); 1.6 km and 5 km E of Bloedkoppie, farm Donkerhoek (SMW); Goanikontes (SMF, TM); 1.6 km SE of Gobabeb, farm Greylingshof, Gross Tinkas (TM); 5 km NW of Gorob Mine (Gorob Mine AM is probably from same site) N and S end of Gungochoab Mountain, 3 km SE of Gungochoab Mountain (TM); Haigamkaab (AM); btwn. Hebron-Onanis River, 8 km SE and 8 km SW of Hebron, Homeb, Husab Drift (TM); Kahn Mine, 30 km W of Kahn Pforte (SMF); Klein Tinkas (TM); Kuiseb Canyon and Bridge (TM, DERU, SMW); farm Komua (TM); Langer Heinrich, 9 km E of Klein Klipheus (TM); Mirabib (TM, SMW); Mirabib Hills (TM, DERU); “New Road Site” (TM, SMW); 1 km W of “New Road Site” (TM); Namib Station (TM, SMF); btwn. Nonidas—Namib Station (TM); Nonidas Station (TM, SMF); Onanisberg (DERU); Palmehorst, Riet, farm Rostock, Rossing Mountain and Mine, 5 km NW of Schieferberg Pass (TM); Swakopmund (SMF, PEM); 20 km N of Swakopmund (TM); 16 km E of Swakopmund (NMP); Uibib, 3
km W, 10 km SE, 5 km NNE of Uibib, N side of Witpoort (TM).

3.2 Density estimates

Table 1 shows the density estimates for some of the sites, indicating variations in population densities between species. The cause for the variation in relative densities between sites with more than one species represented may be sought in the availability of suitable preferred habitat. Some sites with the same species composition vary drastically in relative densities. For instance, *R. bradfieldi* occurs in much higher numbers than *R. afer* at Bad Earth Site while at New Road Site they occur in nearly even numbers (Table 1). These differences may be explained by comparing the suitability of the substrata. At Bad Earth Site the low vertical ridges are occupied by *R. bradfieldi* while *R. afer* occurs on the gravel sheets between the ridges. It appears that a lack of flat rocky areas with loose lying slab shelters in the presence of *R. bradfieldi* reduces the suitability of the site as *R. afer* habitat, resulting in low densities. Although *R. afer* will ascend even large rock outcrops in the absence of *R. bradfieldi*, as at Swartbankberg, Vogelfederberg, Carp Rock, Rooikop and even Gobabeb Site B, and others, this species in areas of sympathy will take to flat rocky areas as at Bloedkoppie and Bad Earth Site. In contrast at New Road Site the numbers of the two species are reasonably even. This site has large flat to near horizontal surfaces suitable for *R. afer* which are avoided by *R. bradfieldi*, which occurs on the many monolithic boulders with vertical and overhanging surfaces which are available.

During March/April 1977 generally higher density estimates were obtained for both *R. afer* and *R. bradfieldi* in contrast to December/January 1976/7 at Gobabeb Site A and Mirrabib Site (Ondenbal, unpubl. data). This could be due to the high relative abundance of hatchlings during early autumn. At present hardly anything is known about the population dynamics of the three species and whether their reproductive patterns show noticeable peaks which might be synchronised or staggered as in the lacertid *Ichnotropis* (Broadley, 1979).

3.3 Description of seven sites

These sites were given code names and used by the junior author for more intensive studies.

**Gobabeb Site A (Plate 4)**

Locality: 4 km SE of Gobabeb in an interdune valley.
The site consists of low but extensive granite outcrops situated in an interdune valley. These granite outcrops are surrounded by sand. The rock type is of a weathered flaky nature, providing suitable shelters for the lizards. The site is fairly homogenous without proper boulders and the granite is not quite as weathered as that of Mirrabib and is of a lighter colour (more or less grey to whitish-grey). The time of insolation is more or less the same for the entire site, since it is flat. Hardly any shade is available at mid-day except under the flanks and on the vertical surfaces of the few concave larger rocks. There are also a few small outcrops of white quartzite (± a metre in diameter). This site is completely isolated by sand from any other suitable habitat with respect to *Rhopitopus*. Only *R. afer* occurs on this site and in high numbers (Table 1).

**Gobabeb Site B (Plate 5)**

Locality: Gobabeb, directly across the road from the Research Station.

As Gobabeb Site A lacks boulders, a similar site with granite boulders was selected for the sake of comparison. With respect to the morphology of the rocks it differs from Gobabeb Site A only by the presence of large numbers of boulders. Again only *R. afer* occurs here and in high numbers (Table 1), although *R. bradfieldi*'s range extends to within 1 km from this site along the Kuseb River.

**Mirrabib Site (Plate 6)**

Locality: 40 km NE of Gobabeb, an isolated koppie on the SE side of the range, about half-way between Mirrabib and Gorob Mine.

This site is a prominent outcrop consisting of many boulders of varying sizes and a substantial amount of flat areas, much of which is of the flaky nature comparable to that of the sites of Gobabeb. Many of its boulders and rock-faces are much larger than those at Gobabeb Site B. Shade is available throughout the day.

<table>
<thead>
<tr>
<th>SITE</th>
<th>SPECIES</th>
<th>Method</th>
<th>( \bar{x} )</th>
<th>SE</th>
<th>n</th>
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</thead>
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<tr>
<td>Gobabeb</td>
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<td>A</td>
<td>65,6</td>
<td>3,95</td>
<td>5</td>
</tr>
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<td>0,91</td>
<td>9</td>
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<tr>
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<td>4</td>
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<td>Site</td>
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<td>4,14</td>
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<td>7</td>
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<td>A</td>
<td>6</td>
<td>1,50</td>
<td>3</td>
</tr>
<tr>
<td>Site</td>
<td></td>
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<td>0,25</td>
<td>0,25</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td><em>R. bradfieldi</em></td>
<td>A</td>
<td>40</td>
<td>6,57</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>B</td>
<td>3,25</td>
<td>0,57</td>
<td>4</td>
</tr>
<tr>
<td>New Road</td>
<td><em>R. afer</em></td>
<td>A</td>
<td>25</td>
<td>2,02</td>
<td>3</td>
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<td>Site</td>
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<td>0,37</td>
<td>5</td>
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<tr>
<td></td>
<td><em>R. bradfieldi</em></td>
<td>A</td>
<td>27</td>
<td>0,57</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>B</td>
<td>2,6</td>
<td>1,02</td>
<td>5</td>
</tr>
<tr>
<td>Bloedkoppie</td>
<td><em>R. afer</em></td>
<td>A</td>
<td>2,5</td>
<td>1,50</td>
<td>2</td>
</tr>
<tr>
<td>Site</td>
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<td>A</td>
<td>28,5</td>
<td>7,51</td>
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</tr>
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<td></td>
<td><em>R. barnardi</em></td>
<td>A</td>
<td>25,5</td>
<td>2,50</td>
<td>2</td>
</tr>
</tbody>
</table>

TABLE 1: Estimates of densities for some of the main study sites done during March/April 1977. A=thumb counter method; B=estimated total number per 1000 m².
Habitat diversity and temperature microclimate is much more diverse than that of the relatively homogenous sites at Gobabeb. As far as *Rhoptopus* is concerned, this site is completely isolated by sandy plains from any other suitable rock outcrop. Since this site lies further east than Gobabeb, New Road, Bakenkoppie and Bad Earth Site, its vegetation is much more diverse. Only *R. bradfieldi* occurs here and in high numbers (Table 1). This site lies east of the known range limit of *R. afer*.

**New Road Site (Plate 7)**

Locality: 20 km from Gobabeb on the road to Vogelfederberg.

Very similar in all morphological respects to Gobabeb Site B. It consists of granite boulders and flaky areas, situated next to a dry river-bed on the gravel flats. Both *R. afer* and *R. bradfieldi* occur here in approximately equal numbers (Table 1), although it is near the SE range limit of *R. afer* and at the southern tip of a band-like extension of *R. bradfieldi*’s range from the Langer Heinrich area in the Swakop Valley across the plains of the central Namib (cf. Figs. 1 and 3).

**Bad Earth Site (Plate 8)**

Situation: 40 km NNW from Gobabeb on road to Vogelfederberg.

Formation consists of low ridges, usually less than one metre in height, separated by gravelly sand. Rock type is black schistose amphibolite, marble and small patches of granitic formations. These ridges form part of the dark formations in the centre of the Namib Park gravel flats (cf. satellite photo, Plate 11), their strike is NNE to SSW and they disappear 4 km SSW of the intersection.
possible fourth system can be described consisting of loose granite boulders at ground level strewn around the base of the koppie and the immediately adjacent area. The main hill is comparable to the Mirabib Site in morphology consisting of a large granite dome with large boulders of varying sizes and flat flaky surfaces, but of much greater dimensions. The hills to the west with ridges of shales and amphibolites were well vegetated during the survey, mostly by grasses. Just within these hills on the side facing the main granite dome is a small isolated granite area (some 20 m × 20 m) encircled by shales and amphibolites. This site has a greater plant species diversity than any of the others (Odendaal unpubl. records).

*R. bradfieldi* occurs exclusively on the main hill while *R. barnardi* occurs exclusively on the shales and amphibolites of the hills to the west of the main hill. Some *R. bradfieldi* occur on the small granite patch encircled by the shales and amphibolites. *R. afer* occurs exclusively on the flat granite surfaces south of the main hill. Both *R. bradfieldi* and *R. barnardi* occur in high numbers while *R. afer* is rare, possibly due to the fact that this is a marginal population at the eastern range limit.

### 3.4 Co-occurring species

The following lizard species occur sympatrically with *Rhoptropus* at the following four sites: Gobabeb Sites A and B, Mirabib and Bloedkoppie and a brief general indication of their spatial and time niches is provided in Table 2.
TABLE 2: Lizards co-occurring at four study sites

<table>
<thead>
<tr>
<th>Lizard Family</th>
<th>Gobabeb Site A</th>
<th>Gobabeb Site B</th>
<th>Minabib</th>
<th>Blood-lopie</th>
<th>Terrestrial</th>
<th>Rupicolous</th>
<th>Diurnal</th>
<th>Nocturnal</th>
</tr>
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<tbody>
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<td>GEKKONIDAE</td>
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<tr>
<td><em>Rhoptropus afer</em></td>
<td>X</td>
<td>X</td>
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<td>X</td>
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<tr>
<td><em>R. barnardi</em></td>
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<tr>
<td><em>R. bradfieldi</em></td>
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<tr>
<td><em>Afroedura a. africana</em></td>
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<tr>
<td><em>Chondrodactylus a. namibensis</em></td>
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<tr>
<td><em>Narudasia festiva</em></td>
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<td><em>Pachydactylus bibronii</em></td>
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<td><em>P. bicolor</em></td>
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<td><em>P. kochii</em></td>
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<td><em>Palmatogecko rangei</em></td>
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<td><em>Ptenopus carpi</em></td>
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<td><em>P. kochii</em></td>
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<tr>
<td><em>M. s. sulcata</em></td>
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<td><em>M. variegata</em></td>
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<tr>
<td>LACERTIDAE</td>
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<td><em>Eremias breviceps</em></td>
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<tr>
<td><em>E. undaia</em></td>
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<td>X</td>
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<tr>
<td><em>Meroles cunetosistris</em></td>
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<tr>
<td><em>M. sobrutilis</em></td>
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</tbody>
</table>

X = Confirmed presence
/ = Sight record

The combination of the diurnal/rupicolous *Rhoptropus* species present at these four sites in relation to the number of lizard species representing certain time/niche preferences is listed in Table 3.

Although *R. afer* has terrestrial tendencies in the absence of suitable rock, all species of *Rhoptropus* may be considered to be rupicolous and diurnal in comparison to other potentially competitive species (Table 2). With reference to Table 3 *R. afer* does not have any competitive lizard species with a similar niche preference at Gobabeb Site A, while at Gobabeb Site B two species are listed as potential competitors. Of these *Agama anchietae* is of very rare occurrence at that locality and is therefore of no consequence. Even within its normal distribution this species tends to occur in isolated pairs or as single individuals which are widely spaced. *Mabuya variegata* tends to be more common along the bed of the Kuiseb River with isolated individuals occurring on Gobabeb Site B.
### TABLE 3: Distribution of lizard types on four study sites.

<table>
<thead>
<tr>
<th>Study sites:</th>
<th>Occurrence of <em>Rhoptropus</em> species on study sites:</th>
<th>General indication of time and spatial niches of co-occurring species</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>R. afer</td>
<td>R. barnardi</td>
</tr>
<tr>
<td></td>
<td>Diurnal</td>
<td>Nocturnal</td>
</tr>
<tr>
<td></td>
<td>Diurnal</td>
<td>Nocturnal</td>
</tr>
<tr>
<td>Gobabeb Site A</td>
<td>X</td>
<td>/</td>
</tr>
<tr>
<td>Gobabeb Site B</td>
<td>X</td>
<td>2</td>
</tr>
<tr>
<td>Mirabib</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Bloedkoppie</td>
<td>X</td>
<td>X</td>
</tr>
</tbody>
</table>

At Mirabib no congeneric competitors have been recorded for *R. b. bradfieldi* (Table 2), while five other potential competitors are recorded. Of these both *Agama anchietae* and *Mabuya hoechii* are non-social species which occur as widely spaced pairs or individuals and are therefore of little consequence as competitors. The small non-social *Mabuya variegata* also tends to occur as single individuals and apparently because of its low density its occurrence has not yet been confirmed by a voucher specimen. The larger rock living skink *Mabuya sulcata* which may occur in high densities in similar situations as *R. bradfieldi* may be of competitive significance under such circumstances, although, due to greater body thickness in adult form, it may lose its importance as competitor for narrow crevice retreats. At Mirabib it has only been recorded as a sight record by the second author, indicating a low density situation unimportant to *R. bradfieldi*. *Eremias undata* is an actively foraging lacertid avoiding vertical and overhanging rock faces where it would encounter *R. bradfieldi*.

The presence of three *Rhoptropus* species at Bloedkopnie appears to significantly affect one another’s occurrence at that site resulting in a patchy distribution with no direct overlap as discussed in the site description (cf. Page 00). All other diurnal rupicolous species recorded here are non-gekkonids of which *Agama anchietae* could co-occur with *R. afer* and *R. barnardi* but would only enter *R. bradfieldi* area on smaller rocks around the base of the granite dome. *Agama planiceps*, a social species, occurs in relatively high concentrations mainly in *R. bradfieldi* area as does *Mabuya sulcata*. Both the latter species could be considered to be potential competitors within the rupicolous / diurnal niche, although all occur in high densities. *Mabuya variegata* and *Eremias undata* have been discussed above, as being relatively insignificant and the unconfirmed sight record of *Mabuya spilogaster*, which usually prefers trees but in their absence will also use rocks, must be rated of similarly low significance.

In conclusion it appears as if other diurnal / rupicolous lizards do not significantly affect the distribution of *Rhoptropus* species and that the congeneric species give way locally to *R. bradfieldi* with *R. afer* restricting itself to low boulders and sheet-rock while *R. barnardi* restricts itself to rock types avoided by the others (cf. Table 3).

#### 3.5 Substrate types

According to Logan (1960) “the rocky outcrops and canyons of the central Namib consist of coarse-grained, well-eroded granite, mica schists, feldspar formations or lime deposits”.

The second author had rock samples from 38 sites in the Namib-Naukluft Park analysed. According to this analysis *R. afer* occurs almost exclusively on granitic plutonic rocks as are found from south of the Kuiseb at Gobabeb over most of its documented range, although within this area occasionally it has also been encountered on other rock types such as quartzites and marbles. *R. bradfieldi* usually associates with granitic substrates but has also been observed on marble (Bad Earth Site, Witpoortberge), quartzite (Gungochaob, and others) and other rock formations. Very coarse, crumbly granitic sites are avoided by all three *Rhoptropus* species. *R. barnardi* over its entire range shows hardly any habitat preference and will utilise practically any rock type except very coarse crystalline granite formations.

### 4 DISCUSSION

The occurrence of this genus is dependent on the presence of a rocky substrate. Rocky areas utilised by *Rhoptropus* are often partially or completely isolated from one another by sandy terrain thereby creating biological island populations. These areas could only have been colonised at a time when rocky “passages” existed which provided migration routes or when ancestral forms of these geckos were still less specialised and therefore more likely to cross sandy stretches. The lack
PLATE 11: Satellite photo of the central Namib Desert. The Kuiseb River bed forming the border between the sand-sea and the gravel plains, the eroded Swakop and Khan River Valleys and the dark rock formations which affect the distribution of Rhoptropus are clearly visible. (NASA-Photo: 65-2652, SCI-1195, Gemini V, taken by G. Cooper and C. P. Conrad 27.8.1965).
of fossil evidence and uncertainty of the geomorphologic history of the area make discussions of the development of the present distribution pattern only a speculation.

The evolutionary centre of the genus appears to lie further north in the pro-Namib area, where several other species of *Rhoptropus* occur (Haacke, in prep.). For this reason the present-day pattern of distribution in the central Namib may be viewed as the dispersal front of a southern expansion which has reached its potential limits. The limiting effect may be due to pure physical conditions, such as the absence of suitable substratum, limits of suitable ecological conditions or biological pressures such as the presence of competitive species. Another aspect may be the withdrawal by extermination from areas which appear to be suitable but are not occupied today ("island effect" MacArthur, 1972).

In the light of these concepts the southern range limits may be analysed as follows: Considering the entire range of *R. afer*, it is the most deserticous species since it is restricted to the most arid parts of the Namib along the coast from the Kuiseb River into southern Angola reaching its eastern range limits at about 80 to 100 km from the coast. This is the area most affected by the coastal fog. The eastern margin of this area reaches an area with a marked increase in rainfall approaching what is referred to as Pro-Namib (Coetzee, 1969) or Inner Namib (Logan, 1960). The southern limits of *R. afer* (Fig. 1) are obviously determined by the disappearance of available sheet-rock surfaces due to the northward expansion of the sand-sea. In this case the possibility actually exists that *R. afer's* range has been pushed back by sand encroachment if it is considered that for instance the mouth of the Kuiseb River formerly was at Sandvis and that the course of the Kuiseb used to run due west from Swartbank as indicated by subtropical water seepage (R.M. Huysen, geologist, C.S.I.R., pers. comm.). The record of *R. afer* from Lüderitz (HM4005, 3 specs, coll. 1911, Werner, 1915) must be regarded as unreliable. The collector, C. Manger, a naval engineer during colonial times, provided material from the Swakopmund as well as the Lüderitzbucht area and since neither the ardent collector F. Eberlanz, who lived there his whole life nor the present authors ever managed to secure any specimens from there, nor from any of the rock islands in between, such as Hottentot Bay, Saddle Hill and the Meoh-Conception Bay enclave, this record must be disregarded. Other doubtful records are those from Salem (Falk, 1914 in Mertens, 1971) on the Swakop River NE of Langer Heinrich Mountain since the description dates from a time when no other species had been described yet and it is highly likely that another species was actually involved. The specimens (SMF 22681–3) supposedly from Otjimbingwe also pose a problem, since they are from a considerable distance further east than the known and apparently acceptable eastern range limits of the species and the general ecology of that area is classified by Giess (1970) as semi-desert and savannah transition which is quite different to that of the coastal Namib. Although these specimens are correctly identified their origin is suspect and not acceptable, since no confirming material from the same locality has been obtained yet.

Although *R. afer* will utilise rocks such as those found at Gobabeb Site B and even ascend large outcrops such as Swartbank Mountain, Vogelfederberg and Carp Rock in the absence of the more specific boulder dwelling *R. braedfieldi*, it will yield in situations of sympathy by largely giving up the boulders and staying on the sheet-rock areas or gravel with flakes, to where *R. braedfieldi* is not inclined to follow. This latter situation can be demonstrated at various points of sympatric occurrence as at Bloodkoppie, 5 km NW of Schieferberg Pass, Gungochaob Mountain and even Bad Earth, Bakenkoppie and New Road Sites, where *R. braedfieldi* will be found in areas with vertical and overhanging surfaces while *R. afer* utilises the plains closer to the horizontal and preferably away from *R. braedfieldi* occupied boulders. It appears thus that the range of *R. afer* is not seriously affected by sympatric populations of congeneric rupicolous species, provided sheet-rock areas or gravel with flakes are available.

The distribution of the larger rupicolous *R. braedfieldi* in the central Namib shows some interesting patterns (Fig. 3) illustrating its dependence of well-developed rock formations with near vertical surfaces. Penetrations of the central Namib plains can be followed along geological formations and in some cases the southern range limits can be defined to within metres (cf. Plate 11).

In general terms the pattern may be described as ending in the Swakop River Valley with two southward extensions towards the Kuiseb Valley. This pattern correlates well with the dark formations which are clearly visible on satellite photos (Plate 11) which extend SW from the Langer Heinrich–Tinkas area and reach beyond the New Road Site and beyond Bad Earth Site to the tip of the Gungochaob Mountain. The other prong of the southward extension appears to extend along the lower altitudes of the escarpment along the eastern boundary of the park into the erosion valley of the Kuiseb. It extends down-stream along rocky outcrops of the banks to close to Gobabeb. An unsolved question at present is the presence of high density populations on Mirabib and the Mirabib Hills, since no clearly defined access routes have been identified to date and in fact this might be a trapped island population which has been cut off from the rest. It appears most likely that a connection existed towards the Kuiseb Valley from where these koppies might have been colonised.

As much as the presence of these geckos at one or other site might be particularly interesting, the absence from what appears to be perfectly good *Rhoptropus* biotopes can certainly cause difficulty explaining. A major problem of this kind is the absence from all the mountains, hills and boulder fields between Mirabib Hill and probably the Onanis mountain. This includes the Archadamab range N of Ganab, the Tumas, Amigab,
Heinrichsberg and all the rocky hills and boulder fields from Kriess-se-rus westwards and southwards. If *R. bradfieldi* does occur on them it has not been found yet, although the rupicolous skink *Mabuya sulcata* extends from Hebron, Bloodkopjie and Gr. Tinkas past Tumas to Kriess-se-rus. If it did occur there in the past it might have died out due to an inability to survive natural pressures.

From the observations so far it appears that *R. bradfieldi*’s range limits are not affected by sympatry or parapatry of congeneric species. The deciding factor appears to be the presence of suitable rock formations with available access routes. Some excellent examples may be demonstrated. At Witpoort a wide valley separates two high rocky ridges which are part of the dyke which extends south from the Huisb Mountains. On the N side *R. bradfieldi* is found on the top of the ridge with *R. afer* at the foot, while across the valley only *R. afer* is found. South-west of Bad Earth Site the presence can be followed to where the ridges disappear into a river-bank, while SW of the New Road Site a cliff on the bank of a dry wash is the terminal site. The rocky banks of the Kuiseb Valley as such act as a migration route and provide access to the cliffs in the vicinity of Gobabeb but not far enough to leave the river-bed and invade Gobabeb Site B no more than 2 km away.

*R. barnardi*, the smallest species, is extremely adaptable and occurs on a wide variety of rock types. In the
central Namib (Fig. 2) it only occurs in the areas referable as “Inner Namib” (Logan, 1960) beyond the main fog-belt, thereby more or less excluding contact with R. afer. In general it may be said that R. barnardi avoids boulders occupied by the large R. bradfieldi. It will utilise small outcrops which are avoided by the larger species and exist along often very low ridges, as near Zebra Pan. This species also penetrates into the central parts of the Namib-Naukluft Park along the same formations as discussed for R. bradfieldi which extend SW from Langer Heinrich Mountain. Although it may occur sympatrically on the same ridge with R. bradfieldi, it usually appears to avoid direct contact and possibly physical aggression from the larger species, as was observed between R. boulitini and R. taeniosticatus at Caraculo, Angola (Haacke) by inhabiting formations which are not utilised by R. bradfieldi.

A striking example is a site at (2257S, 1517E) where R. bradfieldi occurs exclusively on the large boulders of a small granite outcrop situated in between and in contact with quartzite hills of lower rocky formations on which apparently only R. barnardi occurs.

The pattern in the central Namib-Naukluft Park appears to be that R. barnardi occurs in the inner Namib only, penetrating southwards in two tongues, one southward
from Langer Heinrich-Tinkas to just N of Ubib, the other along the eastern border but staying W of the upper Kuiseb Valley, extending past Anigab to Bakenkop and to the Zebra Pan area. Avoiding the Kuiseb Valley as such it extends southwards along the escarpment to Solitaire. Although this species is small and easily overlooked it does not appear to have managed to colonise the hills and mountains from N of Mirribib to the Arechadamab range either. Since *R. barnardi* is a species with greater ecological plasticity than the other two, as it occurs from desert coast to the high rainfall area of the Otavi Mountains and the Angolan Huila Plateau, its minor role in the central Namib is rather surprising. It may well be affected by the presence of *R. bradfieldi* by which it is forced to utilise less suitable substrata. Although to the north of the Namib-Naukluft Park the three species under discussion show large areas of sympatry, within the present study area only one locality was documented where three species occur, namely Bloedkoppie. At this site spatial niche separation is complete with *R. bradfieldi* occupying the actual Bloedkoppie granite dome in high concentrations. *R. barnardi* has been found only on the schistose rocks of the Schieferberge SW of the main hill while *R. afer* occurs on sheet granite one to two kilometres to the SE of the main dome (Plate 10). Here each species has the pos-
sibility of avoiding direct competition with congenerics. Since at other sites all species are known to occur on the rock type apparently avoided here, the situation suggests that the occurrence of *Rhopropus* in the central Namib Desert is a combined result of habitat selection and competition.

5 ACKNOWLEDGEMENTS

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6 REFERENCES


7 GAZETTEER

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DISTRIBUTION OF RHOPTROPUS, CENTRAL NAMIB

Farm Greylingshof
Gross Tinkas
N end of Gumbochoab Mtn
5 end of Gumbochoab Mtn
2.5 km SE of Gumbochoab Mtn
3 km SE of Gumbochoab Mtn
5 km NW of Gumbochoab Mtn
Halagamkab
Hamilton Mtn
btwn Hebron-Onanis River
8 km SE of Hebron
8 km SW of Hebron
16 km SW of Hebron
Homeb
1 km SE of Homeb turn-off
Husab drift
Khan Mine
30 km W of Khan Fièrete
3 km SE of Klein Klipneus
5 km SE of Klein Klipneus
9 km E of Klein Klipneus
Klein Tinkas
Farm Komunah
Kuiseb Canyon and bridge
Kuiseb River nr Rooibank
Langer Heinrich
Mirabib
Mirabib Hills
Namib-Naukluft Park
Namib Station
"New Road Site"
1 km W of "New Road Site"
Nonidas Stn
Onanisberg
Ojimbingswe
Palmenhorst
Riet
Rooibank
2.5 km SE of Rooibank
Rooikop
Rössing Mtn
Rössing Mine

Farm Rostock
Schierferberg Pass
3 km NW of Schierferberg Pass
Schierlutz
Bwem Sphinx-Pforte
Swakopmund
5 km E of Swakopmund
10 km E of Swakopmund
13 km E of Swakopmund
16 km E of Swakopmund
42 km E of Swakopmund
30 km SE of Swakopmund
40 km SE of Swakopmund
38 km SE of Swakopmund on Khomas Hochland
Road
20 km N of Swakopmund
22 km N of Swakopmund
11 km from Swakopmund–Usakos
16 km from Swakopmund–Usakos
3 km E of Swakop River bridge
Swartbankberg
Swartbank, S of Kuiseb River
3.5 km E of Swartbank Vill.
8 km E of Swartbank Vill.
Swartkopjes
Ulub
3 km W of Ulub
5 km NNE of Ulub
11 km NNE of Ulub
16 km NNE of Ulub
10 km SE of Ulub
nr Vogelfelderberg
Von Strylk Mine
Walvis Bay area
80 km E of Walvis Bay on Gamsberg Rd
Welwitschia flats
Welwitschia Stn
N side of Witpoort
5 km SSW of Witpoortberg
Zebra Pan
2 km SSE of Zebra Pan
14 km SSE of Zebra Pan

2329S 3046E
2250S 1528E
2312S 1439E
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2748S 1506E
2253S 1504E
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2332S 1530E
2377S 1531E
veteran collector, Mr. Horst Bachran from Okahandja. By picking up and preserving a dead snake run over on the tarred road on farm Klein Okapuka between Windhoek and Okahandja he provided an indication of the existence of a third species namely the black file-snake (*M. nyassae*) within the limits of central South West Africa/Namibia. However, since the known range of this species lies in eastern tropical Africa ranging from Kenya and Burundi southwards to the Transvaal and Durban in Natal with the nearest documented record (FitzSimons, 1962) about 1 200 km distant in the NW Transvaal, the validity of this record is rather suspect.

Having been found on the main transport route through South West Africa, the possibility of it being an escapee from a vehicle after it had been introduced to the territory is a possibility which must be kept in mind. Nevertheless, it may just as well be a perfectly reliable authentic record which, however, needs confirmation by additional material. For this reason an appeal is made to the public to retain any specimens which might fit the general descriptions provided below and to donate them to a natural history research museum.

As a result of this remarkable find the new records accumulated since FitzSimons’ (1962) publication were checked for the whole of southern Africa. In addition to the records in the Transvaal Museum and the other institutions mentioned above the greatest number of new records are based on material in the collection of the National Museum of Zimbabwe. The latter collection actually has a record of *M. nyassae* from the Caprivi Strip as well as two from north-eastern Botswana which, although they represent range extensions on previous records, are within acceptable ecological areas.

At a time when the initial draft for this paper had been typed, a further specimen of *Mehelya nyassae* representing a further range extension, this time into the southern Kalahari of south-western Botswana, was presented to this museum by Mr. John Lougher, a geologist from Johannesburg. Although this specimen appears to bridge the gap between the accepted eastern range and the new record from central Namibia, it is also from an ecologically unusual area and therefore considered worthwhile reporting on both these specimens in detail.

The following abbreviations are used for institutional or collection prefixes to indicate the origin of new locality records. The records listed by FitzSimons (1962), although shown on the distribution maps, are not listed again in this publication. All loci are indicated by their relative quarter-degree grid reference.

| AMNH | = American Museum of Natural History, New York |
| KNP  | = Kruger National Park (Pienaar, 1978) |
| NMSR | = National Museums of Southern Rhodesia |
| QM   | = Queen Victoria Museum, Salisbury |
| SAM  | = South African Museum, Cape Town |
| SMF  | = Senckenberg Museum, Frankfurt on Main |
| SMW  | = State Museum, Windhoek |
| TM   | = Transvaal Museum, Pretoria |
| UM   | = Umtali Museum |

The NMSR, QM and UM collections, although quoted individually by Bradley are now joined in the biological section of the National Museum of Zimbabwe at Bulawayo.

3 SYSTEMATIC ACCOUNT

3.1 Generic description and key

Head very distinct from neck and flattened above, snout strongly depressed and with a broadly rounded edge, eye small to medium with a vertically elliptic pupil, nostrils noticeably large.

Body subtriangular in sections with strongly keeled, rough but widely spaced body scales, exposing the skin in between. The mid-dorsal scale row consists of enlarged scales with two parallel keels which form the middle “edge of the file”. The ventrals show some extent of lateral keeling, while the paired subcaudals of the moderately long tail are smooth. All the known species appear to be oviparous.

Key to the *Mehelya* species in southern Africa (after FitzSimons, 1962)

1. a) Scales in 19 rows at mid-body; 3 upper labials enter the orbit; ventrals over 250 ........ *vernayi*
   b) Scales in 15, rarely 17, rows at mid-body; 2 upper labials enter the orbit; ventrals less than 230 ....................................................... 2

2. a) Secondary keels (on either side of main keel) on body scales all strongly developed; ventrals 195 –224; subcaudals 44–58; a pale vertebral stripe present .................... *capensis capensis*
   b) Secondary keels (on either side of main keel) reduced to two short ones near the tip of each body scale; ventrals 165–184; subcaudals 51–77; no pale vertebral stripe present ........... *nyassae*

2 MATERIAL AND METHODS

All published records such as Mertens (1955, 1971), Pienaar (1978) and the type of *M. vernayi* (Bogert, 1940), as well as the records in the National Museum of Zimbabwe as supplied by Dr. D. G. Bradley and the new acquisition of the Alexander Koenig Museum, Bonn (P. van der Elzden, pers. comm.) were accepted as correct. The material in the Transvaal Museum, Pretoria; the State Museum, Windhoek, and the South African Museum, was personally examined.
3.2 *Mehelya capensis capensis* (A. Smith, 1847)

Cape file-snake  
Kaapse vylslang  
Kapfellennatter  
(Plate 1)

This is the largest of the species and over 1.5 m in length may be reached although average sized adults are usually about 1 m in length. The overall appearance is usually a slate-grey to purplish-brown above with a characteristic pale, dirty to yellowish stripe running down the middle of the back. In prime condition or when gorged with food the body scales become well separated exposing the pinkish to mauve skin. Underparts light although the belly-scales may have dark leading edges.

Dorsal scale rows 15 (rarely 17) at mid-body; ventrals 195–224 (less than 209 in males, more than 206 in females); anal entire; subcaudals 49–58 in males and 44–54 in females. The basic scale counts of the Namibian specimens fall well into these range limits mentioned by FitzSimons (1962).

Although this is a very docile snake, even when first handled it is an enthusiastic cannibal which appears to be practically immune to envenomation by poisonous snakes since it will tackle highly poisonous species, which no doubt will retaliate by biting their attacker. Plenaar (1978:139) reports the case of a very large specimen (1.58 m) killed near to the Kruger Park, which contained an 1 068 mm olive sand-snake (*Pseudophilis phillipsii*), a python (*Python sebae*) of 825 mm, a brown water-snake (*Lycodon arfutus*) of 531 mm and a Mozambique spitting cobra (*Naja mossambica*) of 481 mm.

Range: From Tanzania southwards into southern Natal and through Zambia and Zimbabwe into the northern and north-eastern Namibia. An unconfirmed sight record indicates an extension into the central parts of the country.

Records from South West Africa/Namibia (Fig. 1):  

Unconfirmed sight records:

Farm Otjozondi, No. 36 Karibib distr. (2216Aa), April 1966; Tsumeb (1917Ba), 1966; Tsumeb (1917Ba),
Alexander König Museum (no number) & Farm Omandumba-West (2115 Da), P. van der Elzden, 6.4.1979 (P. v.d. Elzden, pers. comm.).
Swakopmund Museum (no number) & Farm Ojitambi (1915 Cc), C. A. Schlettwein, 1962 (Finkeldey, 1963).
AMNH 51795 (Type) & Hana, Benguela dist., Angola, coll. A. S. Vernay, H. Lang and R. Boulton, 13.5.1925 (Bogert, 1940).

Unconfirmed sight record:
Farm Otjozondjupa, 36 Karibib dist., April 1966, H. Finkeldey (pers. comm.).

Remarks:
This species is sympatric with *M. capensis* in the Otavi Mountains and from there southwards in the mountainous areas as far as the Swakop River valley from where both species have been reported but not been confirmed by voucher specimens.

TM 16032 contains a half-grown *Bufo g. garmani* Meck.

TM 45100 was found run over on the tar road, but still alive at about 09h00 indicating at least partial diurnal activity, while van der Elzden caught his specimen at night.

TM 48614 was found in the Aigamas Cave, famous for its white cave-barbels (*Clarias cavernicola* Trewavas). It had apparently fallen into the water, was unable to find a way out and was found wrapped around a knot at the end of a rope suspended into the water where it must have spent some time since it was so weak that it died during the following night after capture.

3.4 *Mehelya nyassae* (Günther, 1888)

Black file-snake
Swart vleklang
Schwarze Feilennatter
(Plate 3)

Material examined:
Size: 641 (510+131) mm, 180 V, 64/64 Sc, anal single, dorsal scale rows 15–15–15, 2 nasals, 6 and 7 upper and 6 and 7 lower labials, single loreals, pre-, post- and supra-ocular scales, pupil sub-circular. Dorsum (preserved) purplish-black to dark-brown interstitial skin pale but does not show normally, ventrum dark with paler edges to each ventral scale.

Size: 453 (359+94) mm, 173 V, 65/65 Sc, anal single, dorsal scale rows 15–15–15, 7 upper and 8 lower labial scales and 2 nasals on either side, pupil sub-circular.

PLATE 3: Black file-snake *Mehelya nyassae* (Günther) TM 54903 Bohelobatho Pan, Botswana.
Dorsum (alive and preserved) faintly purplish-black on head and neck and distal part of body and tail with the main parts of the body being black. Ventrum white from chin to tail, first row of dorsals on either side of body white with a few dark dorsals extending into the white lateral scale rows as scattered individual or small groups of scales.

The stomach contents of TM 52734 included the remains of the subfossorial skink *Lygosoma sundavalli*, beetle elytra which probably had been eaten by the skink and the tiny piece of unidentified snake skin.

TM 54093 had an empty digestive tract and was found under camping gear on red Kalahari sand.

Other material examined (22 specimens in Transvaal Museum):
Variation (FitzSimons, 1962 variation in brackets) V = 165–184 (167–181), Sc 51–65 (55–77), anal single (1), dorsal scale rows 15–15–15 (15), nasals 2 (2), upper labials usually 7 (n=34) occasionally 6 (n=4) (7 rarely 6), lower labials 8 (n=32) occasionally 7 (n=3) (usually 8), loreals single and horizontally elongate, in touch with posterior nasals and pre-ocular, in TM 42981 (Farm Cavan) loreals are fused with the frontonasals on both sides while in TM 53938 (nr. Nelaprui) the loreals are shortened to such an extent that the frontonasal and the 2nd upper labials are in touch, the usually single postoculars are divided into two in eight cases while only a single case of a divided preocular was observed.

The dorsal colouration is consistently dark purplish to brownish-black with occasional specimens showing white lateral scale rows with irregular intrusions of black scales. The ventrum may be dusky to white with any variation in between.

Range: An eastern form ranging from Kenya and Burundi southwards into northern Natal. Until now not recorded from west of 24°E for which reason these new apparent range extensions need confirmation.

The following is a list of localities in addition to those listed above and those published by FitzSimons (1962), based on specimens in the collections of the Transvaal Museum (TM), Transvaal Department of Nature Conservation and the National Museum of Zimbabwe (UM, QM, NMSR) and those published for the Kruger National Park.

Farm: Canterbury 2228Db, (Tvl. Dept. Nat. Cons.); farm: Cavan 2229Db, (TM); Chiredzi 2131Ba, Chizarika Nat. Park 1727Db, Christmas Pass 1832Dc, (UM); Fatima Miss. 1827C, (NMSR); Fishan, Gonarezhou Nat. Park 2131Ac, Hippo Valley, Chiredzi 2131Ba, Kariba 1628Db, 15 km WSW of Katima Mbulu 1724Ca, Khumaga on Boteti Riv. 2024Bc, (UM); farm: Klein Okapuka 2217Ac, Lake Sibaya 2732Bc, Lake Tesa 2832Ac, (TM); Malelane 2531Bc, (KNP); Manzengwenya for. str. 2732Bd, (TM); nr. Mathlakaza Pan 2231Cb, (KNP); Mdumalane 2732Bc, (TM); Mooiplaas Experimental Plots 2331Cb, (KNP); Mtubatuba 2832Ac, (TM); S end Nwatimire Rd. 2531Bb, (KNP); Nyamandlovu Sawmills 1928Cd, Old Umtali 1832Dc, 145 km SW of Panda-Ma-Tenga 1925Dc, (UM); Plot Rietgat, nr. Pretoria 2528Ad, ±15 km E of Sabie 2530Bb, (TM); Tshameni 2531Dd, (TM, UM); Ubombo 2732Ca, (TM); Umtali 1832Dc, (UM); Zanzibar Border Post 2228Cb, (TM).

4 SUMMARY

The purpose of this publication is to draw attention to the new records of file-snakes from Namibia, from where the presence of a third species is now recorded. At the same time all new published and unpublished distribution records accumulated since FitzSimons’ account in 1962 are being documented. The southerly range extension of *M. nyassa* from southern Mozambique to Durban is, ecologically speaking, not very surprising. However, the two new most westerly records, which extend the range into the more xeric areas of western Botswana and central Namibia are remarkable and require confirmation. Of *M. vernayi* five further specimens have been added to the five previously known records. Although only one further specimen of *M. c. capensis* was added to those recorded by Finkelday (1962) and Mertens (1971), an unconfirmed sight record indicates that its range extends into central Namibia.

5 ACKNOWLEDGEMENTS

I am indebted to Dr. D. G. Broadley, National Museums of Zimbabwe for putting the museum records at my disposal, and to Mr. N. Jacobsen, Transvaal Department of Nature Conservation, Mr. C. G. Coetzee and Mr. M. Penrith, State Museum, Windhoek, and Dr. G. McLaughlan, South African Museum for providing loan material, Mr. P. van der Elzen for putting at my disposal information of his *Mehelya* specimen, Mr. H. Finkelday, Windhoek, who provided me with additional information from his records on these snakes and in particular Messrs. Horst Bachran and John Lougher who found these new and interesting records and made them available for research purposes. Miss Lomi Wessels assisted with technical aspects and Mrs. E. du Plouy typed the manuscript. I am grateful to the Director of Nature Conservation, Mr. B. de la Bat and his staff, who over many years allowed me to work in South West Africa/Namibia.

6 REFERENCES

BOGERT, C. M.
FIGURE 2: Distribution of the Angola file-snake *Mehelya vernayi* (●) and the black file-snake *Mehelya nyassae* (▲) (open symbol = sight records).

FITZSIMONS, V. F. M.

FINXELDEY, H.

MERTENS, R.

MERTENS, R.

PIENAAR, U. de V.
The incidence of veld-fire in the Etosha National Park, 1970—1979*

by
W. R. Siegfried
FitzPatrick Institute
University of Cape Town
Rondebosch 7700

Received: 22 April 1980

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1 INTRODUCTION

Among many arguments in favour of the creation of nature reserves is the one that such areas are needed for scientific study of natural phenomena, undisturbed or influenced minimally by man. Veld-fire is a common phenomenon in ecosystems in southern Africa, with many, if not most, being caused by man. Even in nature reserves, fire occurs either accidentally or is used deliberately in practical management. Generally, however, and more particularly for the drier regions of southern Africa, there is a dearth of scientific information substantiating burning regimes applied in nature reserves (Trollope, in press).

It can be argued that optimal practices for the management of nature reserves are often those which most closely imitate natural processes. Hence, burning regimes might be applied advantageously if they are modelled on the natural incidence of fire. But what is the natural incidence of fire? Very little information is available on this subject in southern Africa, primarily because there are few, if any, areas that are entirely free of man's Pyrrhic activities.

This paper documents the temporal and spatial incidence of veld-fire in the Etosha National Park, SWA/Namibia, from 1970 to 1979. The park is unusual among large nature reserves in southern Africa in that it has experienced relatively few fires, caused either accidentally or deliberately by man, at least during the last 25 years or so. Indeed, since 1970, official policy in Etosha has specifically forbidden the use of fire as a tool in management practices. However, the policy makes provision for combating and restricting fires when they do occur. To this end, the park is partitioned into eight sections by fire-breaks and roads. Detailed descriptions of the physiography and vegetation of the Etosha National Park are given by Le Roux (1977).

2 THE DATA BASE

Particulars of all 56 veld-fires in Etosha from September 1970 to September 1979 were recorded on prescribed forms (Appendix 1), under the supervision of the Prin-

ABSTRACT

This paper documents the temporal and spatial incidence of veld-fire in the Etosha National Park from 1970—1979. The data analysed indicate that most veld-fires are caused by lightning and occur chiefly from October—December. There were three times as many naturally caused fires in 1975—1978 as in the preceding five-year period. Virtually all vegetated areas of the park burned at least once during the period 1970—1979. These and other findings are discussed in relation to climate and management practices.

*This paper constitutes part of the commemoration of the 21st anniversary of the establishment of the Percy FitzPatrick Institute of African Ornithology.
principal Nature Conservator at Etosha. The information in the forms was analysed by computer at the University of Cape Town, and is stored on magnetic tape in the office of the Director of Nature Conservation, SWA/Namibia.

3 RESULTS

At least 54%, and more probably 73%, of all veld-fires in Etosha were caused by lightning (Table 1). Thus, relatively few fires were due to human activities, including one caused by tourists visiting the park. 78% of all fires occurred from September–December (Table 2), with most fires occurring during the commencement of the seasonal summer rainfall (Table 3) which normally peaks three months later (Fig. 1). On average, about four fires occurred each year as a result of lightning (Table 2), but there were three times as many naturally-caused fires from 1975–79 as in the preceding five-year period (Table 4). The elevated incidence of fire started in the middle of the decade, with a record number of fires in 1975 following a year (1974) during which Etosha received almost double its normal annual rainfall (Table 4). Rainfall in 1976 was again well above normal.

The spatial incidence of veld-fire in Etosha was such that virtually all vegetated areas of the park burned at least once from 1970–79 (Fig. 2). About 50% of all fires spread individually over less than 1 000 ha, but five fires each covered more than 100 000 ha (Table 3). A statistically significant positive correlation was found between the area burnt and the number of man-hours spent combating the fire (Fig. 3). Only four fires covered more than 5 000 ha from 1970–74, whereas 17 fires each did so in the subsequent five-year period. The total areas burnt from 1970–74 and 1975–79 amounted to 244 100 ha and 1 004 630 ha respectively. Mean area burnt per fire from 1970–74 was 22 122 ± 39 938 ha (N=9) and 21 375 ± 39 808 ha (N=47) in 1975–79. There is no significant difference in the extent of individual fires between these two periods (t=0.05, P>0.05, DF=54). Most veld-fires occurred, but did not necessarily start, in woodland vegetation (Table 6). Although a statistically significant difference ($x^2 = 9.6$, P<0.01) between the extent of fires in each of the three main composite vegetation types of the park is indicated, in actual fact naturally ignited fire occurred with equal frequency (P<0.05) in all three vegetation types, and there was no significant difference ($x^2=1.4$, P>0.05) between the area of the fire in each vegetation type when corrected for difference in the vegetation area (Fig. 4).

4 DISCUSSION

Lightning strikes appear to be a common ignition source for veld-fires in Etosha. The nearest station recording lightning flashes is at Oshakati, some 100 km north of Etosha, where a mean lightning-flash density of 2.2 km$^2$ yr$^{-1}$ was obtained over the period July 1975 to June 1978. Comparable figures in the South African high-veld region are three to four times higher (Kroninger, 1978).

In Etosha seasons of well-above normal rainfall, and therefore increased vegetation, are followed apparently some six months later by the onset of a relatively high frequency of veld-fires. Unfortunately, the data available are too scant to predict any definitive long-term pattern concerning the temporal distribution of abnormally high rainfall seasons in Etosha, but in 44 years (1934–1978) of rainfall records at Okaukuejo there are four periods in which annual rainfall exceeded the norm. This suggests an 11-year cycle. According to long-standing residents in the area, super-normal wet seasons occur with a frequency of 8–12 years. If this indeed is the case, then probably all vegetated parts of the Etosha National Park would be burnt at least once every 10 years, as a result of ignition by lightning alone.

The veld-fire season in Etosha appears to be relatively long, as is the case in the Australian arid savanna (Lacey, Walker and Noble, in press). However, the duration of an “average” fire season may be largely a reflection of between season differences influenced partially by annual variation in the onset of the lightning season. In other words, the individual fire seasons may be shorter, but the data available are too few for testing this suggestion. In any event, annual variation in the onset of the fire season can be expected to influence the response of the vegetation to fire.

While it can be argued that the southern African savanna evolved as a dynamic mosaic of vegetation under the influence of a multispecies complex of herbivores interacting with the effects of fire, caused by natural phenomena (primarily lightning) and a relatively sparse human population, it is remarkable how little research has been carried out to establish the state of “natural” fire regimes. Instead, studies have concentrated on short-term effects, primarily on forage plants of domestic livestock, or man-made fires in savanna vegetation (Trollope, in press).

Since veld-fire is a long-standing factor in the evolution of southern African savanna ecosystems, it follows that their biota are adapted selectively to the pressures of burning regimes. Therefore, a cornerstone of a policy for management of nature reserves in these ecosystems should be the acceptance of naturally caused fires which are controlled and, where necessary, supplemented and complemented by artificial burning. A primary objective of fire-management strategy for a nature reserve should be an imitation of the local natural fire regime, coupled with the regulation of herbivore populations, adjusted in accordance with the size and shape of the reserve and its edaphic features.

Some of the information in this paper could be useful as a first step towards a predictive model of the natural fire
regime in arid savanna vegetation in northern SWA/Namibia. Such a model can be expected to assist in the formulation of a clearly defined role for fire in the management of the Etosha National Park. The model depends essentially on information on the temporal and spatial incidence of fire-ignition sources, and the production and accumulation of combustible herbage fuel. These parameters can be measured and their dynamics monitored. Fuel production is determined mainly by climate, especially rainfall, and edaphic features in relation to fire frequency. The quality and the rate of accumulation of herbage fuel are influenced by herbivores and decomposers.

5 ACKNOWLEDGEMENTS

I am grateful to the Director of Nature Conservation, SWA/Namibia, for kindly placing records covering the incidence of veld-fire at the Etosha National Park at my disposal. I am indebted to H. H. Berry and T. M. Crowe for their advice and grateful to S. R. Williamson and I. P. Newton for practical assistance.

6 REFERENCES

KRÖNINGER, H.

LE ROUX, C. J. G.

LACEY, C. J., WALKER, J., and NOBLE, I. R.

TROLLOPE, W. S. W.


FIGURE 2: Number of veld-fires (caused either naturally or by man) occurring in at least 10% of each 100 km² section of Etosha National Park from September 1970 – September 1979. The dashed lines embrace saline pans.
Report on veld-fire

Place where fire occurred

Time and date of first report

Time and date of report to head office

Time and date extinguished

Area devastated

Number and type of machines used

Number and type of vehicles used

Number of supervisors involved in combating fire

Total man-hours

Number of labourers involved in combating fire

Total man-hours

Names of officials on 24-hour patrol

Last precipitation in area of fire. Light/Heavy

Type of vegetation destroyed

Fire first sighted at _________________________________ am

_____________________________ _____________________ pm

Date

Direction of wind _______________________________ Estimated wind speed

Possible cause of fire

Fire reported at

To whom reported

First help arrived at

Fire extinguished at _________________________________ Date

Recommendations:

Signature:

NB. A map showing the area burnt must be attached to this form.

<table>
<thead>
<tr>
<th>Origin</th>
<th>Number of fires</th>
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</thead>
<tbody>
<tr>
<td>Lightning</td>
<td>30</td>
</tr>
<tr>
<td>Unknown but probably lightning</td>
<td>11</td>
</tr>
<tr>
<td>Artificial or from outside park</td>
<td>15</td>
</tr>
<tr>
<td><strong>Result</strong></td>
<td></td>
</tr>
<tr>
<td>Halted by fire-breaks and roads</td>
<td>31</td>
</tr>
<tr>
<td>Halted by other means</td>
<td>23</td>
</tr>
</tbody>
</table>

TABLE 2: Number of veld-fires occurring bi-monthly and caused either by lightning or human agencies in Etosha, September 1970—September 1979.

<table>
<thead>
<tr>
<th></th>
<th>Lightning</th>
<th>Artificial</th>
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</thead>
<tbody>
<tr>
<td>Jan.—Feb.</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>March—April</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>May—June</td>
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<td>1</td>
</tr>
<tr>
<td>July—August</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>Sept.—Oct.</td>
<td>15</td>
<td>9</td>
</tr>
<tr>
<td>Nov.—Dec.</td>
<td>19</td>
<td>1</td>
</tr>
</tbody>
</table>


<table>
<thead>
<tr>
<th>Rain</th>
<th>Lightning</th>
<th>Artificial</th>
</tr>
</thead>
<tbody>
<tr>
<td>Same time as fire</td>
<td>16</td>
<td>0</td>
</tr>
<tr>
<td>&lt;1 week</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>&lt;1 month, &gt;1 week</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>&lt;3 months, &gt;1 month</td>
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<td>0</td>
</tr>
<tr>
<td>&lt;5 months, &gt;3 months</td>
<td>1</td>
<td>6</td>
</tr>
<tr>
<td>&lt;7 months, &gt;5 months</td>
<td>5</td>
<td>4</td>
</tr>
<tr>
<td>&lt;10 months, &gt;7 months</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>No data available</td>
<td>8</td>
<td>2</td>
</tr>
</tbody>
</table>

FIGURE 3: The calculated relationship (r=0.85 P<0.001) between the area burnt and number of man-hours spent combating the fire. Based on all veld-fires in the Etosha National Park from September 1970 — September 1979.

FIGURE 4: Map of the three major composite vegetation types in the Etosha National Park. The unshaded areas are saline pans.
TABLE 4: Number of veld-fires each year in relation to rainfall in Etosha, September 1970 — September 1979. Normal annual rainfall at Namutoni is 433 mm and 419 mm at Okaukuejo (data from S.A. Weather Bureau).

<table>
<thead>
<tr>
<th>Year</th>
<th>Lightning</th>
<th>Artificial</th>
<th>Actual (mm)</th>
<th>Difference between actual and normal (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1969</td>
<td>—</td>
<td>—</td>
<td>481a</td>
<td>+48</td>
</tr>
<tr>
<td>1970</td>
<td>1</td>
<td>0</td>
<td>505a</td>
<td>+72</td>
</tr>
<tr>
<td>1971</td>
<td>3</td>
<td>0</td>
<td>400a</td>
<td>—33</td>
</tr>
<tr>
<td>1972</td>
<td>3</td>
<td>0</td>
<td>457a</td>
<td>+24</td>
</tr>
<tr>
<td>1973</td>
<td>0</td>
<td>0</td>
<td>332a</td>
<td>—101</td>
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<td>1974</td>
<td>2</td>
<td>0</td>
<td>766a</td>
<td>0 +333</td>
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<td>1975</td>
<td>8</td>
<td>8</td>
<td>418a</td>
<td>—16</td>
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<td>1976</td>
<td>9</td>
<td>2</td>
<td>633b</td>
<td>+213</td>
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<td>1977</td>
<td>6</td>
<td>2</td>
<td>336b</td>
<td>—83</td>
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<td>1978</td>
<td>3</td>
<td>1</td>
<td>419b</td>
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</tr>
<tr>
<td>1979</td>
<td>6</td>
<td>2</td>
<td>447b</td>
<td>+28</td>
</tr>
</tbody>
</table>

a Rainfall at Namutoni
b Rainfall at Okaukuejo


<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1—499</td>
<td>5</td>
<td>11</td>
<td>0</td>
<td>7</td>
</tr>
<tr>
<td>500—4999</td>
<td>2</td>
<td>8</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>5000—24999</td>
<td>2</td>
<td>4</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>25000—99999</td>
<td>1</td>
<td>3</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>&gt;100000</td>
<td>1</td>
<td>3</td>
<td>0</td>
<td>1</td>
</tr>
</tbody>
</table>

TABLE 6: Number and extent of veld-fires in the three main composite vegetation types in Etosha, September 1970 — September 1979. Figures in parentheses are the numbers of fires which occurred in more than one vegetation type.

<table>
<thead>
<tr>
<th>Vegetation type and area</th>
<th>Number of fires (ha x 10^4)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Lightning</td>
</tr>
<tr>
<td>Woodland</td>
<td>40.7</td>
</tr>
<tr>
<td>Grassland</td>
<td>12.0</td>
</tr>
<tr>
<td>Scrub</td>
<td>24.4</td>
</tr>
</tbody>
</table>

* given as percentage of the total area (2 227 000 ha) of Etosha including saline pans which account for 23% of the park.
The distribution and ecology of the brown hyaena *Hyaena brunnea* and spotted hyaena *Crocuta crocuta* in the central Namib Desert

by

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and
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Received: 28 July 1980

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1 INTRODUCTION

The niche occupied by the hyaenas as scavengers and/or predators has for the past two decades been the subject of much research (Elff, 1964, 1975; Kruuk, 1972; Skinner, 1976; Bearder, 1977; Mills, 1978; Skinner & Ilani, 1980; Tilson, von Biottnitz & Henschel, 1980). This has resulted in the hypothesis that a result of differing social systems the brown hyena, *Hyaena brunnea* and striped hyaena, *Hyaena hyaena* are effective scavengers but ineffective hunters (Kruuk, 1976; Mills, 1978a; Skinner, 1976; Skinner & Ilani, 1980); whereas the spotted hyaena *Crocuta crocuta* is an efficient hunter, particularly under circumstances such as those pertaining for example in the Ngorogoro crater (Kruuk, 1970). More recently Tilson and his co-workers (Henschel, Tilson & von Biottnitz, 1979; Tilson *et al* 1980) have examined the diet of spotted hyaenas in the Namib Desert. During surveys conducted in January 1976 and 1979 into the status of the brown hyaena in the Namib Desert information was collected on their distribution, diet and habits and compared with those of spotted hyaenas. The object of the present paper is to present this information which may lead to a better understanding of the degree of separation between the two species.

2 AREA SURVEYED AND METHODS

During 1976 a survey was made of the area from the Kuiseb River to Cape Cross and in 1979 from Wolf’s Bay — Elizabeth Bay (26°52’S, 15°10’E) to Koichab Pan (26°19’S, 15°36’E). Additional information was provided by the Division of Sea Fisheries and Consolidated Diamond Mines for the coastal area between the Orange River and Wolf’s Bay and for the dunes between Koichab Pan and Sossus Vlei by a member of the Department of Entomology, University of Pretoria. The presence of hyaenas was established by sightings, presence of latrines or occasionally faeces and other evidence such as fresh spoor and carcass remains. The diet of the two species was established through faecal analysis following Keogh (1979). Both species

ABSTRACT

*Hyaena brunnea* are found mainly along the coast while *Crocuta crocuta* range further inland being associated with *Oryx gazella* and freshwater. Differences in latrines are described and the seats of *H. brunnea* are significantly lighter than those of *Crocuta* (45.8 cf. 160.9; P<0.001). Analysis of identifiable prey remains showed that in *H. brunnea* taxa *Aethococcus pulillus* hair predominated (75%) cf. *Crocuta* seats in which *Oryx gazella* hair (94.5%) predominated. Reasons for the geographical separation of the species are discussed.
make distinctive faecal pellets which are easily identified (Plate 1). A total of 68 brown hyaena scats from Wolf’s Bay and 36 spotted hyaena scats from the Kolnabab Pan area was collected. In addition to analysis of prey remains the scats were analysed for calcium content as described by Nel (1967). This test was followed up through the analysis of the calcium content of the faeces of two captive brown hyaenas fed over seven days with a diet of known calcium content. Further observations were made on latrines of the two species and on prey remains left in the veld.

3 RESULTS

The distribution of both species throughout the Namib Desert is illustrated in Fig. 1. It is apparent that there is little overlap between the species; brown hyaenas being largely confined to the extreme south and coastal regions whereas spotted hyaenas are found further inland where there are more naturally protected habitats. Brown hyaenas are closely associated with seal (Arctocephalus pusillus) colonies at Black Rock and Wolf’s Bay which are separated by some 45 km. There is little reason to doubt that a similar association exists for all the seal colonies along this coast particularly as brown hyaena spoor were also noted at Cape Cross, but there were probably only one or two individuals in attendance whereas at Wolf’s Bay there was a large occupied warren in addition to visiting hyaenas from further afield. At Wolf’s Bay we also had to vacate the area before sunset as a security measure so we were unable to make any attempt at counting hyaenas; in the municipal coastal belt surrounding Lüderitz (26°39’S, 15°9’E) following evidence of hyaena spoor on the beach and reports of three hyaenas seen one night near a beach cottage and of one hyaena later being shot near the jail, we did make lengthy nocturnal searches. On one occasion we observed a brown hyaena on the beach through a Scotos I night telescope; this individual was loping along being worried by three jackals which seemed to be having a game with it. Some three kilometres further along the beach we observed another brown hyaena.

It would appear that in this area, at least, brown hyaenas are beachcombers and the name “strandjut” originally accorded them by the first settlers in the Cape Province truly applies. The association with the seal colonies is an obvious one for any scavenger; moreover, there is a high density of jackals in the vicinity of such colonies as well as a few large feral dogs, all of which are at least scavenging on the large percentage of seal pups which die apparently from drowning when falling into the sea at too young an age. In addition, a large number of seal bulls are culled annually and it is well known that boat fishermen on the west coast destroy seals caught in the trawl nets. There is also the meat from pups culled for pelt production. A vast quantity of seal meat is therefore available for exploitation which is a big attraction for the brown hyaenas, large numbers of jackals and occasionally feral dogs.
FIGURE 1: Distribution of hyaenas in South West Africa. *Hyaena brunnea* ■ specimen ▼ sight record ▴ tracks *Crocuta crocuta.*
There are several distinguishing features, apart from morphological and size differences, between *H. brunnea* and *Crocuta*. First there are small but important differences in size and shape of spoor. These are illustrated in Fig. 2.

Both species utilise latrines, but while those of *H. brunnea* are small, clearly demarcated (Plate 2) and possibly only used by single individuals, those of *Crocuta* cover an area of the order of 100 m² (n=3) over which faecal stools are deposited by members of a clan (or individuals) and there is no clear demarcated boundary. Moreover, the number of stools per latrine is far less for *H. brunnea* 5.0 (n=10) cf. 12.4 (n=5) than for *Crocuta*.

There is also a significant difference (p<0.001) in the size of individual stools (Plate 1) between the two species, those of *H. brunnea* having an individual mass of 45.78 ± 4.15 (n=33) cf. 160.92 ± 21.65 g (n=36) for *Crocuta*. Part of the reason for the lighter mass of *H. brunnea* scats was the large percentage of hair contained in them whereas *Crocuta* scats contained much less hair. This could be related to possible behavioural and/or digestive differences; for example, a feature of *Crocuta* is that they frequently regurgitate oral casts (Bearder, 1977) whereas oral casts from *H. brunnea* have only rarely been found.

The analysis of the identifiable contents of the scats from *H. brunnea* and *Crocuta* is presented in Table 1. It is apparent that, despite the availability of an unlimited supply of dead (and living?) scats from the seal colony (Plate 3) at Wolf's Bay *H. brunnea* has a more catholic diet than *Crocuta*. This is, however, not reflected in the calcium content of the scats which is of the same order for both species (Table 1).
PLATE 2: Typical latrines of *H. brunnea* showing the hollowed out area in the centre (2 plates).
would indicate the possibility of their being a sought-after prey item of *H. brunea*.

In contrast to the more catholic diet of *H. brunea*, *Crocuta* fed almost exclusively on gemsbok in the Namib. These results are in close agreement with the analyses of Tilson *et al.* (1980) and, as pointed out previously, the situation at Koichab Pan is similar to that in the vicinity of Natab in the Kuiseb River area but with fewer ungulates. If, as Tilson *et al.* (1980) and the available data suggest, *Crocuta* are catching gemsbok, then there must be some weakness *Crocuta* are exploiting as the absence of springbok hair or ostrich feathers in our results and Tilson’s value of 0.8 and 2.1 per cent for springbok and ostriches respectively means that these species are not procurable by *Crocuta*. Their absence from the diet and the fact that gemsbok remains were also found largely on a sandy substrate indicates that the weaker or maimed individuals may be being brought down here; again, the few observations we made are in close agreement with those of Tilson *et al.* (1980) for Natab. No significant quantities of vegetable items were found in the scats from Koichab Pan, but our visit was preceded by two very dry seasons, so this may also reflect availability; even more so for the more arid Wolf’s Bay where herbage was largely absent.

It is interesting that *Crocuta* also sampled jackals and rodents, in the latter case *Tatera*, while *Desmodillus* and *Gerbillurus* which are present at Koichab Pan (Skinner, Lindeque, Van Aarde and Dieckmann, 1980) did not feature at all in their diet.

5 CONCLUSIONS

It has been established that the brown hyaena, although a rare and endangered species, is more widespread than was at first thought (Joubert & Mostert, 1975), but we still have no idea what numbers occur in the area or details of their habits or range. In addition the relationship with other carnivores particularly scavenging or preying on seals is unique as is the ability of a land carnivore to subsist in such an arid environment. Despite security precautions there is an urgent need for: (1) a helicopter survey using night flares or at first dawn along the entire coastal strip to count brown hyaenas and inland from the Kuiseb River southwards and north of Swakopmund to ascertain distribution and numbers of both species; (2) Wolf’s Bay presents an ideal situation for a study of hyaena ecology, ethology and physiology and an exciting and unique project could be undertaken on this rare carnivore; (3) failing these steps which should enjoy the highest priority, further surveys of an extensive a nature as circumstances will allow, should be undertaken to enhance our knowledge of this important species to enable its continued conservation; (4) the municipal area surrounding Lüderitz should be declared a Nature Reserve under the jurisdiction of the SWA Directorate of Nature Conservation and in which all species including the carnivores are protected.

6 ACKNOWLEDGEMENTS

We would like to thank the following for their encouragement of and interest in this project: the Director and staff of the Directorate of Nature Conservation of South West Africa, who also provided facilities in areas under their jurisdiction, particularly Dr. E. Joubert and Mr. R. Stirly; the Director and staff of Consolidated Diamond Mines (Oranjemund), particularly the General Manager, Mr. J. O. Richards, and Security Superintendent Mr. Du Toit who gave permission to work in areas under their jurisdiction; Mr. Van Dyk, Chief Inspector of Mines SWA, the Director Dr. M. Seeley and the staff of the Desert Ecological Research Unit; Dr. H. Koepl, Mr. and Mrs. R. C. Dieckmann and Messrs. E. S. Lane, A. F. Seabrook, C. P. and D. C. Skinner, Dr. C. Scholtz (Dept. of Entomology) and the late Mr. R. L. Cooper for assistance.

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STUART, C. T.

STUART, C. T.

TILSON, R., VON BLOTTNITZ, F. & HENSCHEL, J.
Abnormal levels of disease and predation as limiting factors for wildebeest in the Etosha National Park

by

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1 INTRODUCTION

An aim of the investigation into the ecology of the blue wildebeest Connochaetes taurinus in the Etosha National Park (Berry, 1980) was to establish whether disease and parasites had contributed to the sharp decline in wildebeest numbers in Etosha. Veterinary aspects of wildlife management have sometimes been regarded as a specialist field by ecologists and are consequently viewed in isolation when identifying the factors which may limit or reduce populations. Thus, whilst some investigations of wildebeest reproduction and population ecology have excluded the disease/parasite factor (Attwell, 1977), others have drawn attention to the significant role it can play (Talbot and Talbot, 1963; Watson, 1967). For example, the disappearance of rinderpest virus from the Serengeti wildebeest at about the end of 1961 (Watson, 1967) resulted in a 263% increase in the population over a 10-year period (Sinclair, 1973). I therefore enlisted the aid of veterinary specialists to make a study of the pathology and parasite loads existing seasonally in Etosha's wildebeest. In addition, I referred to the extensive veterinary investigation carried out by Ebedes (1976a, b) which reviewed the

ABSTRACT

Investigations between 1975—78 established that a combination of disease, namely anthrax, and excessive numbers of predators, especially lion, were responsible for the sharp decline in wildebeest numbers. On average, 62% of all wildebeest carcasses tested positive for anthrax, while predators were not susceptible to anthrax. The levels of other disease and parasites were low. Predator—prey ratios were estimated to be between 1:72—105 which are higher than average. Primary factors for raised anthrax and predator levels were the fencing of Etosha which precludes migration, the development of alkaline gravel pits for road building, and the construction of artificial water points.
epizootiology of anthrax *Bacillus anthracis* in large herbivores in Etosha.

I also considered the role of predators and scavengers. Predation of herbivores and the presence of scavengers are natural phenomena and are desirable in any large area set aside for the conservation of wild animals (Estes, 1967; Hirst, 1969; Pienaar, 1969; Kruuk, 1972; Schaller, 1972). However, because all terrestrial systems have been influenced by man, it is possible that this natural equilibrium can become unstable, resulting in an abnormal predator—prey ratio (Smuts, 1975, 1976, 1978a, b, c). I consequently examined the numbers, age—sex ratios, group size, prey preferences and estimated the food intake of large predators and scavengers in Etosha. These data were used to establish whether the predator—prey ratio was within acceptable limits when compared to other African conservation areas. In Etosha, information on large predators and scavengers is limited to the lion and cheetah, with a few records of observed kills by spotted hyena, leopard, wild dog and black-backed jackal. No other relevant data exist for these species, apart from casual sightings. I have therefore been obliged to refer to subjective observations made by staff and tourists when dealing with the lesser known species. In addition, since virtually nothing is known about the predator—prey relationship in the bush and woodlands of Etosha, I have dealt only with the situation relating to the plains, which are the major habitat of wildebeest.

2 METHODS

2.1 Carcasses

During a three-year period (1976—78), field diagnosis of anthrax was based on the procedure established by Ebades (1976a). Because the presence of lions at a carcass did not necessarily indicate death by predation, all such cases where the "kill" had not been witnessed, were examined microscopically for anthrax by taking bloodsmears. Only undecomposed carcasses were suitable for field diagnosis of anthrax.

2.2 Immobilisation

A total of 60 wildebeest were immobilised on a seasonal basis during the period 1976—78. From these, ectoparasites were collected and where dermal lesions or apparent mange were present, skin scrapings were taken and preserved in 70% ethanol for laboratory investigation.

2.3 Sampling by shooting

In 1978 eight wildebeest were selectively shot at the height of the wet season (February) and similarly, eight were shot at the height of the dry season (November). Subsequent to these samplings, a further nine wildebeest were shot in February 1979 to provide additional veterinary material. These 25 animals were individually selected by veterinarians as being representative of the population and likely carriers of disease and parasites. The carcasses were autopsied by a team of three veterinarians, and organs, tissues, blood, urine and faeces were taken for detailed laboratory analyses.

2.4 Number of predators, age—sex ratios and group size

To estimate the predator and scavenger populations in the areas inhabited by wildebeest and other large herbivores sharing the grasslands, I relied on counts made by nature conservators, research workers and my ground and aerial observations during the period 1974—78. Data on age—sex ratios and group size were recorded on punch cards and subsequently coded on to Fortran sheets for sorting by a Univac 1106 computer. Additional information was obtained from questionnaires which were handed out to tourists.

2.5 Preferred prey species

Prey preference could be obtained for lion, cheetah and spotted hyena and were calculated from the formula used by Pienaar (1969), Rudnai (1974) and Smuts (1975):

\[
PR = \frac{F}{A}
\]

where \( PR \) = preference rating
\( F \) = relative frequency with which a particular prey species is killed (%)
\( A \) = relative abundance of the prey species (%)

As pointed out by Schaller (1972), the term "preference" is misleading in that a kill also signifies the prey's availability and vulnerability. I have accordingly considered the preference rating to be an expression of these two factors as well.

2.6 Estimated food intake per predator species

With no data available from Etosha, I referred to the comprehensive investigations of Wright (1960), Kruuk (1972), Schaller (1972), Eloff (1973) and Bryden (1976). From their data it was possible to extrapolate the estimated amount of food required annually by lion, cheetah and spotted hyena on the plains of Etosha. Although the preferred prey species of large predators differs greatly between various areas in Africa (Bourliere, 1963), the amount of food required by large carnivores
is probably consistent at 4–6 % of their body mass per day (Kruusk, 1972; Schaller, 1972; Smuts, 1975).
Consequently, by applying a mean daily food intake of 5 % of body mass I was able to estimate the amount of food required by the major predators and scavengers at Etosha with a reasonable degree of confidence and then balance this requirement against the live mass of available prey.

3 RESULTS

3.1 Anthrax diagnosis

The diagnosis level of anthrax is given for wildebeest and the other large herbivore species occurring on the grasslands of Etosha (Table 1). From the data collected it is clearly evident that wildebeest were severely decimated by anthrax, followed by zebra, springbok and gemsbok. No anthrax was diagnosed in red hartebeest and ostrich during this period but this may have been due to the small sample. As can be expected the number of carcasses found where the cause of death was unknown was high (48 % in wildebeest, 46 % in zebra, 31 % in springbok, 54 % in gemsbok, 50 % in red hartebeest and 52 % in ostrich; x=47 %). This was due to the rapidity with which carcasses decomposed or were scavenged in Etosha.

3.2 Other infections and general pathology

The findings of Basson (1979) indicate that the pathologically poor condition of seven of the 25 wildebeest examined could be related to increased parasitism and/or diseases such as infectious pustula vulva-vaginitis (IPV) (=infectious bovine rhinotracheitis) and brain lesions. This was regarded as being significant.

3.3 Endoparasites

The reports of Thomas (1978) and Biggs and Anthonissen (1978, 1979) show that all parasite burdens were very low if judged against standard criteria for herbivores.

3.4 Ectoparasites

The reports of Biggs and Anthonissen (1978, 1979) indicate that tick and lice burdens were exceptionally low. In spite of regular Gediaestesia pathology, the loads of this dipteran larva were regarded as low to typical and the parasite—host relationship appeared stable. Nevertheless, the possibility of mortality in calves as a result of gedaestiasis does exist.

<table>
<thead>
<tr>
<th>TABLE 1: Incidence of anthrax in relation to total recorded mortality in wildebeest and other large herbivores in Etosha (1976–78)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mortality</td>
</tr>
<tr>
<td>Season Species Anthrax positive Anthrax negative Other causes including predation Cause unknown Total positive and negative and other causes Anthrax positive as percentage of total</td>
</tr>
<tr>
<td>---</td>
</tr>
<tr>
<td>Wet, hot season (Jan. to April) Wildebeest 22 3 4 14 29 76</td>
</tr>
<tr>
<td>Zebra 60 21 36 82 117 51</td>
</tr>
<tr>
<td>Springbok 16 3 21 13 40 40</td>
</tr>
<tr>
<td>Gemsbok 0 0 8 7 8 0</td>
</tr>
<tr>
<td>Hartebeest 0 0 1 0 1 0</td>
</tr>
<tr>
<td>Ostrich 0 0 4 4 4 0</td>
</tr>
<tr>
<td>Dry, cold season (March to Aug.) Wildebeest 8 1 4 24 13 62</td>
</tr>
<tr>
<td>Zebra 10 3 29 32 42 24</td>
</tr>
<tr>
<td>Springbok 2 2 41 17 45 4</td>
</tr>
<tr>
<td>Gemsbok 0 0 5 6 5 0</td>
</tr>
<tr>
<td>Hartebeest 0 0 1 0 1 0</td>
</tr>
<tr>
<td>Ostrich 0 0 10 3 10 0</td>
</tr>
<tr>
<td>Dry, hot season (Sept. to Dec.) Wildebeest 11 2 11 23 24 46</td>
</tr>
<tr>
<td>Zebra 11 0 17 45 28 39</td>
</tr>
<tr>
<td>Springbok 6 1 24 23 31 19</td>
</tr>
<tr>
<td>Gemsbok 2 0 6 12 8 25</td>
</tr>
<tr>
<td>Hartebeest 0 0 1 3 1 0</td>
</tr>
<tr>
<td>Ostrich 0 0 7 16 7 0</td>
</tr>
<tr>
<td>Total for three years Wildebeest 41 6 19 61 66 62</td>
</tr>
<tr>
<td>Zebra 81 24 82 159 187 43</td>
</tr>
<tr>
<td>Springbok 24 6 86 53 116 21</td>
</tr>
<tr>
<td>Gemsbok 2 0 19 28 21 10</td>
</tr>
<tr>
<td>Hartebeest 0 0 3 3 3 0</td>
</tr>
<tr>
<td>Ostrich 0 0 21 23 21 0</td>
</tr>
</tbody>
</table>
3.5 Estimated predator—scavenger populations and their composition

3.5.1 Lion

The dry season pride areas of resident lion and ranging nomadic groups (as defined by Schaller, 1972) which inhabited the Etosha plains during the period 1974–78 are shown in Fig. 1. Pride areas were fairly distinct during the dry season when availability of drinking water restricted the movements of predators and most prey species. In all, there were 21 known areas on the Etosha plains which were inhabited by resident prides or nomadic groups. Pride areas became obscure during the wet season when distribution of prey changed and wet conditions prevented vehicles from leaving the roads. The mean pride or group size in each area or range was calculated from observations during the five-year period (n=356 observations on 2 562 lions). The overall mean pride/group size was 7,2 (range 2–30, SD ± 4,53), with a yearly mean of 285 individuals present. I was able to age and sex 565 lion. Adult sex ratio was 1 male : 1,03 female (n=354) which was not disparate at P>0,70. Immature lion (0–3 years) made up 37% of my sightings. By comparison, Schaller (1972) found that Serengeti lion pride sizes was 15 (range 4–37) and nomadic group size was 2,8 (range 2–13) giving an overall average of four lion in prides and groups. Their sex ratio was 1 male : 0,92 female (P>0,50), whilst 43% of the lion on the Serengeti plains were sub-adult (0–4 years). Thus the mean pride/group size in Etosha was larger than in Serengeti, although the age–sex ratios were similar. Etosha’s pride/group size of 7,2 is also greater than the figure of 4–5 given for Zambia by Mitchell et al. (1965), but is more in keeping with the group size of 6 reported in East Africa by Wright (1960). In contrast, Smuts (1975) reported an average of 11,8 lion per pride/group in the central Kruger Park.

My figure of 285 lion inhabiting the Etosha plains is likely to be an underestimate since only limited observations were available from some of the areas and lion are usually undercounted from the ground or by aircraft (Schaller, 1972; Smuts, 1975). Because no correction factor for undercounting bias is known for free-ranging lion, I assumed that approximately 70% of the total population were seen by ground counts. Consequently I applied an arbitrary correction factor of 1,4 to the average count of 285 lion, which provided a theoretical total of 400 lion that may have been present on the plains of Etosha during this study. I subsequently used a range of 285–400 lion when calculating predator density and food intake, since it is likely that the actual number of lion present fell within these minimum and maximum figures.

The plains of Etosha cover 8,1% of the total area, namely 1 793 km² (Le Roux, 1977). Applying my estimates of between 285 and 400 lion, the density is one lion/4,5–6,3 km². These first approximations are well within the range of lion densities found elsewhere in Africa. For example, one lion/2,6 km² in Manyara Park, one lion/3,7 km² in Ngorongoro Crater, one lion/4,6 km² in Nairobi Park (Schaller, 1972) and one lion/7,9 km² in Kruger Park (Smuts, 1975). My estimates of the lion population on Etosha’s plains therefore appear to be of the right order of magnitude.

3.5.2 Cheetah

The records show that, on average, there were 70–80 cheetah inhabiting Etosha’s plains between 1974–78. Allowing for double-counting as well as for undercounting, I consider that a population figure of 50–100 cheetah is realistic. These estimates give a density of one cheetah/18–36 km². In comparison, Nairobi Park supported one cheetah/4,42 km² (McLaughlin, 1970), while Kruger Park had one cheetah/72 km² (Pienaar, 1969) and Serengeti’s density was one cheetah/102–107 km² (Schaller, 1972). Group size at Etosha varied from 2–5. The most adults reported together were three, whilst groups of 4–5 animals were females with up to four cubs.

3.5.3 Spotted hyaena

The number of spotted hyaena, hereafter referred to as hyaena, inhabiting the plains of Etosha is unknown and I have used the ratio of hyaena : lion from other areas to estimate a figure. Nonetheless, my casual observations and those of other observers at Etosha indicate that the hyaena population is substantial and my initial estimates can therefore be regarded as realistic. The ratio of hyaena : lion in Ngorongoro Crater is 6,1:1 and in Serengeti it is 1,25–1,50:1 (Kruuk, 1972; Schaller, 1972). In the Kruger Park it is 2,73:1 (Smuts, 1975), while in the adjoining Timbavati Nature Reserve it approximates 1:1 (Bearder, 1975). Thus it appears that in large, relatively natural conservation areas there are at least as many hyaena as lion and often more. Consequently, I estimated the hyaena population on Etosha’s plains to be the same as for lion, namely 285–400. These figures are probably conservative.

Hyaena packs of more than three adults were frequently seen in Etosha. The largest pack encountered in daytime was 12 and at night a pack of 23 was observed. By comparison, up to 25 hyaena in a pack were recorded at Serengeti — Ngorongoro (Kruuk, 1972). Since pack formation indicates either active hunting or patrolling of territory boundaries (the latter in itself indicates a fairly dense hyaena population according to Kruuk, 1972), it appears that Etosha’s hyaena hunt frequently. The records at Etosha show that healthy, adult zebra, wildebeest, kudu and springbok have been successfully hunted and killed by hyaena packs. This in turn indicates that at certain times of the year scavenging from lion kills is insufficient to meet the food demand of hyaena.
3.5.4 Other predators and scavengers

No information exists on the numbers of leopard and brown hyena in Etoisha, while in the case of wild dog it is virtually certain that they did not inhabit the plains during 1974–78. I estimate that there may be 1,000 – 2,000 black-backed jackal on the plains, giving a density of 1 jackal/0.9 – 1.8 km². Up to 52 jackal have been recorded at a zebra carcass and groups approximating 30 are frequently encountered at anthrax carcasses. There is no doubt that the jackal population is high and my estimates may well be conservative.

I have not considered vultures and other avian carrion eaters in my estimates of predator–scavenger biomass, since they are not necessarily resident on the plains. The omnivory of the other mammalian and avian species and scavengers lends conservative bias to the estimated predator–scavenger biomass and consequently to the predator : prey ratios. This bias may, however, be offset to an extent by the fact that the major carnivores I have considered also predate and scavenge species other than the large herbivores included in my estimates.

3.6 Preferred prey species

The prey preferences of lion, cheetah and hyena are given in Table 2. Lion showed the greatest preference for gemsbok, followed by wildebeest, zebra, ostrich and springbok. In other areas where gemsbok are common, for example the Kalahari Park, they are frequently taken by lion (Eloff, 1964). However, prey preference is largely dictated by availability of species. For instance buffalo made up 9% of the lion’s diet in Kruger Park (Pienaar, 1969), 15% in Serengeti (Schaller, 1972; Sinclair, 1977), but constituted 62% of the prey species at Manyara Park, an area where buffalo outnumbered all other prey species (Makacha and Schaller, 1969). Likewise at Kruger Park, where impala were the most plentiful prey species, they constituted the highest frequency (31.3%) of food for lion (Smuts, 1978b).

I suspect that the preference shown for gemsbok in Etoisha may be due to the establishment of artificial drinking places where gemsbok, a species which is relatively independent of drinking water, are found in the dry season. Consequently, these boreholes support large groups of lion. Under natural (waterless) conditions, no lion could be resident in such areas of Etoisha during the eight months of dry season. A similar situation was found to exist in Wankie Park, where gemsbok and eland suffered disease and predation stresses beyond their adaptive capabilities (Davison and Davison, 1968). Furthermore, eland in Etoisha have also been greatly reduced in numbers and increased predation may well be a major contributory factor.

Wildebeest are marginally preferred to zebra by hunting lion in Etoisha (preference rating = 2.98 compared to 2.53). In Kruger Park the PR for wildebeest ranged from 2.21 – 4.35, while that for zebra was 1.43 – 2.37, making wildebeest preferred above zebra, on a yearly basis, for a period of 20 years (Smuts, 1975). The PR values were of a similar magnitude in Nairobi Park, where wildebeest PR = 1.83–4.20 and zebra PR = 0.81–1.98 (Rudnai, 1974). Wildebeest were also preferred above zebra by lion in the Timbavati Reserve, Eastern Transvaal (Hirst, 1969).

<table>
<thead>
<tr>
<th>Predator</th>
<th>Prey species</th>
<th>No. of kills recorded</th>
<th>Relative kill frequency (%)</th>
<th>Relative abundance of prey (%)</th>
<th>Prey preference rating*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lion</td>
<td>Wildbeest</td>
<td>21</td>
<td>19.1</td>
<td>6.4</td>
<td>2.98</td>
</tr>
<tr>
<td></td>
<td>Zebra</td>
<td>67</td>
<td>60.9</td>
<td>24.1</td>
<td>2.53</td>
</tr>
<tr>
<td></td>
<td>Springbok</td>
<td>12</td>
<td>10.9</td>
<td>65.0</td>
<td>0.17</td>
</tr>
<tr>
<td></td>
<td>Gemsbok</td>
<td>9</td>
<td>8.2</td>
<td>2.3</td>
<td>3.57</td>
</tr>
<tr>
<td></td>
<td>Red hartebeest</td>
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<td>0.9</td>
<td>0.2</td>
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</tr>
<tr>
<td></td>
<td>Ostrich</td>
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<td></td>
<td></td>
<td>0.45</td>
</tr>
<tr>
<td>Cheetah</td>
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<td>7</td>
<td>3.2</td>
<td>6.4</td>
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</tr>
<tr>
<td></td>
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<td>0.0</td>
<td>24.1</td>
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</tr>
<tr>
<td></td>
<td>Springbok</td>
<td>61</td>
<td>96.8</td>
<td>65.0</td>
<td>1.49</td>
</tr>
<tr>
<td></td>
<td>Gemsbok</td>
<td>0</td>
<td>0.0</td>
<td>2.3</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>Red hartebeest</td>
<td>0</td>
<td>0.0</td>
<td>0.2</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>Ostrich</td>
<td>0</td>
<td>0.0</td>
<td>2.0</td>
<td>0.00</td>
</tr>
<tr>
<td>Spotted hyena</td>
<td>Wildbeest</td>
<td>2</td>
<td>22.2</td>
<td>6.4</td>
<td>3.47</td>
</tr>
<tr>
<td></td>
<td>Zebra</td>
<td>5</td>
<td>55.6</td>
<td>24.1</td>
<td>2.31</td>
</tr>
<tr>
<td></td>
<td>Springbok</td>
<td>2</td>
<td>22.2</td>
<td>65.0</td>
<td>0.34</td>
</tr>
<tr>
<td></td>
<td>Gemsbok</td>
<td>0</td>
<td>0.0</td>
<td>2.3</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>Red hartebeest</td>
<td>0</td>
<td>0.0</td>
<td>0.2</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>Ostrich</td>
<td>0</td>
<td>0.0</td>
<td>2.0</td>
<td>0.00</td>
</tr>
</tbody>
</table>

*Preference rating = Relative kill frequency Relative abundance of prey
Predictably, cheetah prey mainly on springbok in Etosha, although wildebeest, especially calves, may be taken. Wildebeest appear to head the list of prey preferences of hyaena in Etosha, ranking above zebra and springbok. The small sample size (n=9 kills) may, however, have biased the findings.

3.7 Live mass of food required annually

Applying a mean daily food intake of 5% of body mass, I estimated the food requirement in Etosha’s large, plains-dwelling carnivores (Table 3). As mentioned previously, leopard, wild dog, brown hyaena, jackal and vultures were omitted from these estimates. Furthermore, I presumed that 37% of the lion population was immature, basing this on field observations in Etosha. For cheetah, 32% of the population was taken to be immature (Schaller, 1972) and in the case of hyaena this figure was 25% (Kruuk, 1972). Live mass of the three carnivore species was based on the means recorded by Kruuk (1972) and Schaller (1972).

Because lion and cheetah, on average, leave 33% and 35% of a carcass uneaten respectively (Schaller, 1972), I have estimated the total food actually killed to be accordingly higher. In the case of hyaena, my assumption was that almost 100% of a carcass was consumed (Kruuk, 1972; personal observation).

The estimates result in a total food requirement plus uneaten residues of approximately 1–1.5 million kilogram prey annually. I wish to reiterate that these figures should be considered initial approximations, since my calculations are based on several unproven assumptions.

3.8 Predator—prey live mass ratios

Estimates of the ratios of predator to prey on the Etosha plains are given in Table 4. To calculate these ratios I used the estimated maximum and minimum total live mass of the three major predators, namely lion, cheetah and hyaena as derived in Table 3. This range of predator live mass was related to the live mass of wildebeest and the other five major herbivore species which inhabit the plains. In estimating the live mass of prey, I took into account the contribution made to each species’ population by the different age and sex classes, using the appropriate body mass of each age—sex class (Berry, 1980). Furthermore, I used the mean population of each prey species during the period 1974–78 to correspond with the mean predator populations for the same period.

Thereby, the total predator—scavenger live mass was estimated to lie between 49,255 and 71,310 kg and the total live mass of prey was estimated at 515,013 kg, as shown in Table 4. This gives a minimum predator:prey ratio of 1:72 and a maximum of 1:105. A comparison of these ratios to those found elsewhere in Africa is made in Table 5. Etosha appears to have a greater proportion of lion to prey than most other conservation areas for which data are available. It must, however, be remembered that Schaller’s (1972) ratios for Serengeti include all major predators, whereas the other sources refer specifically to lion:prey ratios. For this reason I have presented Etosha’s ratios in both ways.

In central Kruger Park, which has similar ratios to Etosha, a total of 335 lions and 297 hyaena, representing 63% and 80% of the numbers in one area, were cropped between 1974–77 (Smuts, 1975, 1978c). Despite this high rate of predator control, lion regained 90% of their former level within 17 months while hyaena were slow to colonise (Smuts, 1978a). Therefore it seems that the question of direct predator control at Etosha would have to be approached with caution in view of the limited success achieved elsewhere.

The 1–1.5 million kilogram prey removed annually (Table 3) is 21–30% of the estimated herbivore live mass of 5 million kilogram (Table 4). This rate of removal by predators is two to three times that in the Serengeti where 9–10% of the prey biomass is taken by predators (Schaller, 1972), whose findings indicated a dearth of large carnivores. The relative paucity of prey at Etosha can be illustrated by the prey biomass which is estimated at 2,873 kg/km² compared to 20,712 kg
TABLE 4: Estimated mean predator—prey live mass ratios on the grasslands of Etosha (1974—78)

<table>
<thead>
<tr>
<th>Predator species</th>
<th>Prey species</th>
<th>Prey live mass (kg)</th>
<th>Predator—prey ratios</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lion</td>
<td>Burchell's zebra</td>
<td>3 564 112</td>
<td></td>
</tr>
<tr>
<td>Cheetah</td>
<td>Wildebeest</td>
<td>521 250</td>
<td></td>
</tr>
<tr>
<td>Spotted hyaena</td>
<td>Springbok</td>
<td>700 681</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Gemsbok</td>
<td>261 295</td>
<td>1:72</td>
</tr>
<tr>
<td></td>
<td>Red hartebeest</td>
<td>18 160</td>
<td>to</td>
</tr>
<tr>
<td></td>
<td>Ostrich</td>
<td>85 515</td>
<td>1:105</td>
</tr>
</tbody>
</table>

Total predator live mass 49 255—71 310  
Total prey live mass 5 151 013

TABLE 5: Comparison of predator—prey ratios on the grasslands of Etosha with other areas of Africa

<table>
<thead>
<tr>
<th>Area</th>
<th>Lion: Prey ratio and Predator : Prey ratio</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Albert Park</td>
<td>1 : 360*</td>
<td>Bournier (1965)</td>
</tr>
<tr>
<td>Kagera Park</td>
<td>1 : 300*</td>
<td>Bournier (1965)</td>
</tr>
<tr>
<td>Tarangire Game Reserve</td>
<td>1 : 292*</td>
<td>Lampey (1964)</td>
</tr>
<tr>
<td>Ngorongoro Crater</td>
<td>1 : 260*</td>
<td>Lampey (1964)</td>
</tr>
<tr>
<td></td>
<td>1 : 100**</td>
<td>Schaller (1972)</td>
</tr>
<tr>
<td>Serengeti Park</td>
<td>1 : 250—300**</td>
<td>Schaller (1972)</td>
</tr>
<tr>
<td>Manyara Park</td>
<td>1 : 174**</td>
<td>Schaller (1972)</td>
</tr>
<tr>
<td>Nairobi Park</td>
<td>1 : 100**</td>
<td>Schaller (1972)</td>
</tr>
<tr>
<td>Heuses Park</td>
<td>1 : 100—116*</td>
<td>Piennar (1969)</td>
</tr>
<tr>
<td></td>
<td>1 : 57—149*</td>
<td>Smuts (1976)</td>
</tr>
<tr>
<td></td>
<td>1 : 107—153*</td>
<td>Smuts (1976)</td>
</tr>
<tr>
<td>Etosha Park</td>
<td>1 : 72—105*</td>
<td>Present study</td>
</tr>
</tbody>
</table>

* Lion : prey ratio  
** Predator : prey ratio

prey/km² in Serengeti (Schaller, 1972). Moreover, the lion biomass in Etosha is estimated between 18,8—26,8 kg/km² which is higher than the range of 13,6—20,5 kg/km² found in four areas of the Kruger Park (Smuts, 1978c) despite the fact that he applied a mean adult body mass of 158 kg for lion which is 9 % higher than the figure of 145 kg which I used.

4 DISCUSSION

4.1 Anthrax

The viable nature and ecology of anthrax have been adequately dealt with by Van Ness (1971) and Ebedes (1976b). In Etosha, soils in the areas inhabited by wildebeest are highly alkaline, thereby providing conditions under which anthrax bacilli flourish. Furthermore, the creation of numerous gravel pits for road building in Etosha boosted the disease’s incidence by creating favourable incubator areas for sporulation. Ebedes (1976b) confirmed that the manner in which anthrax could be transmitted, namely, by infected carcases, faeces, predators, scavengers, birds and insects, as well as by water and wind, made it practically impossible to eliminate the disease in an area the size of Etosha. He also related the greatly increased incidence of anthrax in Etosha since 1966 to the emergence of over-utilised grazing areas. These “slum areas” (Ebedes, 1976a) were created by the construction of drinking troughs in the areas previously occupied by migrant herds in the rainy season only.

The findings of Ebedes (1976a, b) were supported by my observations during this five-year investigation. In addition, I am of the opinion that anthrax has resulted in an ideal situation in which predators and scavengers can increase to an unnatural level. My supposition is partly derived from the high incidence of anthrax in relation to recorded mortality (Table 1), where it is apparent that a surplus of meat from carcases would be available. When it is considered that anthrax-infected carcases were especially abundant during the wet season, a period in which predators would normally experience greater difficulty in obtaining food (Schaller, 1972; Smuts, 1975, 1978c), the advantage to lions and hyenas is obvious. The combination of anthrax and increased predation pressure has in turn been reflected in declining herbivore populations, notably wildebeest and zebra. The impact of anthrax on the reproductive component of the wildebeest population should also be considered. For ex-
ample, the majority of wildebeest cows died of anthrax during the wet season when they were nearing full-term pregnancy or had recently calved. This resulted in "double deaths" and may have contributed to a high antenatal and neo-natal mortality since milk-dependent calves are suckled only by their mother and are not fostered by other cows. There was no significant difference in mortality of the sexes in the sample collected by Ebedes (1976b): 308 bulls : 303 cows (P>0.80). In the present study the sample reflected a more distorted sex ratio of 24 bulls : 15 cows which was not significant at P>0.02. This may have been due to the much smaller sample size.

It appeared that wildebeest were more susceptible than zebra to anthrax (Table 1) because the total number of anthrax-positive carcases located in relation to the total population was 1,93 times higher in the case of wildebeest. Ebedes (1976b) mentioned that possibly 50% of all anthrax-infected carcases were located, but I am of the opinion that in wildebeest a much lower percentage was located. I base this on the fact that 48% of my sample was made up of dehydrated or decomposed carcases from which no positive field diagnosis was possible.

Furthermore, a predated carcase was seldom found in a relatively intact, mumified state which characterised an anthrax epidemic, when more meat was made available to scavengers than could be utilised. None of these frequently occurring dried-out carcases or remains could be positively diagnosed in the field. Moreover, while herbivores were fatally affected by anthrax, no records of predators or scavengers dying of the disease were obtained during a seven-year investigation by Ebedes (1976b) or during the present study. Consequently, carnivores fed freely from anthrax-infected carcases, or drank from infected water, thereby gaining advantageously over the susceptible herbivore populations.

Thus I consider anthrax to be a primary and major factor in the decline of wildebeest in Etosha. The data in support of this are quantifiably demonstrable from both Ebedes' (1976a, b) findings and my results, namely, that in our respective samples 74% and 62% of all diagnosed deaths in wildebeest were positive for anthrax. Other herbivores, especially zebra, appeared to be similarly affected and this was reflected in their declining numbers (Berry, 1980).

4.2 Other pathological conditions and parasites

The autopsy findings indicated that two age classes especially showed levels of viral infection and/or parasitism which could be considered potentially fatal (Basson, 1979, pers. comm.). These were the very young calves (<2 months) in which disease, notably IPV, resulted in prominent brain lesions and the 1–2 year old immatures which exhibited widespread lesions from migrating Guederstria larvae. In comparison, the older, weaning calves (2–9 months) and wildebeest older than two years were noticeably less prone to these conditions. These findings dovetail well with my surmise that there was a high mortality of neo-natal calves, which, because it could not be quantitatively determined, has been included in a theoretical population model as a reduced birth-rate in adult cows, namely 0.35 (Berry, 1981). Similarly, the pathology of 1–2 year old wildebeest was well correlated to my field counts where there was a greater decline in the number of calves achieving immaturity (8% decrease) than in the number of immatures achieving sub-adulthood (4% decrease).

The autopsy findings also confirmed a high incidence of Guederstria larvae, and the burden carried by young calves pointed to the possibility of occasional deaths in young animals as a result of gedoetlasis. However, this ectoparasite was not present in abnormally high levels in Etosha's wildebeest. The remaining parasite loads, especially ectoparasites, were exceptionally low in all specimens examined and were regarded as having no significant effect on the population's mortality (Biggs, 1979, pers comm.).

4.3 Combined effect of predation and disease

In Etosha, a portion of the carnivores' food is provided by diseased animals which die of anthrax (Table 1). Thus, during an anthrax epidemic, lion and hyaena are not required to hunt but can live off the abundant supply of diseased meat without suffering any apparent clinical ill-effects. Nevertheless, lion may continue to hunt in the presence of diseased carcases and there are records of Etosha lion ignoring several zebra which had died of anthrax, to commence a successful hunt on healthy zebra in the vicinity. Under these circumstances the live mass of herbivores removed by the combined effect of predation and disease would be higher than the estimates of 1–1.5 million kilogram obtained in Table 3. Even if this were not the case, my estimates can still be considered conservative because, during an anthrax epidemic, more herbivores die than can be eaten by the large carnivores (Section 4.1).

I therefore consider my estimate that 21–30% of the large herbivore live mass was removed annually from the Etosha plains to be realistic. Taking the minimum estimate of 21% removal, it is clear that neither wildebeest nor zebra which together comprise 80% of the lion's recorded diet (Table 2) and 77% of the recorded cases of anthrax (Table 1) can withstand these mortality pressures. Consequently, it is not surprising that wildebeest and zebra, with recruitment rates to the breeding stock of 11–18% and about 8% respectively (Berry, 1980) are decreasing in numbers at Etosha. The wildebeest population decreased by 24% and the zebra population by 43% during the period of study (1974–78). These declines were inversely proportional to the different recruitment rates of wildebeest and zebra. For example, the mean recruitment rate of wildebeest was
14.5% which was 1.8 times higher than that of 8% for zebra and the decline in zebra numbers was 1.8 times greater than wildebeest.

If the wildebeest and zebra populations decline further, which seems likely at this stage because of the endemic nature of anthrax, then they could become relatively unattractive to hunting lion which would be forced to turn to alternative prey species (Smuts, 1978b). This may in turn result in increased predation on bush and woodland dwellers such as giraffe, kudu, gemsbok and eland.

Finally, the status of springbok in Etosha supports my findings that the combined effect of predation and disease is the major cause of declining wildebeest and zebra numbers. Springbok have increased more than three-fold in numbers (9,800 to 32,000) between 1974–78. They also died of anthrax (15% of all anthrax-infected carcases found were springbok; Table 1) but apparently to the extent that wildebeest and zebra died. Also, the relative predation rate of springbok was far lower than either wildebeest or zebra. Springbok constituted 17.8% of the live mass removal by predators, compared to 65.4% by wildebeest and zebra combined (Tables 2 and 3). It can be argued that recording of anthrax and predation in springbok were biased in favour of the larger herbivores because of the rapidity with which springbok carcases are obliterated. This may partly be the case, but it is nullified to a large extent by the fact that Etosha’s springbok population increased by a factor of 3.3 in five years. It appears that the differential disease and predation pressures which exist between the springbok population and the wildebeest and zebra populations are justifiable reasons for the respective increase and decreases in numbers.

5 CONCLUSIONS

Before the introduction of artificial drinking places in Etosha from 1951 onwards, the cyclical nature of herbivore movements to and from preferred grazing areas was evident (Bigalke, 1961). Refer also in this regard to Berry (1980) in which I review the development of Etosha for tourism. Consequently, in pristine times, the short rainy season provided an abundance of temporary drinking places for grazers such as wildebeest as well as attracting them to the apparently preferred annual grasses in the Okaukuejo area, which are high in nutrients (Berry, 1980). However, before the advent of permanent drinking troughs, the migratory herds vacated these “wet season dispersal areas” (Bigalke, 1961) when the ephemeral rainwater pools dried. Thereby a natural, rotational grazing system operated which precluded predators and scavengers from establishing permanent populations in large parts of the Okaukuejo area. Also, in the absence of roads and accompanying gravel pits, the disease factor was not yet epidemic in any part of Etosha (Section 4.1).

The provision of artificial watering points in the form of drinking troughs and gravel pits modified the earlier migratory tendencies of herbivores and, at the same time, stabilised the environment for predators and scavengers. Following on this, the reduced need to migrate has resulted in smaller group sizes of wildebeest (Berry, 1981). This in turn makes them more vulnerable to predation and especially increases neo-natal mortality by rendering calves more easily available to hyaena (Smuts, 1978b). In the present study in Etosha, hyaena scats were found to contain foetal and newborn wildebeest calf hooves as well as amounts of wildebeest calf tail hair (Report No. 1768/77, S.A. Police Forensic Laboratories, 1977). Thus wildebeest and other large herbivores in Etosha have to contend not only with an increased lion population which has expanded spatially, but also with a substantial hyaena population which can alternate efficiently between scavenging and preying. Cheetahs may also exert predation pressure on wildebeest calves.

In addition, wildebeest form a major prey item of lion and hyaena. If the combined effects of this predation are coupled to my findings that 62% of all deaths in wildebeest were caused by disease, namely anthrax (Table 1), then it follows that the pressure exerted by predators and disease is the major reason for the decline of wildebeest in Etosha during the period of study. Moreover, this assertion is supported by the fact that the quantity and quality of nutrients and water were not limiting during my investigation (Berry, 1980). This was also evident in the good nutritional status of the wildebeest.

Whereas predation may have a negligible effect in a system such as Serengeti (Schaller, 1972), where herbivore mortality was attributable mostly to malnutrition and disease (Watson, 1967; Bell, 1969; Sinclair, 1977), predation can, under certain circumstances, such as were encountered in Ngorongoro Crater and Kruger Park, have a considerable effect on the herbivore population (Kruuk, 1972; Smuts, 1975, 1976, 1978b, c). It appears that the special conditions in Etosha, which have resulted from man’s impact on the environment in the form of fences, roads and artificial drinking places, have created abnormal disease and predation levels, causing wildebeest numbers to decline drastically.

6 SUMMARY

An investigation was undertaken to establish whether the declining wildebeest numbers in Etosha could be related to veterinary causes. This was achieved by monitoring a total of 127 wildebeest carcases and 337 carcases of Burchell’s zebra, gemsbok, springbok, red hartebeest and ostrich over a period of three years. In the same period a total of 60 immobilised wildebeest were visually examined for external parasites and peripheral blood smears were made for blood parasites. In addition, 25 wildebeest were selectively sampled for detailed pathological and parasitological investigation. Fresh carcase diagnosis yielded blood smears which were positive for anthrax Bacillus anthracis in 62% of
wildebeest, 43% of zebra, 21% of springbok, 10% of gemsbok and were anthrax-negative in hartebeest and ostrich. Anthrax mortality reached a predictable peak in wildebeest, zebra and springbok during the rainy season when 76%, 51% and 40% of anthrax deaths occurred in these species respectively.

The low endoparasite profile in wildebeest was regarded as an insignificant factor for limiting the population. Similarly, the ectoparasite burden was exceptionally low, except for *Gedoelsisia* larval counts which approached typical herbivore levels.

The special conditions existing in wildebeest habitat in Etosha favoured anthrax viability and the disease was regarded as having become endemic with epidemics occurring during the wet season. An abundance of anthrax-infected carcasses during the wet season probably resulted in increased predator—scavenger populations. Carnivores were apparently not fatally affected by anthrax. There was no significant sex link in wildebeest mortality from anthrax but the deaths of reproductive cows naturally also resulted in the loss of foetuses and neo-natal calves.

Reviewing the disease and parasite pressure on wildebeest in Etosha, it is evident that anthrax was a primary and major factor in the reduction of the population up to the present time and that it will not be possible to eliminate it in the foreseeable future. Other diseases and parasites were found to be insignificant in comparison to anthrax, but *gedoelsiasis* and *IPV* are potentially fatal conditions which, if they were to become severe, could result in increased mortality.

The role of predators and scavengers on the Etosha plains was examined in relation to the declining wildebeest population during the period 1974–78. The estimated 285–400 lion, which included resident prides and ranging nomads, had a group size of 7,2 and an adult ratio of 1 male : 1,03 females. Immatures comprised 37% of the sightings. A total of 21 known pride areas or nomadic ranges were located on the plains during the dry season, but the situation in the wet season was unknown. Density was 1 lion/4,5–6,3 km², which was comparable to other areas in Africa.

Between 50–100 cheetah inhabited the plains, with a density of 1 cheetah/18–36 km². Spotted hyaena numbers were estimated from data of other areas, assuming a ratio of 1 hyaena : 1 lion. This gave an estimated population of 285–400 hyaena. Packs of up to 23 hyaena in Etosha indicated frequent hunting and records of kills on zebra, wildebeest, kudu and springbok were obtained. An initial estimate of black-backed jackal numbers (1,000–2,000) gave a density of 0.9–1.8 km², the large population being indicative of a substantial predator population. Up to 52 jackal were seen at one zebra carcass.

Preferred prey species of lion in Etosha were gemsbok, wildebeest, zebra, ostrich and springbok in declining order of magnitude. Cheetah preferred springbok above all else but sometimes killed wildebeest calves. Hyaena showed a preference for wildebeest, followed by zebra and springbok.

Based on a mean daily food intake of 5% of body mass, the lion, cheetah and hyaena populations on the plains were estimated to require 1–1.5 million kilogram of food annually, including uneaten residues. This demand represented a yearly removal of 21–30% from the total live mass of the six major herbivore species, namely wildebeest, zebra, springbok, gemsbok, hartebeest and ostrich.

In Etosha, lion prey ratios were 1:107–153 and the ratios of lion / cheetah / hyaena : prey were 72–105. These ratios were higher than in most other areas and of the same order as those in the Kruger Park where the predator density was considered high enough to warrant control. Lion biomass in Etosha was also estimated to be higher than in the Kruger National Park, namely 18.8–26.8 kg/km² compared to 13.6–20.5 kg/km².

Predators and scavengers in Etosha benefited from the surplus of meat which was provided by anthrax-infected carcasses. Thereby their numbers may have increased and the combined effects of disease and predation were considered to be the main reason for the decline in wildebeest and zebra numbers. Together, wildebeest and zebra formed 80% of the lion’s recorded diet and 77% of the recorded cases of anthrax. In contrast the springbok population, being relatively much less affected by both disease and predation, increased by a factor of 3.3 during the five-year period.

The overall conclusion reached in this investigation was that the earlier, natural movements of the migratory herbivores in Etosha have been modified by fences, roadbuilding and artificial, permanent drinking places. Disease, especially anthrax, has become endemic in areas where gravel pits occur, while the predator—scavenger populations have stabilised and increased where artificial water has been provided. Furthermore, disease is complementary to predation by providing an abundance of carcasses during anthrax epidemics. Taking into account the findings that neither food nor water were limiting to the wildebeest population and the fact that their nutritional status was good, it was evident that disease and predation had combined under the special conditions existing in Etosha and together were the major cause of the decline in wildebeest and also in zebra numbers.

### 7 Acknowledgements

I acknowledge the work of the veterinarians who willingly gave their time during this investigation. In particular I want to thank Dr. P. Basson, State Veterinarian, Grootefontein, who was responsible for the pathology studies, and Dr. H. Biggs, State Veterinarian, Windhoek Regional Laboratory, who investigated the parasites. Dr. J. Hofmeyr and Dr. T. van Wyk of Nature Conservation immobilised wildebeest and took general
specimens. They are thanked for their expertise. Dr. I. Carmichael and Dr. S. Thomas, Veterinary Research Institute, Onderstepoort, provided specialist services in the examination of parasites and blood specimens.

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Population structure, mortality patterns and a predictive model for estimating future trends in wildebeest numbers in the Etosha National Park

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1 INTRODUCTION

The aim of this investigation was to estimate the total population of wildebeest Connochaetes taurinus in Etosha, to examine its structure, and to identify the factors which may have caused a decline in numbers.

1.1 Decline in total population

Prior to aerial counts which commenced in 1966, only general estimates of the wildebeest population in the Etosha National Park were made. These ranged from 20 000 to 30 000 wildebeest in 1913 (Jaeger, 1926—1927), 7 000 to 10 000 in 1952 (Schoeman, 1952), 25 000 in 1954 (De la Bat, 1977 pers. comm.) and 30 000 in the period ending 1965 (Viljoen, 1967). In 1966 the aerial counts were carried out in limited time and no population estimates were possible (Ebedes et al., 1967). The first dry season aerial census in September 1968, when water dependent species occupied “dry season concentration areas” (Bigalke, 1961), gave a total of 4 073 wildebeest (Ebedes, 1968). According to Ebedes (1977, pers. comm.), he undercounted by 10—20 % and estimated the total population at 5 000. In April 1969 and February 1970 aerial strip counts were flown for the first time over Etosha and were subsequently adopted in preference to the previous method of random counting. Thereby 4 773 (1969) and
4789 (1970) wildebeest were counted (Ebedes et al., 1970), but the increase over previous years was considered to be a result of the improved method. Nevertheless, fixed-wing aircraft have disadvantages, such as limited view and turning ability, when compared to a helicopter. This became evident when the first census of the Etosha plains was undertaken by helicopter in September 1973 (Joubert et al., 1973). They counted 3717 wildebeest, an increase of 21% over the October 1972 count of 3078 (Du Preez, 1972). The subsequent counts I did by helicopter (1974–1978) revealed a declining population of which the numbers dropped from 3300 to 2493 (Berry, 1978). The decreasing trend is Fig. 1.

1.2 Spatial and temporal distribution

The seasonal distribution of the wildebeest population is illustrated in Fig. 2 and reflects the strong influence of rainfall which resulted in dispersal over a large area between January and April (wet, hot season) and subsequent concentration around perennial water sources between May and December (dry, cold and dry, hot seasons). During my investigation (1974–1978) the population was divided into two discrete units. The westerly unit near Otjovasandu comprised one mixed herd of up to 27 animals plus a few solitary bulls which grouped periodically into a bachelor herd. Due to the isolated nature of the westerly unit and because they inhabited terrain which made them difficult to locate, my observations were limited to aerial census and occasional sightings by vehicle. They appeared to be more stable in numbers than the much larger, declining population in the eastern sector of Etosha. The latter constituted 99% of the total population and was concentrated in two areas, namely the Namutoni sub-unit and the Okaukuejo–Halali sub-unit (Fig. 2). Although some interchange occurred between these groups they occupied discrete areas.

2 METHODS

2.1 Aerial census of total population

A total of five censuses using a Hughes 300 C helicopter and a total of three censuses using a Piper Super Cub fixed-wing aircraft were made in the period 1973–78. On average, about 30 hours' flying time by helicopter was required to adequately census the area inhabited by wildebeest, and about 15 hours was needed by fixed-wing aircraft. Wildebeest were counted individually in herds numbering up to 20, and 35 mm photographic transparencies were taken of larger herds for subsequent projection and counting. In relatively small numbers, such as those encountered in Etosha, wildebeest are considered to give reliable counts from a helicopter, with close to 100% sighting, especially with slow flight (Melton, 1978a, b). Since his results were obtained in the thickly vegetated Umfolozi Game Reserve.
FIGURE 2: Seasonal distribution and major migration routes of the wildebeest population in Etosha (1974–78).
in Zululand, I considered the open grasslands and comparatively sparsely vegetated thorn savanna which wildebeest inhabit in Etosha to give very close to 100% sightings of the population. Consequently no upward adjustment of the census figures was made. During aerial censuses I also noted the number of calves, the number of lone, territorial bulls and bachelor herd bulls, as well as the number of neck-banded animals sighted.

2.2 Ground observations for age-sex ratios

Observations on whole herds were made to establish age-sex and social status. Because of the synchronised nature of calving it was possible to identify up to four age classes, namely 0–1 year, 1–2 years, 2–3 years and adult. Sexing of wildebeest is relatively easy, but requires practice (Watson, 1967), and needs no further explanation. I was able to distinguish between mixed herds and bull herds, thereby obtaining a confirmation of the proportion of bull herds found in the population during aerial census. During the dry season when wildebeest concentrated at perennial fountains, a large and representative sample (31%) of the population could be aged and sexed during any one day. This was facilitated by the good visibility at fountains on the edge of the Etosha Pan and by the habit of wildebeest to approach water in file. In this way it was possible to distinguish up to nine age classes during ground observations while a tenth class, namely lone, territorial bulls, could be identified during aerial counts.

2.3 Age determination by tooth attrition

To establish mortality patterns in wildebeest, a total of 283 skulls was recovered from the areas occupied by the eastern population unit of Etosha. I made a chronological table of tooth eruption and infradental attrition, based on data from Talbot and Talbot (1963) and the detailed investigations by Watson (1967) and Attwell (1977) into wildebeest age determination. Because investigation of incremental growth layers of cementum or dentine is time-consuming and not always infallible (Spinage, 1976), especially in older animals which experience root resorption (Watson, 1967), I did not attempt to relate growth layers to age.

Also, the deposition of dental layers may not all be related to tooth attrition; for instance, 18% of the sample investigated by Attwell (1977) was considered unsatisfactory. Furthermore, there is uncertainty whether the deposition rate of dental layers is governed by seasonal factors such as nutrition (Smuts, 1974; Spinage, 1976) or is the result of an endogenous rhythm (Grimsdell, 1973). During my study 10 premolars and molars were sectioned, polished and examined for incremental growth layers under a dissecting microscope at 6–50x magnification. However, the manifestation of several errors in this technique, such as possible mis-

interpretation of accessory and double lines of growth, precluded its objective use and will require more detailed investigation. I therefore relied on tooth eruption sequence which provided an accurate means of ageing wildebeest up to three years. Infradibular attrition, used in conjunction with Attwell’s (1977) data, gave a practical assessment of age classes above three years.

2.4 Predictive modelling

A preliminary model, based on the methods of Starfield et al. (1976) and Shell and Starfield (1977), was tested on a Univac 1106 computer by changing critical parameters which may have influenced the population. The parameters tested were number of lions, yearly kill rate of lions, calf survival rate, and birth rate. The model was initiated with the earliest, reliable census figures and was run for 10 consecutive years (1973–1982) to obtain predictions for change in the wildebeest population. Field data for the period 1973–78 were used to adjust the model to existing situations.

3 RESULTS

3.1 Estimation of total population

The counts made by helicopter and fixed-wing aircraft are given in Table 1.

3.2 Age-sex ratios

Table 2 shows the range and mean yearly ratios of the age-sex and social status of wildebeest in Etosha. The range indicated change in a particular component of the population during the year and was a measure of mortality rate in calves, immatures and sub-adults. In the case of adult bulls the yearly range also reflected their seasonally changing social status.

3.3 Age-sex ratios in mortality

A total of 15 age classes from birth to approximately 14 years was distinguishable and 197 of the 283 skulls could be accurately sexed (Table 3). Although the allocation of yearly age classes to the sample of skulls must be treated with caution because of individual variation in the rate of tooth wear (Watson, 1967; Attwell, 1977) the data are accurate from birth to three years. From three years to 10 years of age there may be a variation of up to one year in the estimated classes and for wildebeest older than 10 years this variation could be up to three years. Nevertheless, the age-sex classes which are subjected to the greatest mortality are clearly evident in Table 3.
TABLE 1: Aerial counts of wildebeest in Etosha (1974–78)

| Year | Month | Numbers counted | Type of aircraft*
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Older than 1 year</td>
<td>Calves</td>
</tr>
<tr>
<td>1974</td>
<td>July</td>
<td>2 574</td>
<td>726</td>
</tr>
<tr>
<td>1976</td>
<td>May</td>
<td>1 782</td>
<td>578</td>
</tr>
<tr>
<td>1976</td>
<td>July</td>
<td>2 034</td>
<td>604</td>
</tr>
<tr>
<td>1976</td>
<td>Dec.</td>
<td>2 078</td>
<td>585</td>
</tr>
<tr>
<td>1977</td>
<td>March</td>
<td>2 576</td>
<td>483</td>
</tr>
<tr>
<td>1977</td>
<td>Sept.</td>
<td>2 673</td>
<td>356</td>
</tr>
<tr>
<td>1978</td>
<td>March</td>
<td>2 069</td>
<td>424</td>
</tr>
</tbody>
</table>

| Mean | 2 247 | 537 | 1 871 | 300 | 74 | 2 783 |
| Mean ± SD | 234 | 124 | 346 | 66 | 49 | 336 |

* H = Helicopter; Fwa = Fixed-wing aircraft.
** Population totals of 3 059 and 2 969 include herds of 423 and 281 wildebeest respectively, which were sighted in Owambela, adjacent to Etosha’s northern boundary. They may have been emigrating or were potential immigrants.

TABLE 2: Structure of the wildebeest population in Etosha in regard to age, sex, reproduction and social status (1976–78)

<table>
<thead>
<tr>
<th>Year</th>
<th>Criteria used</th>
<th>Ground counts</th>
<th>Aerial counts</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>Range %</td>
<td>Mean %</td>
</tr>
<tr>
<td>1976</td>
<td>Calves</td>
<td>1 995</td>
<td>14–27</td>
</tr>
<tr>
<td></td>
<td>Immatures</td>
<td>9–15</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>Sub-adults</td>
<td>7–10</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>Non-pregnant cows</td>
<td>4–10</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>Pregnant cows</td>
<td>24–30</td>
<td>26</td>
</tr>
<tr>
<td></td>
<td>Lone bulls</td>
<td>1–3</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Herd bulls</td>
<td>2–3</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Bachelor bulls</td>
<td>12–17</td>
<td>16</td>
</tr>
<tr>
<td>1977</td>
<td>Calves</td>
<td>2 453</td>
<td>14–26</td>
</tr>
<tr>
<td></td>
<td>Immatures</td>
<td>13–20</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>Sub-adults</td>
<td>11–14</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td>Non-pregnant cows</td>
<td>1–2</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Pregnant cows</td>
<td>28–32</td>
<td>29</td>
</tr>
<tr>
<td></td>
<td>Lone bulls</td>
<td>1–4</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Herd bulls</td>
<td>2–3</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Bachelor bulls</td>
<td>10–15</td>
<td>12</td>
</tr>
<tr>
<td>1978</td>
<td>Calves</td>
<td>7 274</td>
<td>16–24</td>
</tr>
<tr>
<td></td>
<td>Immatures</td>
<td>11–15</td>
<td>13</td>
</tr>
<tr>
<td></td>
<td>Sub-adults</td>
<td>9–11</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>Non-pregnant cows</td>
<td>1–5</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Pregnant cows</td>
<td>28–32</td>
<td>30</td>
</tr>
<tr>
<td></td>
<td>Lone bulls</td>
<td>1–7</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Herd bulls</td>
<td>2–4</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Bachelor bulls</td>
<td>14–18</td>
<td>16</td>
</tr>
</tbody>
</table>

3.4 Wildebeest population model

The trend in the population total was simulated by applying realistic values for the model's selected parameters (Table 4). Thereby the population model totalled 2 501 in 1978 which was close to the final aerial count of 2 493 wildebeest. Having established this preliminary model I then “tuned” the data input as suggested by Starfield et al. (1976) to find which parameter levels would have to exist to maintain the population at its 1978 total (Table 4). Subsequently, I purposely altered each major parameter by an increase of 10% and a decrease of 10% (Fig. 3) to predict the population trend until 1982. A similar procedure (Shiel and Starfield, 1977) was used on wildebeest and zebra population models to test the sensitivity of parameters in the Kruger National Park. In the case of Etosha's wildebeest these increases and decreases were realistic and could conceivably occur if predation, calf survival and reproductive success were favourably or unfavourably influenced. The model I used was kept relatively simple to avoid confounding the predictions (Starfield et al., 1976).

TABLE 3: Mortality patterns in wildebeest in Etosha (1976–78)

<table>
<thead>
<tr>
<th>Estimated age in years</th>
<th>No. of skulls collected</th>
<th>Percentage of sample</th>
<th>Cumulative total*</th>
<th>Sex ratios</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Bull</td>
</tr>
<tr>
<td>0–0.5</td>
<td>1</td>
<td>&lt;1</td>
<td>1</td>
<td>?</td>
</tr>
<tr>
<td>0.5–1.0</td>
<td>4</td>
<td>1</td>
<td>2</td>
<td>?</td>
</tr>
<tr>
<td>1–2</td>
<td>17</td>
<td>6</td>
<td>8</td>
<td>3</td>
</tr>
<tr>
<td>2–3</td>
<td>22</td>
<td>8</td>
<td>16</td>
<td>10</td>
</tr>
<tr>
<td>3–4</td>
<td>41</td>
<td>14</td>
<td>30</td>
<td>20</td>
</tr>
<tr>
<td>4–5</td>
<td>48</td>
<td>17</td>
<td>47</td>
<td>23</td>
</tr>
<tr>
<td>5–6</td>
<td>47</td>
<td>17</td>
<td>64</td>
<td>35</td>
</tr>
<tr>
<td>6–7</td>
<td>30</td>
<td>11</td>
<td>75</td>
<td>18</td>
</tr>
<tr>
<td>7–8</td>
<td>32</td>
<td>11</td>
<td>86</td>
<td>18</td>
</tr>
<tr>
<td>8–9</td>
<td>12</td>
<td>4</td>
<td>90</td>
<td>6</td>
</tr>
<tr>
<td>9–10</td>
<td>8</td>
<td>3</td>
<td>93</td>
<td>2</td>
</tr>
<tr>
<td>10–11</td>
<td>6</td>
<td>2</td>
<td>95</td>
<td>4</td>
</tr>
<tr>
<td>11–12</td>
<td>6</td>
<td>2</td>
<td>97</td>
<td>4</td>
</tr>
<tr>
<td>12–13</td>
<td>4</td>
<td>1</td>
<td>98</td>
<td>2</td>
</tr>
<tr>
<td>13–14</td>
<td>5</td>
<td>2</td>
<td>99</td>
<td>1</td>
</tr>
<tr>
<td>&gt;14</td>
<td>0</td>
<td>0</td>
<td>100</td>
<td>0</td>
</tr>
</tbody>
</table>

|                  |                         | 100       | 100       | 143     | 54     | 197 |
| Totals           |                          | 283       |           |         |        |     |

*The cumulative total is biased in favour of adult skulls because of the rapidity with which carcasses of young animals are obliterated by predators and scavengers. Consequently the data cannot be used to establish a true age structure of the population.
4 DISCUSSION

4.1 Population structure and mortality patterns

The structure of the Etosha wildebeest population was established by taking the mean of three years of ground counts (1976–78) which were considered to be more detailed and accurate than total aerial counts, except in the case of lone, territorial bulls where aerial counts were used (Table 2). Nevertheless, the aerial counts gave a reasonably similar population structure to that obtained from ground counts, thereby confirming that the ground counts were representative of the population. The detailed population structure is given in Table 5 and I have chosen to compare it with the results of a similar investigation by Attwell (1977) which was, however, based mainly on aerial observations. This comparison attempted to establish which components of the two populations were similar, in view of the fact that Attwell (1977) estimated a 3.8% decline in the population he studied.

From the data presented there appeared to be proportionately fewer full-grown bulls in Etosha and consequently relatively more adult cows in the population (1 bull : 1.57 cows in Etosha, compared to 1 bull : 1.49 cows (Attwell, 1977)). This suggests that bulls in Etosha were subjected to a higher mortality rate and is borne out by the sex ratio from skulls collected in Etosha (Table 3) which was 1 bull : 0.38 cows ($X^2 = 146.69$;
TABLE 6: Comparison of birth-rate and calf survival of wildebeest in Etosha with other populations.

<table>
<thead>
<tr>
<th>Area</th>
<th>Mean seasonal rainfall (mm)</th>
<th>Criteria measured (mean)</th>
<th>% Calves in total population</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Birth-rate 2-year-olds</td>
<td>Adults</td>
</tr>
<tr>
<td>Western Masaiiland</td>
<td>762</td>
<td>0,83</td>
<td>0,95</td>
</tr>
<tr>
<td>East Africa¹</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Serogeti National Park</td>
<td>782</td>
<td>0,37</td>
<td>0,96</td>
</tr>
<tr>
<td>Tanzania²</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kruger National Park</td>
<td>584</td>
<td>0,32</td>
<td>0,92</td>
</tr>
<tr>
<td>South Africa³</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Zululand</td>
<td>677</td>
<td>0,11</td>
<td>0,92</td>
</tr>
<tr>
<td>South Africa⁴</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wandic National Park</td>
<td>550</td>
<td>0,0</td>
<td>0,74</td>
</tr>
<tr>
<td>Rhodesia⁵</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Etosha National Park</td>
<td>469</td>
<td>0,0</td>
<td>0,86</td>
</tr>
<tr>
<td>South West Africa⁶</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

¹ Talbot and Talbot (1962)
² Watson (1967)
³ Braack (1973); Starfield et al. (1976)
⁴ Attwell (1977)
⁵ Estes (1965); Higgins (1969)
⁶ Present study

P<0,001). In the Kruger National Park adult wildebeest sex ratios were more disparate (1 bull : 2,6 cows) which indicates an even greater mortality in bulls, probably due to a high rate of predation (Braack, 1973). Disproportionate mortality of males in free-ranging ungulate populations is a well established phenomenon (Watson, 1967; Estes, 1968; Mentis, 1972; Crowe and Liversidge, 1977; Hamilton et al., 1977; Sinclair, 1977). Moreover, increased mortality in adult bulls is, in turn, an indicator of predation pressure (Schaller, 1972) and lone, territorial bulls may be particularly vulnerable to predation (Watson, 1967; Estes, 1968). Thus, when it is considered that lone bulls made up only 3,7% of the Etosha population compared to 5,0% in the Kruger National Park (Braack, 1973) and 9,0% in Zululand (Attwell, 1977), it is apparent that predation was a significant factor in Etosha’s bull wildebeest mortality. This higher mortality in males is also illustrated in the ratio of immatures in Etosha (1 bull : 1,17 cows) which is closer to parity than the sub-adult ratio of 1 bull : 1,53 cows or the adult ratio of 1 bull : 1,57 cows. Thus there appears to be a logical progression of predation on the maturing bulls if it is considered that the sex ratio of wildebeest at birth is not significantly disparate (Braack, 1973).

Bachelor herds in Etosha were larger than those in Zululand and this would afford the individual members a greater measure of protection from predators through increased vigilance (Powell, 1974; Siegfried, 1980). The greater number of bachelor bulls present in Etosha, compared to Zululand may, in part, reflect the survival value of a larger herd size. With regard to breeding herd bulls the lower percentage of this component in Etosha can be explained by the fact that proportionately fewer and larger breeding herds, each with a herd bull in attendance, existed in Etosha than in Zululand.

Calf survival in Etosha appeared to be higher than in Zululand (0,5 compared to 0,4; Table 6) and is confirmed by the higher percentage of calves in the total population and by the ratio of calf : adult cow.

When the mortality patterns in Etosha wildebeest are examined (Table 3) it is evident that the heaviest mortality in adults of both sexes occurred in the three- to six-year-old group (48% of all skulls found). Furthermore, 91% of all adult deaths had taken place at the age of 10 years. No interpretation of mortality in wildebeest younger than three years was attempted from skulls found because of the rapidity with which immature skulls and horns are destroyed. Nevertheless, the available data show that at least 14% of population mortality occurred in the one- to three-year-old age group.

In comparison, Attwell’s (1977) findings in Zululand were that 48% of adult mortality occurred in the four- to six-year-old age group and that at 10 years of age 74% of the adults had died. Therefore mortality in four- to six-year-old wildebeest was the same in Etosha’s and Zululand’s samples, but the four- to 10-year-old mortality rate was higher in Etosha (89%). Consequently, 26% of Zululand’s adult wildebeest attained an age of more than 10 years, while in Etosha only 11% exceeded this age.

In summary, it appeared that the mortality patterns in neo-natal calves among Etosha’s wildebeest were typically high. Also, up to the age of six years mortality was very similar to declining populations in the Kruger National Park (Braack, 1973) and Zululand (Attwell, 1977). Adult mortality in Etosha was greater than other
populations, up to the age of 10 years, with only 9% of the population surviving beyond this age. When compared to other declining populations such as in Zululand and the Kruger National Park it seems as if maximum longevity of Etosha's wildebeest is approximately 14 years and therefore about seven years less than the maximum age of 21.5 years (Braack, 1973) and 21 years (Attwell, 1977) recorded in these other populations. The data from my investigation are strongly suggestive of a normal calf mortality while the adult segment, especially lone, territorial bulls, are subjected to heavy mortality due to a combination of predators and disease. The endemic nature of anthrax in Etosha appears to have led to an unnatural predator—prey live mass ratio (Berry, 1981). This in turn has resulted in a situation where mortality exceeds the birth rate and a consequent decline in population.

4.2 The Etosha population model in comparison with other areas

The model I used simulated Etosha's wildebeest population at its annual peak in numbers, namely, the end of the calving season, which is during March. To keep parameters simple, only four age classes were used and sexes were not distinguished. Three critical parameters were selected to represent intrinsic and extrinsic pressures which may have limited the population. These are birth rate, calf survival which leads to recruitment rate, and mortality of animals older than one year. To simulate conditions in Etosha, the mortality was ascribed to the existing lion population and their yearly kill rate per adult, hunting lion. Furthermore, in doing this, I assumed that all wildebeest older than one year which died were eventually eaten by lions, although the proximate cause of death may have been disease, especially anthrax. In estimating the adult lion population and their kill rate, I referred to punch card data in the Etosha Ecological Institute from 1973—1978 and my observations during this study (n=912 pride compositions; n=139 wildebeest carcasses).

Calf survival rate was taken at 0.5 on average and simulated the mortality from the end of the calving period to one year of age which was established by observation. To simulate adult birth rate I calculated that, on average, 63% of the adult population were cows and that they had a conception rate of 87% (Table 2). Consequently, the upper limit for adult birth rate would be 0.54. However, to reflect losses from aborted pregnancies, still-born calves and calf mortality at a very young age which my observations on calf survival counts did not detect, a lower value of 0.35 was used. In determining this figure, I took into account the fact that up to 50% of new-born calves may die (Taibol and Talbot, 1963). Unlike the wildebeest population at the Kruger National Park where precociousness in two-year-olds resulted in a birth-rate of 0.21 in this age group (Starfield et al., 1976), I did not record any pregnancy or calving by immature wildebeest in Etosha. Although the seasonal rainfall influenced the wildebeest population, it tended to confound the prediction of population trend because compensatory factors may have been brought into play. For example, years of low rainfall decreased calf survival rate, but this was compensated for by a decrease in predation, because the shorter grass cover afforded wildebeest improved visibility. Conversely, in years of high rainfall the increase in calf survival was offset by improved conditions for predators. Impinging on these patterns was the considerable effect of disease, notably anthrax, which varied in intensity depending on the temporal and spatial distribution of the rainfall (Van Ness, 1971).

Consequently, anthrax outbreaks may be as severe under low rainfall conditions as when heavy rains occur (Ebedes, 1976). As a result, I have purposely “tuned” the lion population and their kill rate in the model to include the anthrax component of mortality, leaving the parameters of birth-rate and calf survival constant and based on a calculated mean.

It is clear from the model that extrinsic factors such as rainfall, predation and disease are less predictable than intrinsic properties of the population, namely birth-rate and calf survival, although birth-rate appears to be a very sensitive parameter for change in the population as will be discussed subsequently (Section 4.3).

If the Etosha wildebeest population is compared to other free-ranging populations in regard to birth-rate and calf survival, then the former parameter is somewhat lower while the latter is considerably higher than most other populations with the exception of the Wankie National Park, Rhodesia (Table 6). Etosha and Wankie have similar rainfall regimes and it may be that their aridity resulted in the apparently inability of two-year-old cows to reproduce, as well as a lower birth-rate in adult cows. However, both Etosha and Wankie had very similar calf survival rates and in both areas calves formed 22% of the total population. Reviewing the data in Table 6 a general trend is evident, namely, that well-watered areas which support large populations of wildebeest such as East Africa appear to have higher birth-rates than the arid areas of Wankie and Etosha. In the Kruger National Park and Zululand, both areas of moderate rainfall, wildebeest birth-rates are intermediate to those in East Africa and Etosha. Conversely, the huge wildebeest herds encountered in East Africa result in a low calf survival rate, in which calf—cow separation is a major factor (Watson, 1967). The smaller herd sizes in Zululand, Wankie and Etosha appear to favour calf survival.

4.3 Sensitivity of parameters in the model to change, and future predictions

The effects of a 10% change in each of the parameters selected for the model of Etosha's wildebeest population are clearly evident in Fig. 3. The order of increasing sensitivity to change is calf survival, lion population, lion.
kill rate and wildebeest birth-rate. The parameters required for an hypothetically stable population are detailed in Table 4. It is unlikely that the population of c. 2,500 wildebeest in 1978 will remain at this level, since African ruminant populations display cyclic fluctuations (Sinclair, 1973).

The modelled changes of ±10% which I have applied to selected parameters could conceivably occur within the space of one seasonal year and indeed they could be much greater in the event of a natural catastrophe. It is worth noting that a 10% change in calf survival predicts an increase of 1.0% and a slightly larger decrease of 1.1% in population numbers after one year. Similarly, a 10% decrease in the lion population results in a 1.4% increase in wildebeest, while a 10% increase reduces the population by 1.9%. A decreased kill rate gives 1.6% more wildebeest, whereas an increased kill rate of the same magnitude (10%) gives 2.4% fewer wildebeest. The birth-rate is evidently the parameter most sensitive to change, namely: 3% population increase or decrease in response to a positive or negative change of 10%.

If these relatively small changes in parameters are projected to 1982 then the cumulative effect is noticeable. For example, a continued increase in calf survival of 10% results in a population increase of 5.6% and a continued 10% decrease in calf survival results in a population decrease of 5.1%. In comparison, the more sensitive parameter of birth-rate gives 8.4% increase and 7.8% decrease respectively. These predictions are for changes in single parameters only and if two or more parameters were to change simultaneously in favour or against the wildebeest population the consequences could be considerable. For instance, it is possible that prolonged drought could decrease birth-rate and calf survival and also increase adult mortality through an epidemic of anthrax (the latter effect would be reflected in the model as an increased lion kill rate).

These projections have been made with the view to underlining the sensitivity of the Etosha wildebeest population to relatively small changes in their environment. The consequences of a drastically altered environment in other wildebeest habitats, notably the Kruger National Park, are evident in the findings of Shill and Starfield (1977) that wildebeest are not as resilient to change as, for example, Burchell’s zebra. It follows that any attempt to modify a particular parameter in Etosha, for instance by culling lion, may allow the wildebeest population to recover, but could very well lead to an explosion of the zebra population. Management plans should as a result be made with circumspection, since the model proposed here has been purposely simplified, thereby isolating the wildebeest population from the remaining ecosystem to a great extent. Nevertheless, the model I have presented serves as a first approximation by applying available data. It can be used, albeit cautiously, as a baseline to predict what would happen to the wildebeest population in a particular situation.

5 SUMMARY

Following an apparent drastic decline in the wildebeest population in Etosha from c. 25,000 to 3,000 over a period of 20 years, a series of total counts were made by aircraft to establish the population size more accurately. During the five-year study period the numbers decreased by a further 24% (3,300 to 2,500).

Age-sex ratios were established by seasonal observations over a period of three years. Calf percentage was normal in comparison to other areas in Africa, but lone, territorial bulls were proportionately fewer than another declining population in Zululand. However, because of relatively large bachelor herds, total percentage of bulls in the population did not differ greatly from other areas. The size of Etosha’s breeding herds was, on average, 34 animals compared to 14 animals in the Zululand population. Consequently, proportionately fewer herd bulls were present in Etosha. Maturing wildebeest reflected a disproportionate, sex-linked mortality favouring the cows; the adult ratio being 1 bull: 1.57 cows which was closer to parity than sex ratios in the Kruger National Park, but more disparate than in Zululand.

From a sample of 283 collected skulls, mortality patterns were related to age by tooth attrition and to sex ratios by horn development. Immature animals were under-represented in the sample, invalidating the use of skulls as a means of gauging immature mortalities. Adult mortality in both sexes was greatest between three and six years of age (48% of all skulls found) and by 10 years of age 91% of all adults had died. The maximum longevity recorded was approximately 14 years. These mortality patterns correspond well with those found in two other declining populations except that fewer wildebeest in Etosha survived beyond 10 years and maximum longevity was reduced by about seven years. A combination of diseases (anthrax) and predation pressure appeared to be the most likely cause of this early adult mortality.

A computer model was used to simulate the declining population by manipulating the critical parameters of birth-rate, calf survival and combined mortality in all other age groups. Plausible mean values were 0.35 for birth-rate which took into account neo-natal deaths and 0.5 for calf survival. Mortality rates in animals older than one year were established from field observations and gave a yearly range of 260–700 during the five-year period on which the population was modelled. This mortality exceeded the recruitment rate of two-year-old wildebeest to the breeding stock. Lions were assumed to be the ultimate factor in wildebeest mortality for the purpose of the model although anthrax disease was in many instances the proximate factor. Birth-rate was found to be the population parameter which was the most sensitive to change, followed by lion kill rate, the number of lions and lastly calf survival rate. Furthermore, overall birth-rate in Etosha wildebeest appeared to be lower than most other free-ranging populations, partly because cows in their second year did not reproduce.
This lower birth-rate appeared to be compensated to a certain extent by a normal to above average calf survival rate.

Projections of population trends until 1982 showed that relatively small changes in the parameters, namely a 10% increase or decrease, would result in changes of between 5 and 9% in total population. However, in the event of a succession of major, unfavourable changes in the environment, such as could be expected under drought conditions, the wildebeest population would decline drastically. The model was a gross simplification of the complicated ecological processes governing the wildebeest population and did not consider the species interactions which would be effected in the event of changed parameters.

When viewed against the past history of Etosha, where changed conditions have resulted in the present drastically reduced wildebeest population, it seems unlikely that the former numbers will be regained. Instead, management plans should be directed at maintaining the wildebeest population at its present level. Since disease, notably anthrax, appeared to be the proximate cause of decline during the study, further research in this field is essential. The culling of lion or other predators is not recommended because it may only serve to alleviate the symptoms. The obvious choice is to treat the cause, not the effect.

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SHORT NOTE

Diet of the owl *Claucidium perlatum* in the Etosha National Park

by

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During recent years the analyses of prey items recovered from owl pellets, in particular those of the barn owl, *Tyto alba*, have received much attention (Coetsee, 1963; Dean, 1973; Stuart, 1975; Vernon, 1971 and others).

Perusal of available literature shows, however, that little has been recorded concerning the smaller owl spectrum in southern Africa. The diet of the diminutive pearl-spotted owl (*Claucidium perlatum*) is given as insects, lizards and very small mammals, small snakes and birds (Mackworth-Praed and Grant, 1952) and as mainly large insects, small mammals and birds (Roberts' Birds of S. Africa). Pellets from this owl, collected along the Fish River south of Mariental, contained fragments of lizards, bats, insects and rodents (Vernon, 1971).

Over the period October 1975 to May 1976 a total of 154 prey items was recovered from 85 pearl-spotted owl pellets, collected within the Etosha National Park in Namibia. The results of this analysis are contained in Table 1.

**COMMENTS ON PREY GROUPS**

1 *Arthropods*: These were by far the most important group, representing 65.1% of the total prey items, with diurnal Sollfuges dominating. Of importance, however, was the recovery in the January sample of six specimens of the Formicidae and a single complete Gastrophilidae larva (prey items not included in Table 1). These items are unusual and may have been ingested with carrion. The fragmented specimens (heads only) of the Formicidae would tend to support this.

2 *Mollusca*: The Molluscs, *Namibiella hottentota* and *Xerocerasitus nitens* represented 19.4% of the total prey items recovered. Shells were recovered from pellets collected during November and December only. The frequency of occurrence in pellets was 89% for November and 20% for the December sample. Out of a total of 38 prey items recovered for November 27 (71%) were mollusc shells. The possibility that mollusc shells were of secondary origin cannot be ruled out but the overall large percentage recovered in relation to other prey items makes this improbable. This is further supported by the fact that the November sample contained no prey items that could be remotely suspected of feeding on molluscs (see Table 1). Both *Namibiella* and *Xerocerasitus* are seasonally plentiful (after rains) over much of the Etosha National Park.

3 *Reptilia*: A total of 15 reptiles, representing at least four species and making up 9.7% of the total prey items, was recovered. The majority of this prey group was represented by the well-known diurnal lizards, *Mabuyu varigata* and *Agama hispida*.
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Short Note

Aantekening

A. T. van der Merwe

From a total of 29 oviparous reptiles found at one site in Etosha National Park, only 52.1% were found in the sites visited during the dry season in the south-western part of the Park. 276