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Journal of Nature Conservation and Desert Research, South West Africa

# MADOQUA

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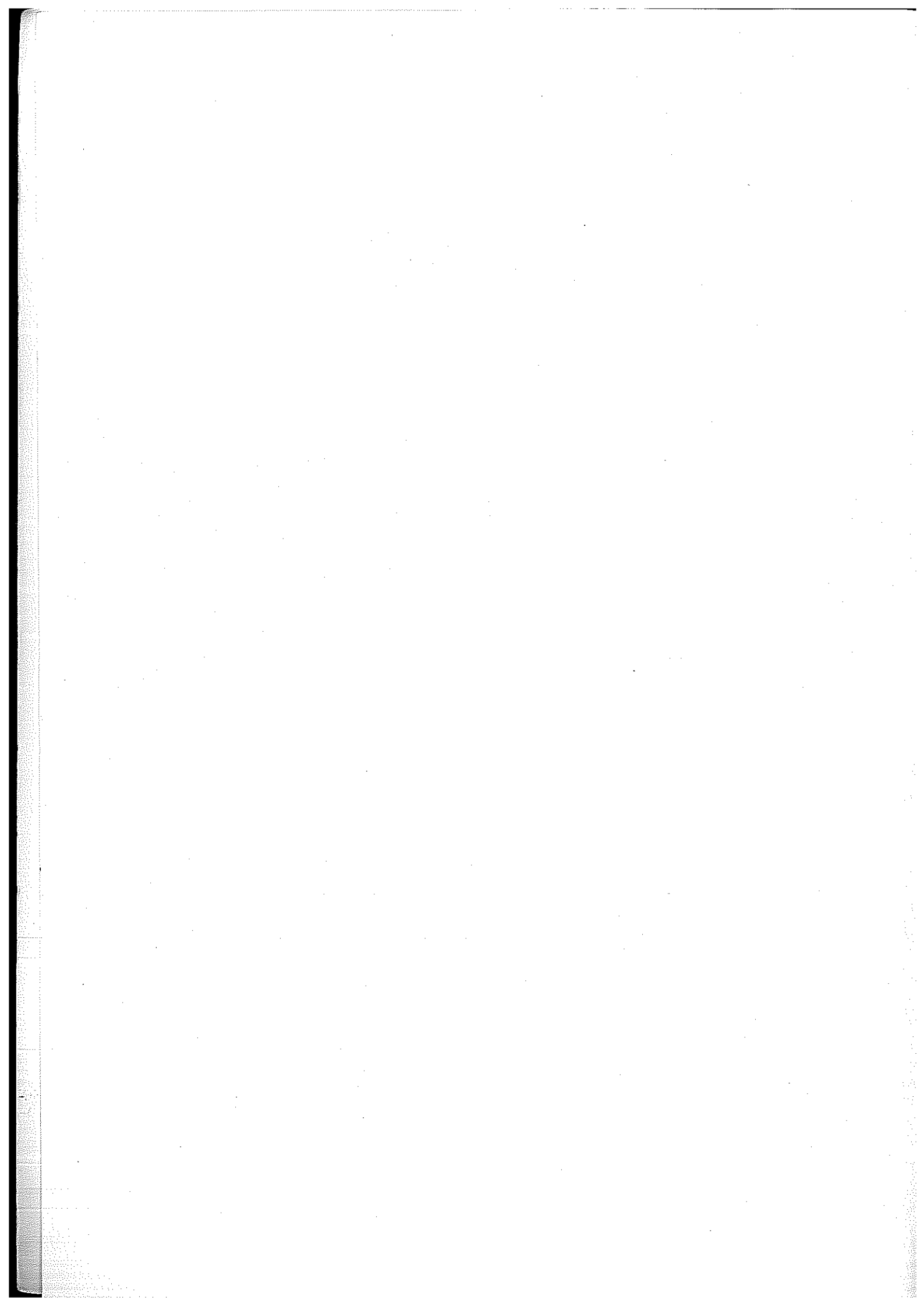
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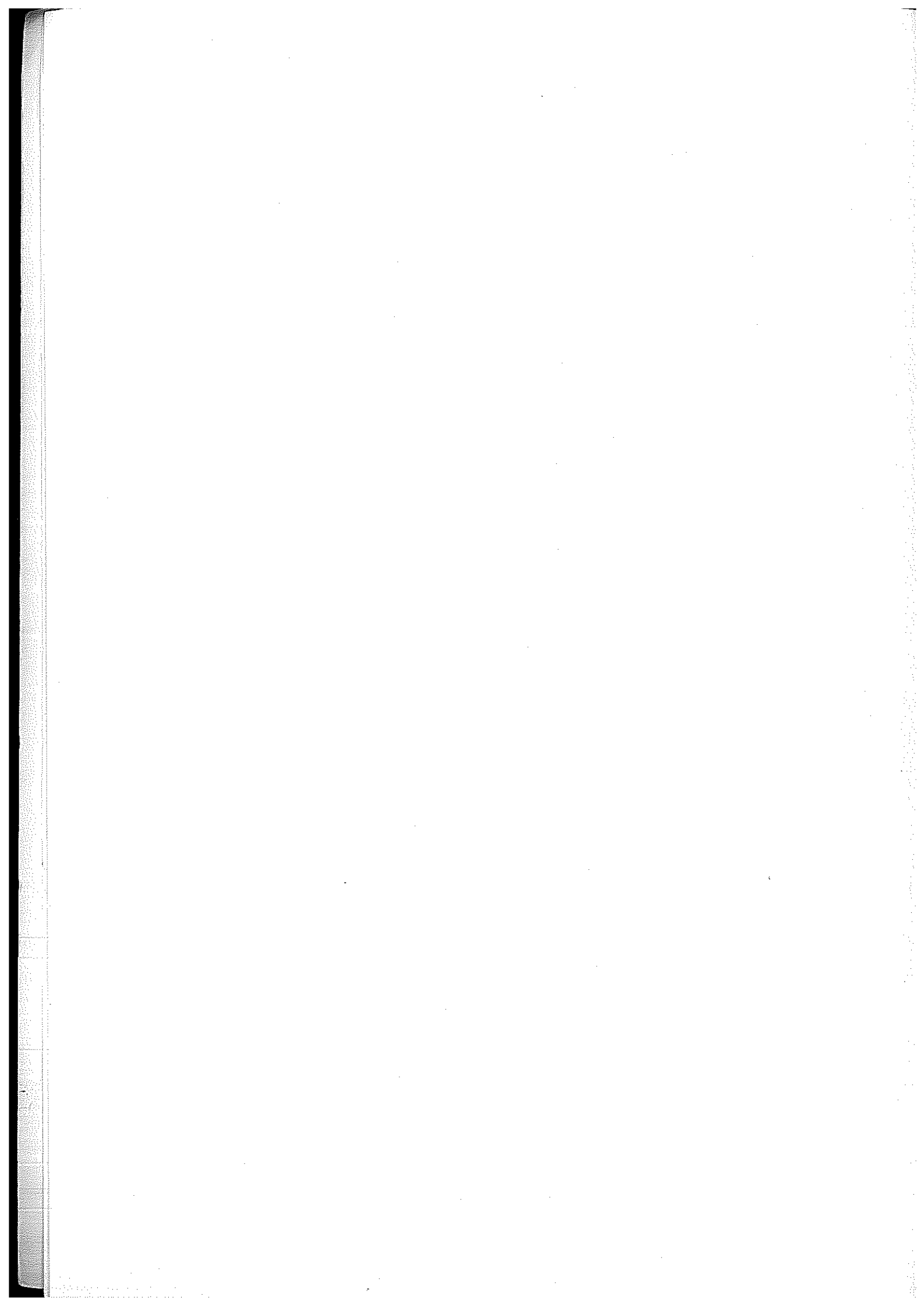


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# Aggressive behaviour of oryx antelope at water-holes in the Etosha National Park

by

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## ABSTRACT

In June and July 1978, 584 agonistic encounters of *Oryx gazella* were recorded in Etosha National Park. Generally, the fighting techniques and the displays were the same as in *Oryx beisa* (Walther 1958, 1978a); however, a particular display, the "symbolic stab over the shoulder", seemed to be unique in *Oryx gazella*. All the fights were horn-to-horn contacts. Body attacks were rare. Among adult bulls, one-sided displays decided many of the encounters. Next in frequency were fights. One-sided displays also decided most of the interactions of bulls with cows. In encounters among females, the same fighting techniques and displays were used as in bulls; however, there were differences in frequency. The immature males usually sparred without prior displays. The most important situational motivations of aggressive interactions were co-ordination of group activities, maintaining or enlarging individual distances, meeting strangers, sparring matches, contagion, and taking offense. These situational motivations were the same at water-holes as away from water-holes. Only the proportion of encounters due to meeting strangers was considerably greater at water-holes as compared to animals in other areas. Competition over water was rare.

## 1 INTRODUCTION

In June and July 1978, I visited the Etosha National Park in South West Africa where I observed aggressive interactions in the South African oryx antelope (*Oryx gazella*) in order to obtain data for a qualitative comparison to the agonistic behaviour of the East African oryx (*Oryx beisa*), studied previously in captivity (Walther, 1958, 1965a) and in the Serengeti National Park (Walther, 1978a, 1979).

A further stimulation came from the article of Hamilton *et al.* (1977) on the behaviour of *Oryx gazella* at Namib Desert water-holes. The sand-dune region appears to be a relatively marginal habitat for oryx. Hamilton's investigation was made during the extremely dry summer 1972–73, when the population was under an unusual environmental stress. Virtually all the calves and quite a number of the adults died, and many of them were in poor condition. Water was only available from very small water-holes and from deep wells which the oryx had excavated with their forefeet in the river-bed sands. Under these conditions, the oryx showed strong competition over water. The males displaced the females from the water-holes, drinking individuals were challenged by the waiting ones, body attacks (stabbing the flank or the rump) were frequent, and the aggressive interactions sometimes resulted in serious and probably lethal injuries (Hamilton *et al.*, 1977).

In the Etosha National Park, water is available in a number of relatively large water-holes, many of them artificially reinforced by windmills. As du Preez and Grobler (1977) rightly state, a minimum distance of about one metre is maintained between oryx individuals at these large water-holes, and drinking usually proceeds without aggression. On the other hand, also in Etosha, intraspecific aggression of oryx antelope in the vicinity of water-holes is so striking and common that it is particularly mentioned in the tourist guide of this park. In order to investigate these, at first sight, somewhat controversial facts, I gathered some quantitative data on the aggressions of oryx at Etosha water-holes and its situational motivations.

## 2 MATERIALS AND METHODS

According to annual counts, the oryx population in the Etosha National Park ranged between 2 500 and 3 900 animals during the last five years (Berry, pers. comm.). In June and July 1978, I spent 36 days and 180 recorded observation hours with oryx in Etosha. The water-holes where I observed the animals were Okondeka, Adamax, Ozonjuitjimbari, Renostervlei and Dinteri. Apart from water-holes and their vicinity, I watched oryx between Okondeka and Adamax, between Adamax and Leeubron, and between Kapupuhedi and Gemsbokvlakte, for 8 days with 47 hours of observation.

I observed from a car at distances between 30 to 300 m with Zeiss Dialyt 10 × 40 binoculars, and dictated the observations into a tape recorder. Pictures were taken with a Leicaflex and Novoflex telelens  $f = 64$  cm.

I distinguished the following age classes: juveniles, adolescents, sub-adults, and adults. Juveniles (calves) differed from all the other classes by their (brown) colour and by lack or incompleteness of the (black) face and body markings.

Adolescents were sometimes not considerably taller than the biggest of the juveniles; however, they had the colour of the adults and their face and body markings were more or less complete. Their horns were more than 10 cm long.

The sub-adults were at least three quarters of the size of an adult, and their horns also were about three quarters of adults' horns. Since the adolescents and the sub-adults comprised a relatively small portion of the population, the numbers of encounters observed in these two age classes were relatively small, and in the following presentation, they were often united to one class (immatures).

Any animal which had reached full size, was considered to be adult. Among the adults, certain, usually highly dominant individuals were strikingly more massive in body than the others. Thus, it was possible to distinguish sub-classes within the adults. However, they were often difficult to determine at larger ranges and/or in fast events, particularly when the latter happened in groups of some size. In the following, therefore, I refer to these sub-categories within the adults only when describing single cases, but I do not use them in more general, quantitative evaluations.

As forms of aggression, I considered several kinds of threat and dominance displays (such as broadside position, erect posture, head-sideward inclination, sideward-angling of the horns, symbolic stab over the shoulder, frontal presentation of the horns, etc. — see below), fighting (any form of horn contact), body attack (stabbing the other's flank or rump with the horns), the rush (a short run with presented horns toward the other), and the chase (running after the other over a longer distance).

Any encounter in which at least one of the animals involved showed at least one of the forms of aggression mentioned above was considered to be an aggressive interaction. Besides the forms of aggression, I always recorded sex and age class of the combatants, the situation which led to the encounter, and its outcome. In this way, I took notes of 584 agonistic encounters.

Some of the following tables are based on encounters, and some on forms of aggression. The numbers of encounters and forms of aggression coincide in those cases in which only one form of aggression was used per encounter. Sometimes, however, several forms of



aggression were used in the same encounter, e.g., when one or both opponents threatened each other, came up to a fight, and then the one turned for flight and was chased by the victor. In this case we have one encounter but three forms of aggression (threat, fight, chase).

Furthermore, an encounter or a form of aggression respectively, can be one-sided or reciprocal. Some forms of aggression are necessarily reciprocal, e.g., a fight. Others are necessarily one-sided, e.g., a chase. Some forms of aggression could theoretically be reciprocal, but were only observed in one-sided form, e.g., the rush or the body attack. Finally, some forms of aggression were both one-sided and reciprocal performances. This was mainly true for the threat and dominance displays, depending whether only one or both partners showed the same or, at least, equivalent displays. When one of the animals involved responded with a clearly inferior display (e.g., head-low posture) to a more offensive or dominant display of the challenger (e.g., broadside display in erect posture and/or with a symbolic stab over the shoulder, etc.), this also was counted as a case of one-sided display or encounter, respectively. More about definitions and methods used in the quantitative evaluations is given with the tables below.

### 3 RESULTS AND DISCUSSIONS

#### 3.1 Distribution of encounters within sex and age classes

##### 3.1.1 Results (Table 1)

Table 1 shows the distribution of the (584) agonistic encounters within the single sex and age classes. Encounters of juveniles were few because oryx calves did not come to the water-holes. Since sub-adults and adolescents comprised relatively small classes within the population, the numbers of encounters were correspondingly small. Thus, the relatively small numbers of encounters in these age classes do not necessarily imply that they would be less aggressive than the others.

I did not always record how many animals were present or how many of them were males or females. However, I can safely say that at least as many females came to the water-holes as males. Thus, the larger number of aggressive encounters of adult males is due to the fact that in oryx, as in so many species, males are more aggressive than females.

Each sex and age class had the majority of its encounters with animals of their own class (260 out of 428 in adult males; 95 out of 158 in adult

TABLE 1: Distribution of the observed agonistic encounters (N=584) within sex and age classes

	: ad♂	: ad♀	: sa♂	: ado♂	: sa♀	: ado♀	: juv
ad♂	260	149	14		5		
ad♀	7 (+18)	95	6	7	11	1	3
sa♂	(2)		14	1		1	
ado♂			(1)	8			1
sa♀		(2)					
ado♀			(1)				
juv		1		(1)			

In the case of a one-sided aggression, an encounter was counted only for that combatant that behaved aggressively. The numbers in parentheses are doubled due to the involvement of opponents from different classes in reciprocal encounters.

Abbreviations: ad = adult, sa = subadult, ado = adolescent, juv = juvenile.

females, 14 out of 18 in sub-adult males, 8 out of 10 in adolescent males).

### 3.1.2 Discussion

In principle, the same results have been obtained in other bovid species which were quantitatively investigated in a comparable manner (e.g., Geist, 1971, Walther, 1978b).

Another result of such previous investigations was that next in frequency were agonistic encounters with the neighbouring class. For example, in Thomson's gazelle (*Gazella thomsoni*), the next neighbouring class to (non-territorial) adult males were the sub-adult males, whereas adult tommy males had considerably less interactions with adult females (Walther, 1978b). Obviously, this was different in *Oryx gazella* where interactions of adult males with females were next in frequency to those of males among each other or of females among each other.

In the *Oryx beisa* I observed in Serengeti (Walther, 1978a), the proportion between the aggressions of adult males toward adult females (6) as compared to the encounters of adult males among each other (95), was 1:15.8. At first sight, this is quite a difference when compared to the *Oryx gazella* in Etosha where this proportion was 1:1.7. However, one may argue that the *Oryx beisa* in Serengeti were well-defined migratory herds invading a new area, and that this special situation may have influenced their behaviour. In captive *Oryx beisa* (Walther, 1958, 1965a), encounters between males and females were quite frequent; however, here usually only one adult male was kept with several females, i.e., the males did not have partners other than females with which to interact. Finally, also in the *Oryx gazella* in Etosha, the aggressions of males toward females were considerably more frequent at water-holes than in other situations (see below). In short, it is not certain whether the comparatively great numbers of intersexual interactions of *Oryx gazella* at Etosha water-holes and at Namib Desert water-holes (Hamilton *et al.*, 1977) are characteristic of this species, or whether they are largely due to special social and/or environmental situations.

## 3.2 Aggressive behaviour patterns

### 3.2.1 Results

According to my observations, the *fighting techniques* of the South African oryx are not qualitatively different from those of the East African oryx. Since these fighting techniques have been described in previous publications (Walther, 1958, 1965a, 1978a, 1979), a short review is sufficient.

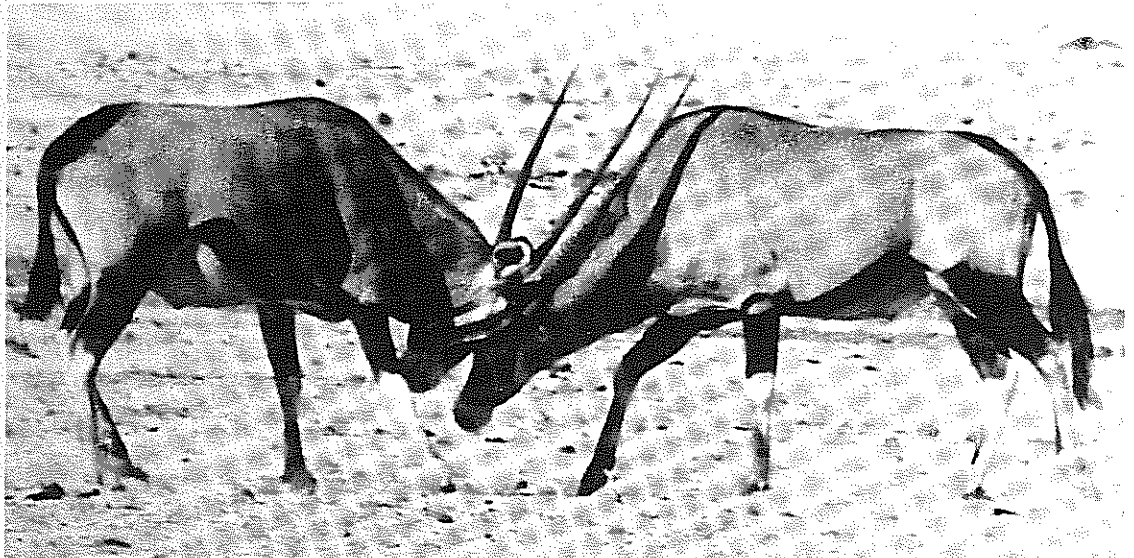
The orientation of the fighters to each other ranges from a frontal (Plate 1a, b) to a rectangular (Plate 3a) to a more or less parallel position (Plate 1c), and these

positions can change during a fight. Contacts are made with the horns in all these positions. Fighting oryx tend to drop down to their knees (Plate 2c, d), however, by far not as readily and regularly as e.g., *Boselaphus*, *Damaliscus*, *Alcelaphus*, and *Connochaetes* species.

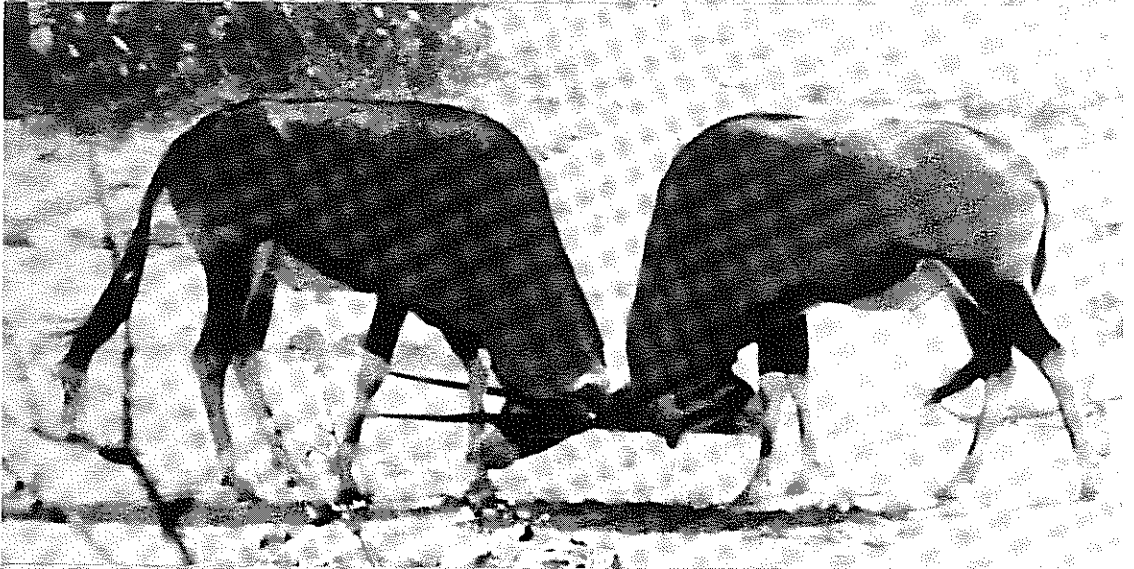
Except for very brief encounters, fights consist of bouts interrupted by pauses during which the opponents stand more or less frontally to each other, or they walk or gallop parallel to each other. Threat displays, object aggressions, pawing the ground, defecation, sideward turning of the head, or (rare in oryx) self-scratching may sometimes be shown in these pauses.

The most important fighting movements of oryx are: simple butt (Plate 2a — a vehement nodding movement of the head), forward-downward blow (in which the whole neck is involved) which is often applied in an oblique form (e.g., from right-above downward to left-below), forward thrust (with horns near and more or less parallel to the ground — Plate 1b), forward dash (with horns held upward), twist (Plate 2c — a levering movement to the right and the left), sideward swing of head and neck ("mowing", Bruhin, 1953 — Plate 3c), stab over the shoulder (Huth, 1976 — a vehement sideward movement of head and horns combined with backward hooking — Plate 3a, b), and finally, head-low posture (with horns pointing upward) similar to the grazing attitude (Plate 2a, b).

The various fighting movements, the orientations of the combatants, and the length and the intensity of the interactions result in several types of fighting. The most common ones are: (a) horning ("Hornen", Schloeth, 1961) in which the animals may show various fighting movements, however, in a very "gentle" form; (b) boxing in which the fighting actions are restricted to simple butts; (c) fencing in which the frontal sides of the combatants' horns (sometimes also their foreheads) hit each other by (oblique) forward-downward blows, and the animals bring their heads back immediately after the blow — sometimes in order to repeat it; (d) clash-fighting which is similar to fencing in that the horn contacts are very short; however, the horns interlock during these brief contacts; (e) horn-pressing (Plate 1a) in which the opponents persistently press the frontal sides of their horns against each other (sometimes also their foreheads), either straight along each other or, more frequently in oryx, crosswise; (f) front- or forehead-pressing (Plate 1b) in which the horns point forward near the ground and more or less parallel to it, and they interlock at their bases so that the foreheads literally or almost touch each other and each adversary's head is between the other's horns, then, the rivals persistently thrust forward against each other; (g) push-fighting in which the rivals press against each other as in front-pressing, but they interrupt this intensive contact by erecting the horns, however, without losing contact; (h) twist fighting (Plate 2c) which develops by levering movements of the head to the right and/or to the left after the horns have been interlocked; (i) parallel



a



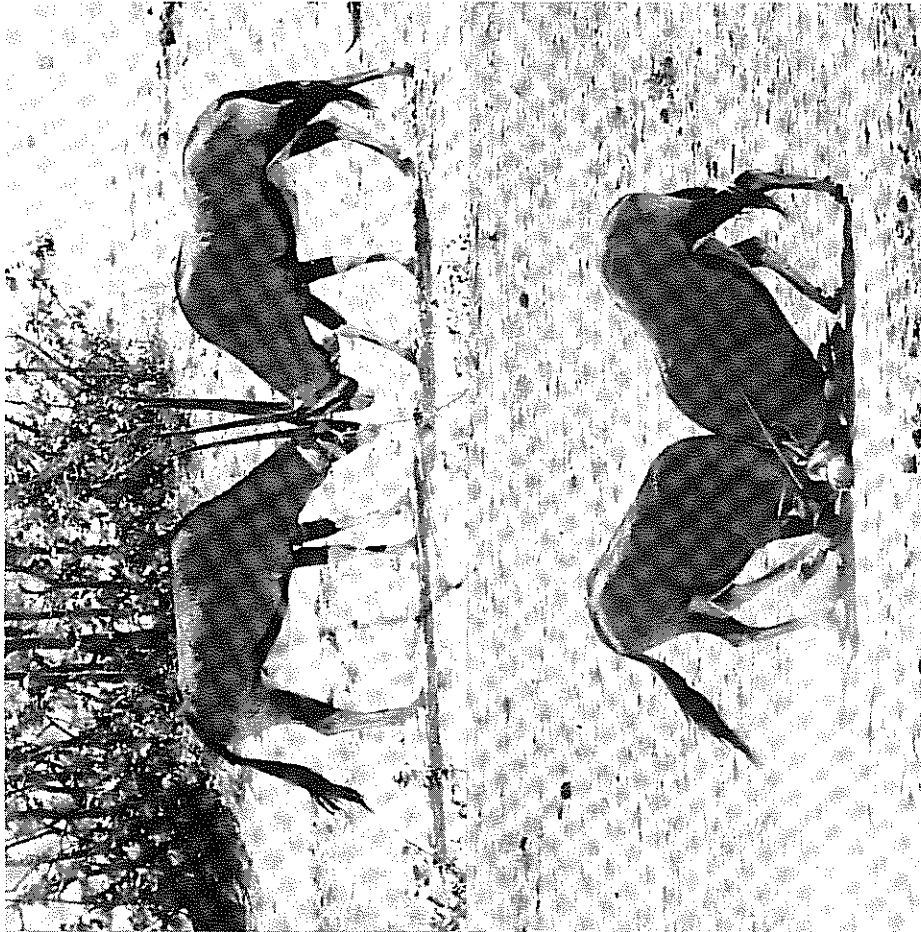
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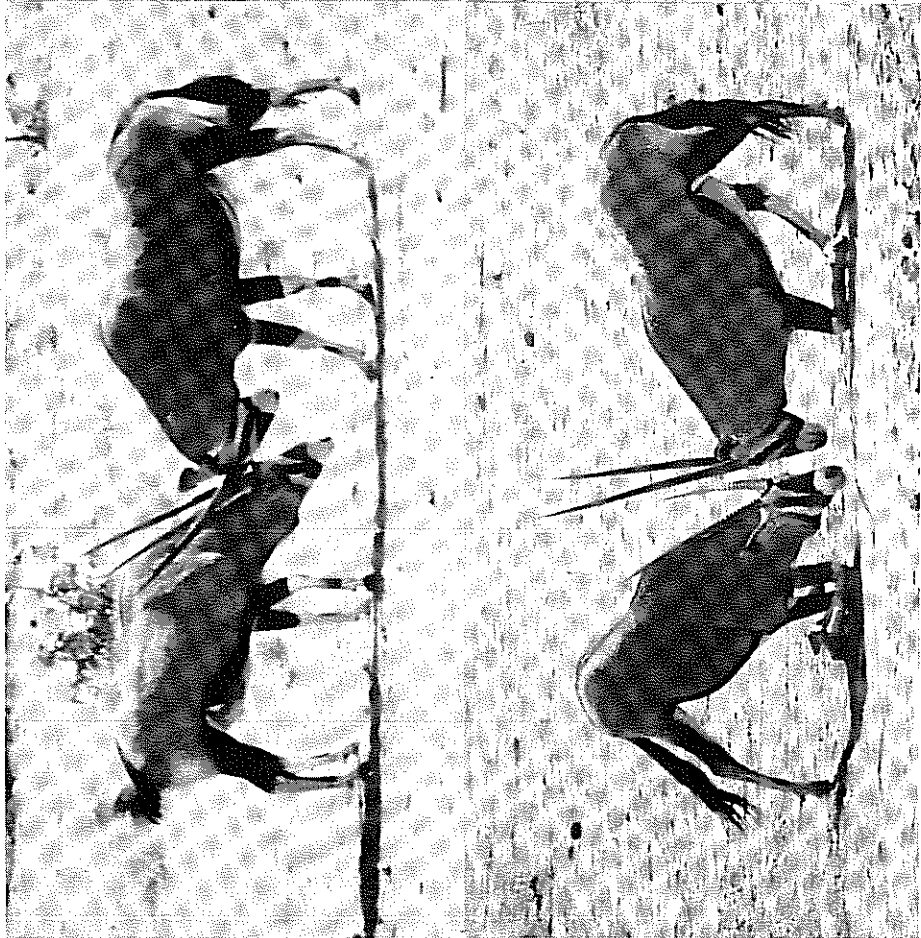
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PLATE 1: Fighting techniques: a) Horn-pressing; b) Front-pressing; c) Parallel fighting (sub-adult males).

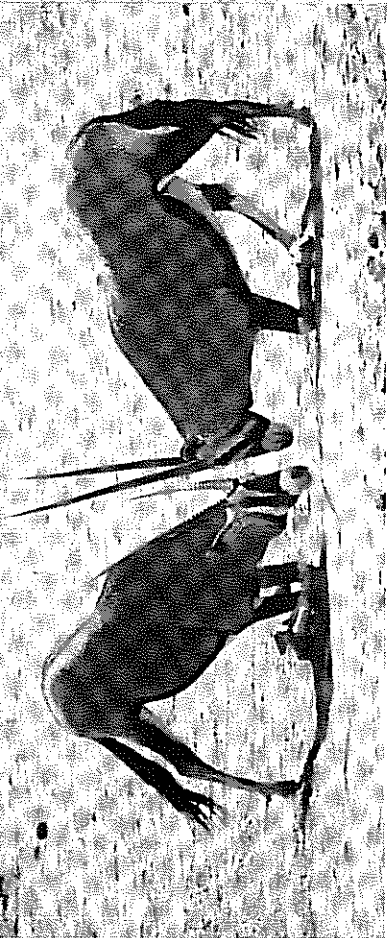
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PLATE 2: Fighting techniques: a) Forward-downward blow (right) parried by head-low (left); b) Initiation of a fight (horn-pressing) by reciprocal head-low postures; c) Defensive initiation (left) of a fight on the "knees" (carpal joints); d) Twist-fighting with shoulder-pressing in a frontal fight on the knees.

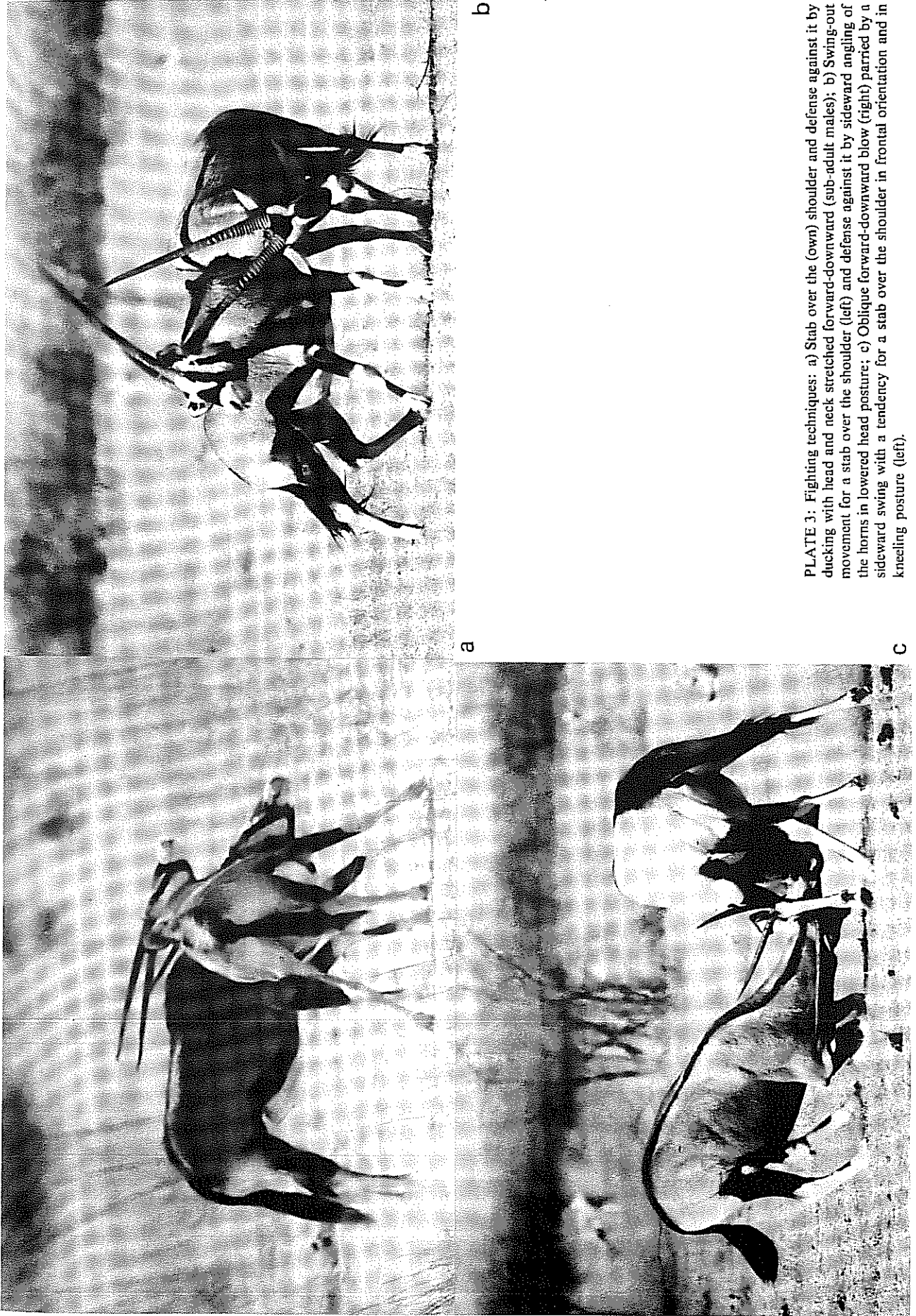
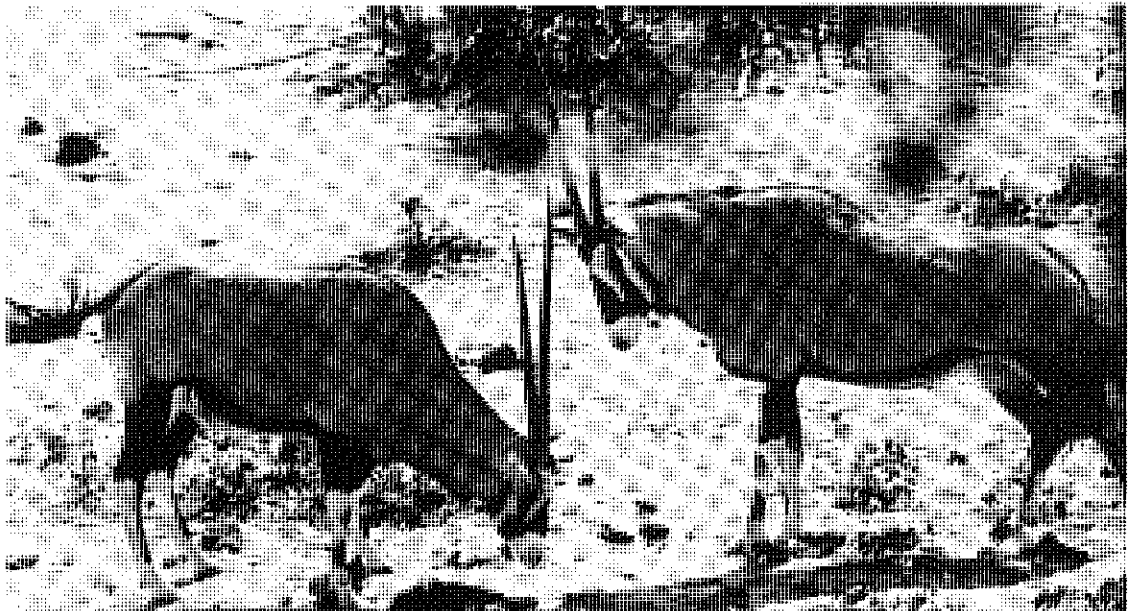
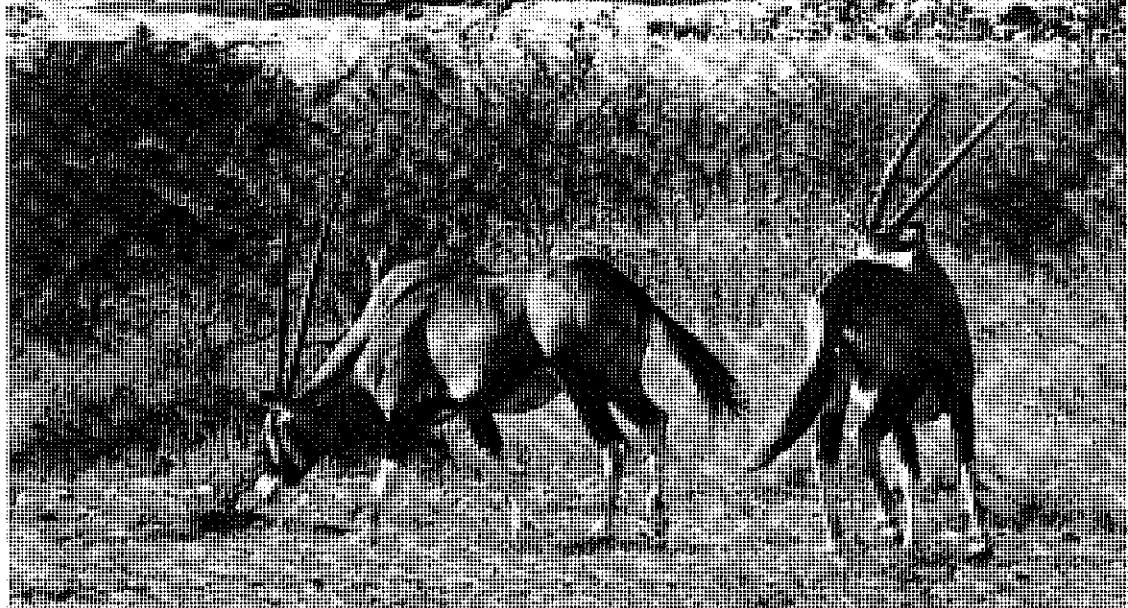


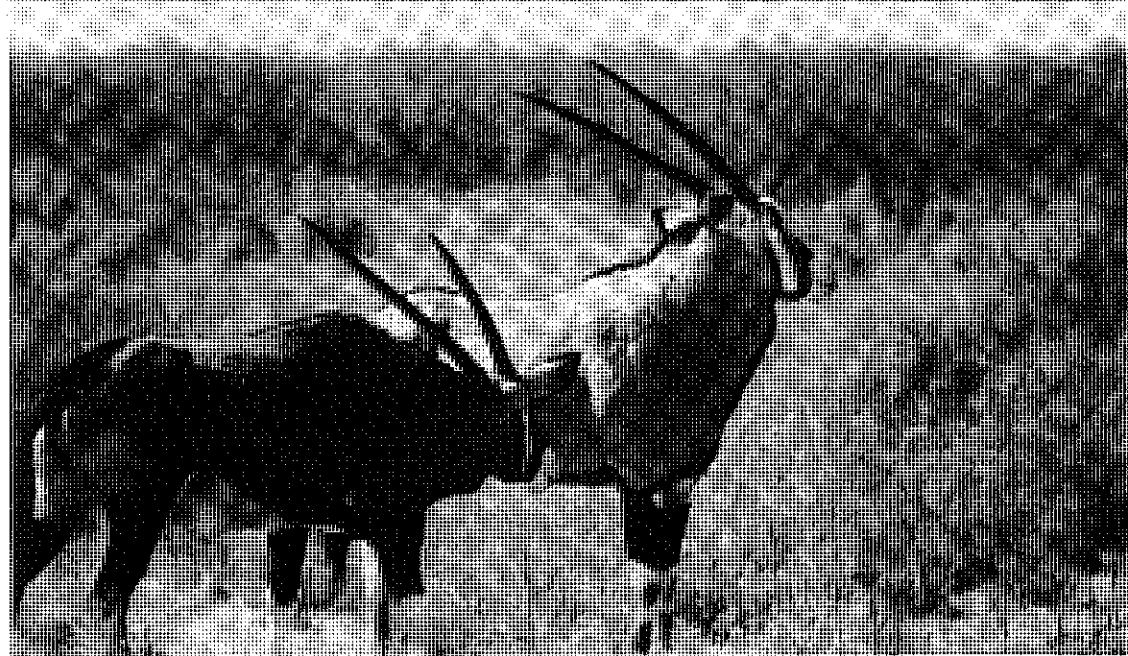
PLATE 3: Fighting techniques: a) Stab over the (own) shoulder and defense against it by ducking with head and neck stretched forward-downward (sub-adult males); b) Swing-out movement for a stab over the shoulder (left) and defense against it by sideward angling of the horns in lowered head posture; c) Oblique forward-downward blow (right) parried by a sideward swing with a tendency for a stab over the shoulder in frontal orientation and in kneeling posture (left).



a



b



c

PLATE 4

fighting (Plate 1c) in which the rivals are in more or less parallel position (frequently in an acute angle) wrestling with their horns by movements which are not principally different from those in a fight in frontal position but are oriented sideways. Of course, sideward swings and stabs over the shoulder are particularly frequent in parallel fighting. Besides their horns, the adversaries also use their shoulders in pressing against each other (Plate 1c, 2c, 3b) which may result in a whirl-around fight. In stabbing over the shoulder, they show a strong tendency to drop to their knees.

Relative to defensive techniques in oryx fights, the rivals can simultaneously perform the same aggressive movement, e.g., an oblique forward-downward blow, as a counter-attack. Furthermore, they often show special parrying manoeuvres in which sideward swings, sometimes also stabs over the shoulder, and, above all, head-low postures, play a great role. The head-low posture apparently is particularly suitable to screen neck and withers against all strokes from above, such as the butt, and the straight or oblique forward-downward blow (Plate 2a). Also, for parrying the stab over the shoulder, the head-low or a posture similar to it (the nose is often not as close to the ground as in the typical head-low posture, or head and neck are somewhat more stretched forward) is almost regularly used (Plate 3a). When fighting in frontal position, sideward swings or even stabs over the shoulder (Plate 3c) are sometimes used to catch the opponent's butt, downward blow, or forward dash. Finally, a movement corresponding to the stab over the shoulder is sometimes performed to get free when occasionally the head or the throat is caught between the rival's horns. In such a case, of course, the stab over the shoulder is directed into the air, and not toward the opponent.

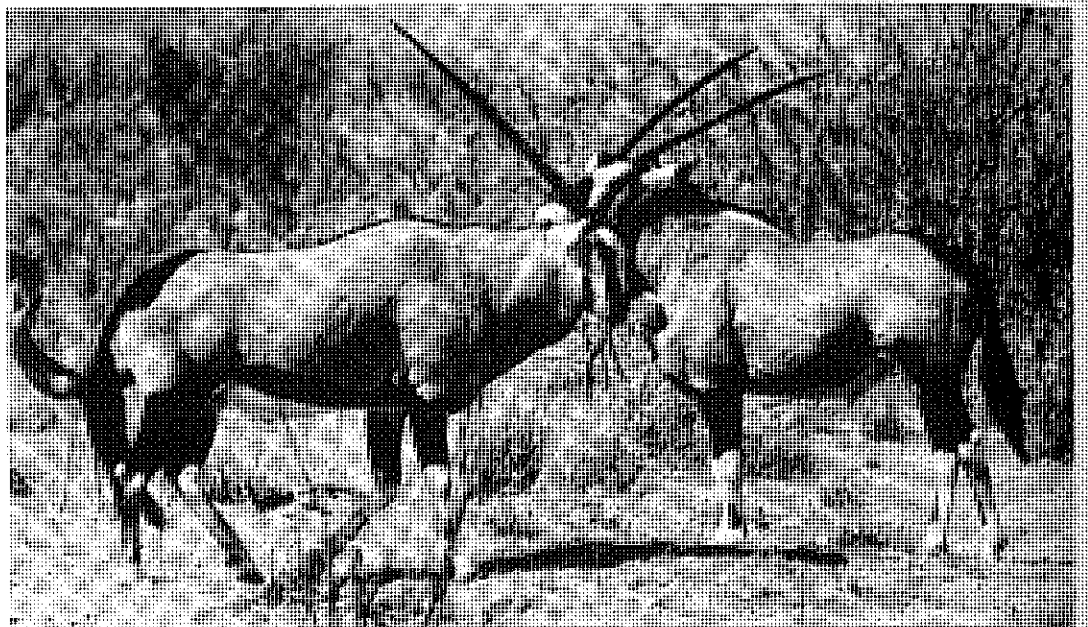
Fighting movements can serve as *agonistic displays* (threats) when performed "symbolically", i.e., the animal shows the same, full movement as in a fight, however without touching the opponent and frequently at a distance from which it cannot possibly touch him. In oryx, this is particularly true for the butt and the forward-downward blow (Plate 6c). The latter is often performed slower than in a fight. Also, aggressions toward inanimate objects in which oryx almost regularly drop down to their knees may be said to be a symbolic action since the animal performs the same movements

as in a fight. The threat character of these object aggressions, however, is much more questionable than that of the other displays under discussion because (a) they can also show up when no rival is present, (b) they frequently are not clearly addressed to a definite recipient, but more "to whom it may concern", and (c) the recipients may simply ignore them which may occasionally happen with any display but seems to be comparatively frequent in object aggressions (Walther, 1978b). Finally, the head-low posture can be used as a threat display, but its recognition as a threat has problems of its own. Besides cases in which the threat character is absolutely clear, there are other and unfortunately not quite rare cases in which it is difficult to determine whether the head-low posture is still a threat display or the beginning of a fight, e.g., when both rivals stand with head-low frontally to each other at close range (Plate 2b). Moreover, in fighting, the head-low is often used as a defensive manoeuvre, and correspondingly, the head-low display often has the character of a defensive threat, particularly when used as a response to a more offensive threat of a (superior) challenger (Plate 4a, 6c). In this situation, the head-low threat may gradually merge into a submissive posture (Walther, 1978a) and, sometimes it may become difficult to determine whether the animal still shows the (defensive) threat or behaves submissively.

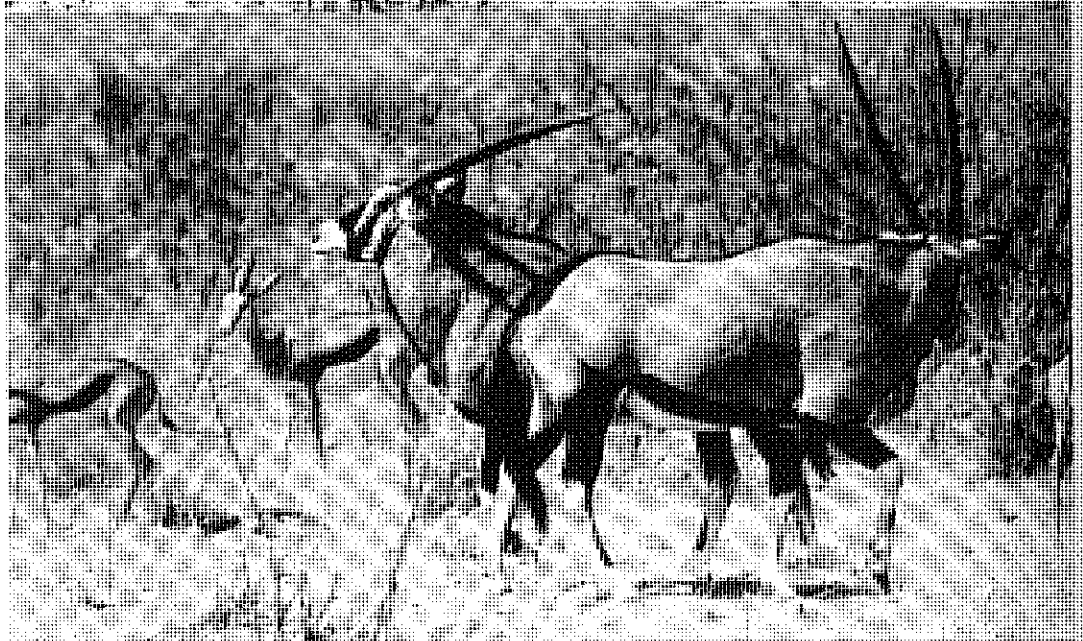
Other threat displays show features of more elaborate ritualisation. Apparently, the butt gave rise to the (in oryx relatively infrequent) head-throwing, a rhythmically repeated vehement nodding movement which usually occurs in combination with other displays such as erect posture or head-low posture (Plate 6c). Furthermore, there are several ritualised intention movements where the initiation of a fighting movement is "frozen" into a posture. These are especially the medial presentation of horns (chin tucked toward the throat, head held approximately on body level — Plate 4a) as an intention movement for a butt, the high presentation of horns (head above body level) as an intention movement for a forward-downward blow, and the sideward angling of the horns (Plate 5e) as an intention movement for a sideward push or swing. Interestingly enough, the stab over the shoulder also can be "frozen" into a display posture in the South African oryx (Plate 5d).

PLATE 4: Agonistic displays: a) (Medial) presentation of horns (right) of a bull toward a (subordinate) cow which responds with a head-low posture. (Compare these expressive postures to the fighting movements in Plate 2a); b) Head-low posture of a subordinate (cow) in withdrawal from a dominant (bull); c) Head-forward posture of a sub-adult bull in response to the erect posture with head-sideward inclination in the broadside display (T-position) of an adult bull. (Compare the posture of the subordinate to the defense against a stab over the shoulder in Plate 3a).

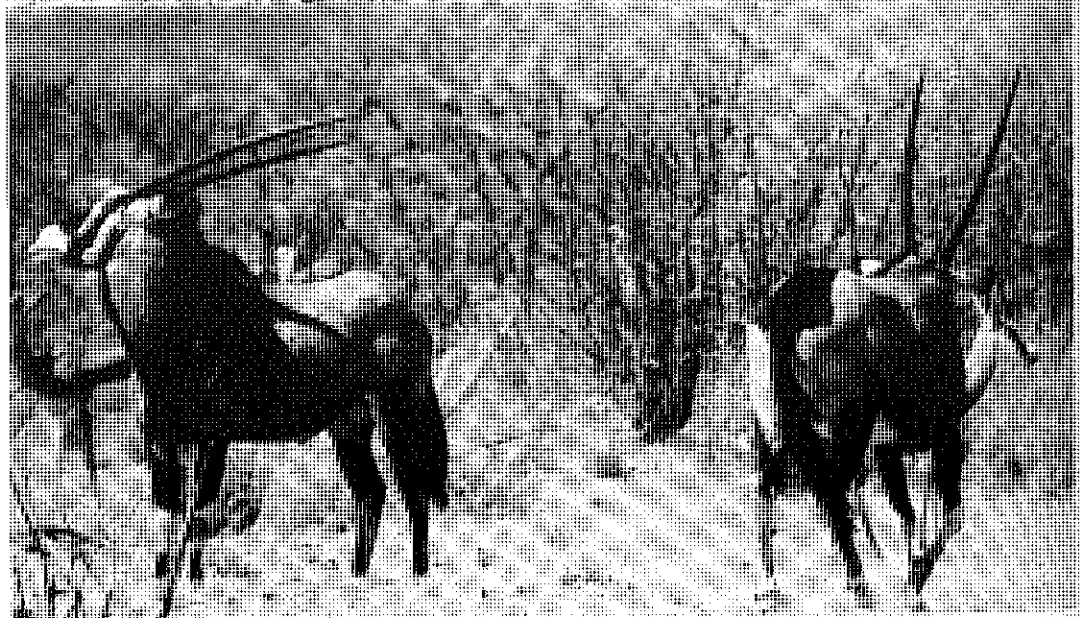
PLATE 5 (see pages 280 and 281): Agonistic displays. Sequence of display "elements": a) A subordinate adult bull (left) passes a dominant bull (right) in the opposite direction at close range. The dominant erects; b) The dominant bull in full erect display in reverse-parallel lateral position; c) The subordinate (right) tries to pass behind the dominant bull (left). The latter circles correspondingly in keeping the broadside position. His erect display merges into a sideward inclination of his head; d) In continued circling, the sideward inclination of the head merges into a symbolic stab over the shoulder on the part of the dominant bull (left); e) The dominant's symbolic stab over the shoulder merges into a sideward angling of the horns. The subordinate (right) responds by lowering the head and waving his tail; f) The dominant has turned frontally towards the subordinate. The latter flees at a gallop.



a

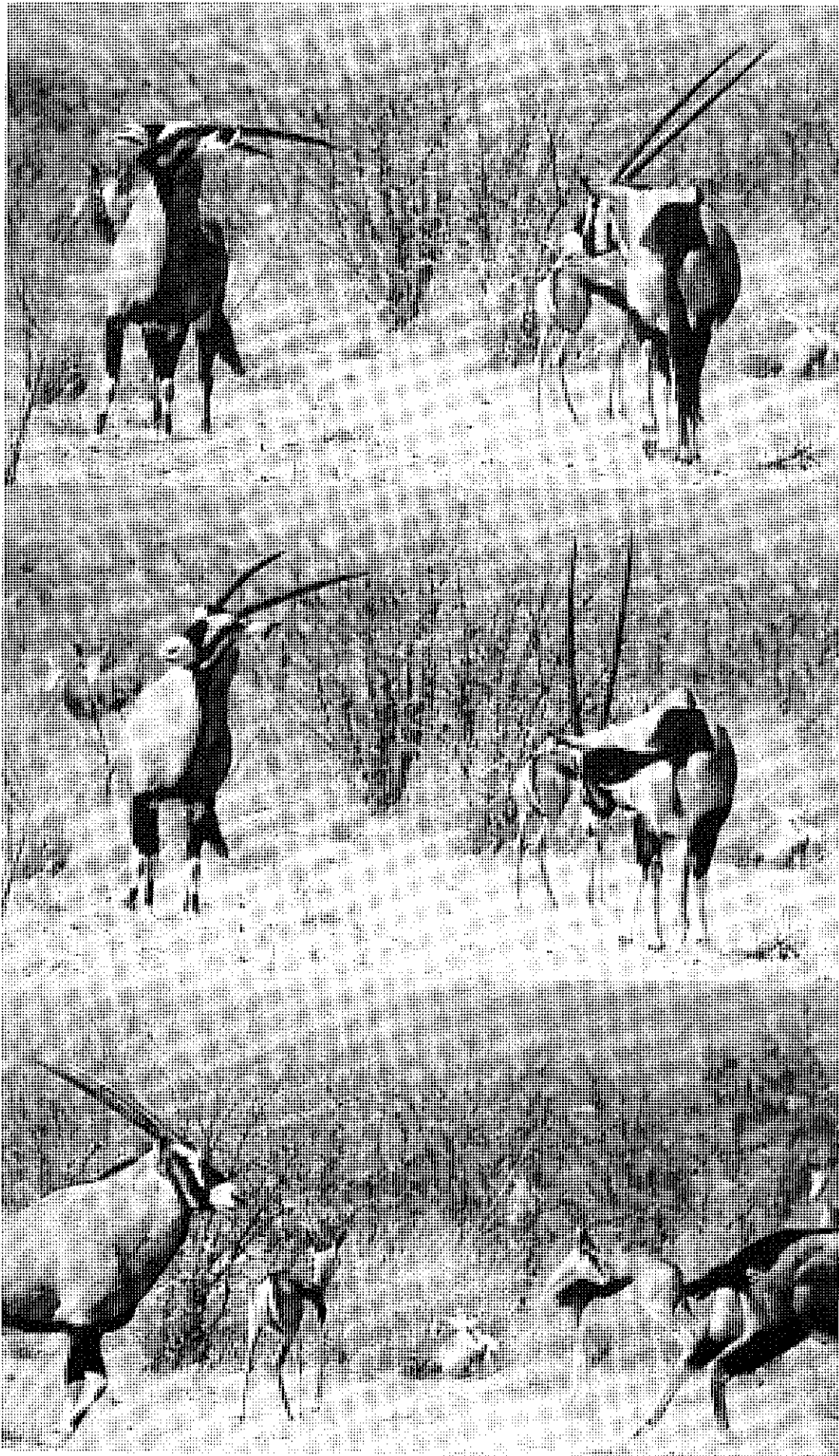


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PLATE 5 (cont.)

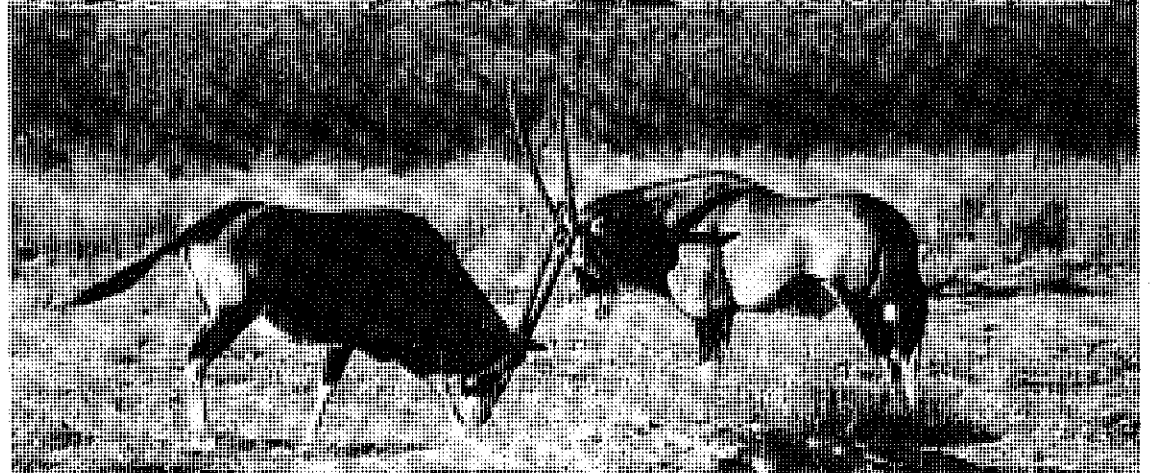
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d



PLATE 6

Dominance displays (= *Imponierverhalten* in German literature), i.e., displays with similar — challenging or intimidating — effects on the recipients as threat displays, but not as closely related to fighting movements as the latter, are broadside (lateral) position, erect posture, and head-sideward inclination. The broadside display is most frequently assumed in reverse-parallel position (head-to-tail — Plate 5a - e) or in front of the recipient (T-position — Plate 4c), blocking the latter's path. In both cases it is combined with the erect posture (Plate 5a, b) and usually also with the head-sideward inclination (Plate 4c, 5c). These two, however, are in principle independent displays, i.e., they also can show up in frontal orientation (Plate 6a, b). In the erect posture, the animal erects withers and neck and raises the head to a horizontal level. This display is almost regularly followed by the head-sideward inclination in which the animal turns the erected head away from the opponent in an angle of about 45° when standing in lateral position (Plate 4c), and in an angle of about 90° when standing or approaching the opponent in frontal orientation (Plate 6a, b). When a subordinate animal is challenged by a superior in reverse-parallel or in T-position, the subordinate may withdraw, and then, the challenger may correspondingly circle, keeping his flank toward the subordinate (Plate 5b - e). The head-turn toward the recipient from an erect posture in lateral position, is not as frequent and pronounced in *Oryx gazella* as in *Oryx beisa* (Walther, 1978a). When it shows up at all, it usually occurs at the end of an encounter when the dominant looks after the withdrawing subordinate (Plate 6d).

In reciprocal as well as in one-sided display encounters, some of the described threat and dominance displays follow one another in a relatively stable sequence. The typical case is as follows: the challenger assumes the erect attitude (usually in broadside position — Plate 5b), and he more or less strikingly turns his head away from the recipient (Plate 5c). In turning his highly erected head further away he points with his horns over his withers toward the opponent. This symbolic stab over the shoulder (Plate 5d) slowly merges into sideward-angling the horns (Plate 5e). Finally, when standing in lateral position as in most of the cases, the challenger may now turn into a frontal orientation, presenting his horns and/or performing a symbolic butt or forward-downward blow (Plate 6c). The single major variation is that sometimes the sequence of sideward-angling the horns and the symbolic stab over the shoulder may be reversed.

Besides that a subordinate may immediately withdraw or even flee when threatened by a superior, he can

respond by a head-low posture (Plate 4a, b, 5e, 6c). As mentioned above, the meaning of this posture may range from a defensive threat to submission depending on some — often rather inconspicuous — details in the performance. The threat character of the head-low can be emphasised by head-throwing. Occasionally, one could even speak of intentions for a body attack on the part of the subordinate, e.g., when a relatively strong bull is dominated by an even stronger one who stands broadside in front of him. I did not witness a true flank attack in such cases; however, I twice observed highly dominant bulls in all-male groups who had fresh, slightly bleeding wounds at their flanks which could have resulted from such a situation. The submissive character of the head-low posture becomes more emphasised, the more the subordinate turns his horns sideways away from the dominant and/or the more he stretches head and neck forward (Walther, 1978a). In *Oryx gazella*, this forward tendency may occasionally become so pronounced that the head-low changes into an almost horizontal posture of head and neck (Plate 4c). Then, the subordinate may even move one or two steps toward the dominant animal.

Sooner or later the subordinate withdraws with head-low posture (Plate 4b) and with a waving movement of the tail. Preferably, he passes behind the displaying dominant. In captive *Oryx gazella*, I have seen subordinates lying with head and neck stretched forward in complete submission. I did not note it during my observations in Etosha, but O. B. Kok (pers. comm.) recorded it in oryx in the wild. When fleeing after a heavy fight, an oryx may sometimes roar loudly. No aggression inhibiting effect of this roaring on the pursuer was recognisable.

Pawing the ground and defecation in low squatting posture may sometimes be seen in connection with agonistic interactions in oryx bulls (Walther, 1958, 1978a). Both behaviour patterns were infrequent in the Etosha oryx during the season under discussion. It is a question of its own whether the deep squatting defecation posture is indicative of territoriality. In migratory *Oryx beisa* in Serengeti, it definitely occurred in high-ranking, non-territorial individuals (Walther, 1978a). When I saw it in the Etosha oryx, I was usually not sure whether these bulls were territorial. In one case, however, a bull had dominated several other bulls in the immediate vicinity of a water-hole. After one of these encounters, he defecated in a deep squatting posture. About ten minutes later, another, even heavier bull arrived and dominated all the other bulls including the up to now dominant one. In my opinion, this speaks strongly against a territorial status of the individual in question.

PLATE 6: Agonistic displays: a) A bull (right) frontally approaches a cow (left). The bull's erect head-sideward inclination becomes a 90° turn of the head due to the frontal orientation. This head posture may be said to be an "abbreviation" — *pars pro toto* — of the lateral display; b) Finally, he stands in this posture in front of the cow; c) He frontally turns toward the cow performing a symbolic forward-downward blow in slow-motion. The cow responds with head-low posture, head-throwing, and waving her tail. She starts moving, passing the bull in reverse-parallel orientation; d) The cow withdraws, the bull looks after her.

### 3.2.2 Discussion

I did not find qualitative differences in the fighting techniques between *Oryx gazella* and *Oryx beisa*. Since my data were gathered under somewhat different aspects in the different observation periods, I cannot give an exact quantitative comparison between the single fighting movements or the types of fighting. As far as my subjective impression goes, the stab over the shoulder is more pronounced and more frequent in *Oryx gazella*, they go more readily down to their knees, their fighting actions are often more vehement, and, on the whole, they appear to be rougher fighters than *Oryx beisa*.

Altogether, I observed 133 fights of oryx in Etosha, 31 fights in the Serengeti oryx, and more than 20 fights in captive animals. Of these there were many fights of medium intensity and about 30 of high intensity. However, I did not witness one case of a serious injury, and not even one case of a minor wound. On the other hand, it is not too seldom that one sees an oryx with a broken horn, with scars or bleeding wounds at shoulders, neck or flank which are likely to be caused by intraspecific fighting. Thus, the fighting behaviour of oryx appears to be ritualised in the sense that it is largely a horn-to-horn fight which diminishes the probability of serious injuries and fatal endings but does not completely exclude them. The latter is not surprising when one takes into account the length and shape of the horns, and the frequency and often also the vehemence of the oryx fights. On the whole, it appears that out of the many fights which these animals have among each other, only a small proportion leads to bloodshed.

Of course, the probability of injuries considerably increases in the unritualised body attack. Under normal conditions, however, body attacks seem to be exceptional. In the same period in which I observed 133 horn-to-horn fights in Etosha, I recorded only three body attacks — and one of them was performed by a calf toward its mother in soliciting milk, certainly not a case of severe aggression. Obviously, body attacks were considerably more frequent in Hamilton's *et al.* (1977) studies at Namib Desert water-holes indicating that also the social behaviour may deviate from normal under an extraordinary environmental stress as it was obviously given in this area during the extreme drought in 1972–73 (see Introduction).

In this context, I may mention a remark in Hamilton's *et al.* (1977) paper which in my opinion could be misleading. The authors state that females tend to fight with the tips of their horns while males push against the bases of one another's horns. Based on my observations, this difference is not primarily a result of different fighting techniques in males and females, but depends on the length of the interaction. In an oryx fight, frequently the first contact is made with the upper third of the horns (Walther, 1958). This "taking measure" can occur in males as well as in females. In short

fights, it easily may remain the single form of horn contact, and since female fights are often short, this is particularly frequent in females. When the fight is continued and intensified, the females push with the bases of their horns as do males.

More striking than those in fighting behaviour are some differences in the threat and dominance displays of *Oryx gazella* and *Oryx beisa*. I have never seen a symbolic stab over the shoulder in *Oryx beisa*, which is a frequent, clear and distinct display in *Oryx gazella*. Huth (1976) did not see it in zoo animals of this species which may have been due to a lack of corresponding situations in captivity; however, strangely enough, Hamilton *et al.* (1977) also do not mention it in their observations on *Oryx gazella* at Namib Desert water-holes. If it was truly lacking there, this may be another indication of how deeply the social behaviour of these animals was affected by the extreme environmental conditions. Other differences in the displays are more gradual, but still well-recognisable. Both *Oryx gazella* and *Oryx beisa* show the erect posture and the head-ward inclination, but *Oryx gazella* carries its nose almost horizontal, sometimes even a little above horizontal level, whereas *Oryx beisa* usually does not carry its nose as high, instead they pull it somewhat toward the throat. Probably due to this difference of the head posture, the erect display easily merges into the symbolic stab over the shoulder in *Oryx gazella*, whereas *Oryx beisa* quite frequently continues the erect posture with high presentation of the horns and an emphasised frontal turn of the head toward the opponent from a lateral position. These two latter displays were infrequently seen in the Etosha oryx. Apparently linked to the more frequent occurrence of the high presentation of horns, the symbolic forward-downward blow also seems to be more common and more ritualised (slower performance) in *Oryx beisa*. Thus, although *Oryx gazella* and *Oryx beisa* show basically the same sequence of threat and dominance displays, it seems that in *Oryx gazella* other "elements" have been elaborated so that, on the whole, this sequence shows a tendency to diverge in the two species (or subspecies according to certain classification systems — Haltenorth, 1963).

### 3.3 Sequences and effects of forms of aggression

#### 3.3.1 Results (Table 2)

As can be seen from Table 2, body attacks as well as one-sided and reciprocal object aggressions were so infrequent that they can be ignored under quantitative aspects.

Reciprocal displays infrequently decided agonistic encounters: in total (point 13 — 18) only 18,0 % of the reciprocal erect displays, 15,6 % of the intensified erect displays, and 2,4 % of the reciprocal frontal horn threats. The display sequence which was quali-

TABLE 2: Sequences and effects of forms of aggression (in %)

Forms of Aggression												
n forms of aggression	300	74	160	8	50	32	41	1	133	3	36	50
	One-sided erect display	One-s. intensified erect displ.	One-s. frontal horn threat	One-s. object aggression	Reciprocal erect display	Rec. intensified erect displ.	Rec. frontal horn threat	Rec. object aggression	Fight (horn contact)	Body attack	(one-sided) Rush	Chase
ending with or followed by												
1) one-sided erect display	/			12.5								4.0
2) one-s. intensified erect display	24.7	/		25.0*								22.0*
3) one-s. frontal horn threat	12.0	23.0	/		2.0	3.1						
4) one-s. object aggression				/								
5) reciprocal erect display					/							
6) rec. intensified erect displ.					64.0	/						
7) rec. frontal horn threat	0.7	2.7			6.0	62.5	/					
8) rec. object aggression								/				
9) fight (horn contact)	1.7	4.1	6.9		8.0	18.8	95.1	100	/		2.8	6.0
10) body attack										/		
11) (one-sided) rush											/	
12) chase	1.3	8.1	1.3						7.5		33.3	/
13) inf. anl. flees; dom. follows	1.0	2.7	1.3						2.3		2.8	14.0
14) inf. anl. flees; dom. remains	2.0	5.4	11.3	12.5					12.0		22.2	54.0
15) inf. anl. jumps away; dom. follows	2.0		1.3						0.8			
16) inf. anl. jumps away; dom. remains	5.3	6.8	25.0	37.5	4.0	3.1	2.4		28.6	33.3	36.1	
17) inf. anl. withdraws; dom. follows	6.7	6.8	11.3		2.0				11.3			
18) inf. anl. withdraws; dom. remains	37.7	40.5	39.4		12.0	12.5			17.3		2.8	
19) third anl. intervenes	1.0								14.3			
20) both walk away in opp. directions	2.3		0.6		2.0		2.4		6.0			
21) challenge ignored; send. stops action	1.7		1.9	12.5	/	/	/	/	/	66.7		/

Abbreviations: one-s. = one-sided; rec. = reciprocal; displ. = display; anl. = animal; inf. = inferior; dom. = dominant; send. = sender; opp. = opposite

\*Intensified erect displays plus the erect displays initiating them.

## COMMENTS ON TABLE 2:

Table 2 shows the totals (i.e., not divided as to sex and age classes) of the forms of aggression and the ways in which they were continued or in which they ended. The threat and dominance displays are combined into erect displays, intensified erect displays, and frontal horn threats. Erect displays comprise the erect posture and the head-sideward inclination. Intensified erect displays comprise the sideward angling of the horns and the symbolic stab over the shoulder, assuming a broadside position is not listed. Since most of the erect and intensified erect displays are performed in lateral orientation, these categories approximately reflect the frequency of the broadside displays. Frontal horn threats mainly comprise medial and high presentation of the horns, symbolic butt and forward-downward blow, and the relatively few cases of the head-low posture in which its threat character was beyond any doubt. Most of the head-low postures however, are not presented in Table 2 — as well as in the other tables — because of the difficulties to distinguish them from initiating a fight or from submissive behaviour. Also, submissive lowering of the head is not presented because it almost regularly preceded withdrawal or flight. Thus, the numbers of withdrawals and of flights give an approximate impression of the frequency of submissive displays.

When a one-sided display was followed by another one-sided display, it was always the same animal (i.e., the challenger) which showed these two consecutive forms of aggression.

The formulation "dominant follows" always means that the dominant animal followed *walking* even when the subordinate ran away at a full gallop. "Inferior jumps away" refers to those cases in which the inferior first moved away from the dominant by a big jump, but then slowed down to a walk.

Point 1 — 12 show those cases in which a given form of aggression was followed by another form of aggression, and thus, the hostilities were continued. Point 13 — 21 show those cases in which the aggressive interactions ended after a given form of aggression. Thus, Table 2 reads the following way: 300 one-sided erect displays were observed. 24,7 % of them were followed by one-sided intensified erect displays, 12,0 % by one-sided frontal horn threats, etc.

tatively described above, was beautifully demonstrated by the quantitative data: 64,0 % of the reciprocal erect displays (erect posture and head-sideward inclination) were followed by reciprocal intensified erect displays (symbolic stab over the shoulder and/or sideward-angling of the horns), and 62,5 % of these intensified erect displays were continued by reciprocal frontal horn threats. Fights developed from 95,1 % of the reciprocal horn threats, and thus, significantly ( $X^2 = 65,15$ ,  $df = 1$ ,  $p < .001$  and  $X^2 = 41,16$ ,  $df = 1$ ,  $p < .001$ ) more frequently than from reciprocal erect displays (8,0 %) and from reciprocal intensified erect displays (18,8 %).

Fights (point 9) and chases (point 12) followed in very moderate proportions after one-sided displays. Also, other cases in which a one-sided display was continued by another form of aggression were proportionally much rarer than in the reciprocal displays. Nevertheless, the said display sequence was still well-recognisable, though in smaller proportions: 24,7 % of the one-sided erect displays were followed by intensified erect displays, and 23,0 % of the latter were followed by one-sided frontal horn threats. These proportions

were considerably greater than those of other forms of aggression following a one-sided display.

One-sided displays decided encounters (point 13 — 18) significantly more often than the corresponding reciprocal displays: one-sided erect displays 54,7 % of the cases (tested against reciprocal erect displays:  $X^2 = 11,25$ ,  $df = 1$ ,  $p < .001$ ), one-sided intensified erect displays in 62,2 % (tested against reciprocal intensified erect displays:  $X^2 = 17,26$ ,  $df = 1$ ,  $p < .001$ ), and one-sided frontal horn threats in 89,6 % (tested against reciprocal frontal horn threats:  $X^2 = 117,17$ ,  $df = 1$ ,  $p < .001$ ). Flights occurred in moderate proportions: 4,3 % after one-sided erect displays, 16,2 % after one-sided intensified erect displays, and 13,9 % after one-sided horn threats. Somewhat more frequent was jumping away of the recipient (point 15 + 16): 7,3 % after one-sided erect displays, 6,8 % after intensified erect displays, and 26,3 % after one-sided frontal horn threats. The latter was a significantly greater proportion than that in erect displays ( $X^2 = 10,79$ ,  $df = 1$ ,  $p < .01$ ). On the whole, however, most one-sided display encounters ended with the recipient's walking away from the sender (point 17 + 18): 44,4 % of the cases after erect displays, 47,3 % after intensified erect displays, and 50,7 % after frontal horn threats.

The only form of aggression which occurred after fights was the chase, and its proportion was relatively small (7,5 %). After 21,8 % of the fights, the defeated combatant fled at a gallop (point 12 — 14). As compared to flight after one-sided displays, only the difference to erect displays is significant ( $X^2 = 30,15$ ,  $df = 1$ ,  $p < .001$ ), but the differences to intensified erect displays ( $X^2 = 0,62$ ,  $df = 1$ ,  $p > .30$ ) and to frontal horn threats ( $X^2 = 2,74$ ,  $df = 1$ ,  $p > .05$ ) were not significant. The proportion (29,4 %) of those cases in which the defeated withdrew by jumping away from the victor (point 15 + 16) and the proportion (28,6 %) of withdrawals at a walk after fights (point 17 + 18) were in about the same range as fleeing. Also, quite a number of fights (14,3 %) were terminated by a third animal's (usually a bull's) "taking offence" and intervening. In other forms of aggression, this was rare or lacking. Furthermore, the proportion of "neutral" endings, i.e., when both opponents turned away and walked off, although small (6,0 %), was greater after fights than after any other form of aggression. Of course, no combatant could "ignore" a fight as it may occasionally happen with threat and dominance displays.

The rush showed a strong tendency to be continued by a chase (33,3 %), and, altogether, the cases in which the addressee fled after the rush (point 12 — 14) comprised 58,3 %. This means a significantly ( $X^2 = .16,44$ ,  $df = 1$ ,  $p < .001$ ) greater proportion of flights after rushes than flights after fights. In 36,1 % of the rushes, the inferior withdrew with a jump (point 15 + 16), and in only 2,8 %, he walked away (point 17 + 18).

Chases occurred after other forms of aggression (e.g., fights or rushes) or on their own, i.e., without other

forms of aggression preceding them. They usually ended when the pursuer stopped or slowed down to a walk while the pursued animal continued to flee (point 13 + 14). In a few cases (6,0 %), the pursued animal stopped, turned around and fought the pursuer. Relatively often (26,0 %), erect or intensified erect displays followed after a chase (point 1 + 2). In all these cases, the pursuer caught up with the fleeing opponent, passed him and blocked his way displaying in broadside position in front of him.

### 3.3.2 Discussion

Most of the above findings appear to be self-explanatory. It should perhaps be emphasised that reciprocal displays infrequently decide encounters because in the majority of such cases, none of the opponents become intimidated, but both challenge each other with one display after the other until they finally fight. Thus, challenge is the effect of reciprocal agonistic displays, but not intimidation (Walther, 1974). This is typical of encounters among peers. Within the reciprocal displays, only the (frontal) horn threats are immediately followed by fights in a great portion of the cases because they are considerably more closely related to fighting than all the other displays under discussion (Walther, 1974).

This last point is confirmed by the comparatively frequent occurrence of fleeing and jumping away (point 12 – 16 in Table 2) of the inferior opponent after one-sided horn threats, as compared to the other one-sided displays. Obviously, the frontal horn threat is more feared by subordinates.

One-sided display encounters are typical of unequal opponents, and the inferior is intimidated by these displays. However, the subordinates often are not in too great fear of the dominants as can be seen from the great proportion of the inferiors' withdrawals at a walk.

## 3.4 Beginnings of fights

### 3.4.1 Results (Table 3)

In total, 49,3 % of the 75 fights of adult oryx bulls among each other were initiated by reciprocal displays, and in a considerable proportion of the cases (21,3 %), both rivals showed the entire display sequence before they started fighting. Next in frequency (13,3 %) were those cases in which they only showed reciprocal frontal horn threats.

Cases in which only one of the combatants displayed before the fight started were rare (in total 3,9 %). Usually, either the adult peers challenged each other simultaneously, or, at least, the recipient immediately accepted the challenge and responded with the same displays.

Fights without any prior display were quite frequent (46,7 %) among adult bulls.

In fights of adult bulls against adult cows (16), interactions without prior displays or rush or chasing were rare (6,3 %). However, in contrast to the fights among adult bulls, the interactions initiated by one-sided displays (68,6 %) preponderated, whereas the proportion of reciprocal displays (12,6 %) was relatively small.

In the fights among adult cows (15), the proportion of fights following reciprocal displays (46,8 %) approximately equalled that of fights among adult bulls, and again, the proportion of fights initiated by the entire display sequence (26,7 %) was relatively great. The proportion of fights initiated by a one-sided display (13,3 %) was small. At first sight, the proportion of fights without prior displays (26,7 %) appears to be smaller than that in fights among adult males. However, when one adds to it those fights which were not initiated by threat or dominance displays, but which followed after a rush or chase, one comes to a proportion (40 %) which, at least, comes close to that of fights without prior displays (46,7 %) in adult bulls (where no forms of aggression other than threat and/or dominance displays preceded fighting).

In the encounters of immature males among each other (21), only a few (19 %) were initiated by reciprocal displays, and even fewer ones (4,8 %) by one-sided displays. The majority of them (66,7 %) were without prior displays. This proportion becomes even greater (76,2 %) when one adds the (2) cases in which the fight followed after the one partner mounted the other.

Thus, on the whole, one-sided displays rarely preceded fighting (in total 14,4 %). They were relatively frequent only between unequal opponents. The proportion of cases in which a form of aggression other than a threat or dominance display preceded fighting, was even smaller (in total 4,5 %). The initiation of fights by reciprocal displays (37,6 % of the total) was particularly frequent in encounters of adult opponents of the same sex. Fights without prior displays totalled 43,6 %.

### 3.4.2 Discussion

The prevailing initiation of fights between adult bulls and cows by one-sided displays is easy to understand. Since the one-sided displaying was executed by the bulls in all the observed cases, it may be concluded that the initiative was mainly on the part of the bulls, and that the bulls fought the cows when the latter did not or not promptly enough react to the males' displays.

Obviously, fights among adult cows (15) were rarer than fights among adult bulls (75). With respect to the initiation by threat and/or dominance displays, however, they followed about the same pattern as those among adult males.

TABLE 3: Initiation of fights (horn contact) (in %)

	ad♂: ad♂	ad♂: ad♀	ad♂: im♂	ad♀: ad♀	ad♀: im♀	im♂: im♂	im♂: im♀+juv	total
n fights	75	16	2	15	2	21	2	133
Fights initiated by								
reciprocal display I	4.0					4.8		3.0
reciprocal display II	5.3	6.3		6.7				4.5
rec. displ. I + rec. fr. horn thr.	2.7							1.5
rec. displ. II + rec. fr. horn thr.	21.3			26.7				15.0
one-s. displ. I + rec. fr. horn thr.	2.7							1.5
one-s. displ. II + rec. fr. horn thr.		6.3				4.8		1.5
reciprocal frontal horn threat	13.3			6.7		9.5		9.8
reciprocal object ag- gression				6.7				0.8
one-sided display I	1.3	12.5		13.3				3.8
one-sided display II		12.5	(1)					2.3
one-s. displ. I + one-s. fr. horn thr.	1.3	25.0						3.8
one-s. displ. II + one-s. fr. horn thr.	1.3	6.3						1.5
one-sided frontal horn threat		12.5			(1)	4.8		3.0
other forms of aggression (rush, chase, one-s. mounting)		12.5		13.3		9.5		4.5
without prior display or other forms of aggres- sion	46.7	6.3	(1)	26.7	(1)	66.7	(2)	43.6

Explanations: display I = erect posture + head-sideward inclination

display II = erect posture + head-sideward inclination + symbolic stab over the shoulder + sideward angling of horns

(1) or (2) = absolute numbers (not percentages)

Abbreviations: displ. = display; fr. horn thr. = frontal horn threat; one-s. = one-sided; rec. = reciprocal.



## COMMENTS ON TABLE 3:

Table 3 presents the initiation of fights (horn contact) by displays and other forms of aggression. It is divided into fights between adult males, adult males with adult females, etc.

For the displays, the same terms have been used as in Table 2 with two exceptions: instead of "erect display" and "intensified erect display", two new categories have been introduced: "display I" and "display II". "Display I" includes the erect posture and the head-sideward inclination, i.e., the same behaviour patterns as "erect display" in Table 2. In contrast to "erect display" in Table 2, however, all those cases are excluded in which erecting and turning the head was followed by another display form. "Display II" comprises those cases in which the erect posture and the head-sideward inclination were followed by a symbolic stab over the shoulder and/or angling the horns. Thus, "display II" does not only refer to the uses of symbolic stab over the shoulder and sideward angling the horns as the "intensified erect displays" in Table 2, but it also includes the erect postures and head-sideward inclinations preceding them.

When display I or II were followed by a frontal horn threat, this is expressed as a special category in Table 3, e.g., "reciprocal display II + reciprocal frontal horn threat".

When the opponents only executed a head-low posture before the horn contact, it was counted as a "fight without prior display" because the threat character of the head-low was often uncertain in such cases (see text).

After previous studies on other bovid species (Walther, 1965b, 1974, 1978b, 1979), it was expected that the proportion of fights initiated by reciprocal displays would be smallest in immature males and greatest in adult males. On the whole, the findings in the Etosha oryx fulfil these expectations. However, the proportion of fights without prior displays among adult bulls (46,7 %) is surprisingly great.

Possibly, this figure does not give a completely correct picture, because sometimes one or both opponents stood with lowered head prior to a fight, which is included in the "fights without prior display". It is possible that in some of the cases, the head-low posture was "meant to be" a threat. On the other hand, in (non-territorial) adult males of Thomson's gazelle, only 9 % of the (221) fights observed were without prior displays (Walther, 1978b). The corresponding proportion is so much greater in the adult oryx bulls that one may safely say that there are comparatively many fights without prior display among them even when one takes a number of uncertain cases into account, and one may conclude that the threshold for fighting is comparatively low in *Oryx gazella*. Furthermore, fighting without prior displays is often typical for "playful" interactions (sparring) as they are generally common in immature males. Under this aspect, the findings in the Etosha oryx may indicate that sparring matches are also comparatively frequent among adult males in this species. Again, this speaks for the highly pugnacious nature of the South African Oryx.

In *Oryx beisa* invading Serengeti National Park (Walther, 1978) almost all the fights among adult bulls

were initiated by reciprocal displays. The behavioural difference to the *Oryx gazella* in Etosha National Park fits the picture in that "playful" interactions are less likely in tense situations. The situation of animals invading a new area certainly is tenser than that of animals in their familiar home range.

### 3.5 Forms of aggression and decisions of agonistic encounters

#### 3.5.1 Results (Tables 4-6)

In the (260) encounters of adult bulls among each other (Table 4a), there are numerous one-sided threat and dominance displays, and most of them decided the encounters (in total 60 % of them). Particularly frequent were one-sided "displays I" (which occurred in 27,7 % of the encounters and decided 27,3 % of them). Next in frequency were the one-sided "displays II" (occurring in 14,2 % of the encounters and deciding all of them). One-sided frontal horn threats occurred (on their own, i.e., not in combination with another display) and decided only a comparatively small portion of encounters (6,5 %). Reciprocal threat and dominance displays were much rarer (occurring in total in 18,5 % of the encounters) and were much less decisive (in total 4,2 % of the encounters) than one-sided displays. Most of them lead to fighting. The relatively most prominent category in this regard was "display II continued by reciprocal frontal horn threat" (occurring in 6,2 % of the encounters). Fights decided a great portion of the encounters (28,9 %). One-sided rushes were comparatively infrequent (occurring in and deciding 4,2 % of the encounters). Chases occurred — mainly after fights — in a somewhat greater proportion of encounters (13,1 %).

In the (149) aggressions of adult bulls toward adult cows (Table 4b), reciprocal displays were rare. The proportions of rushes and chases were in about the same small range as in the encounters among adult bulls. Fights occurred in a significantly smaller proportion than in adult bulls among each other ( $X^2 = 16,92$ ,  $df = 1$ ,  $p < .001$ ). One-sided displays on the part of the bulls decided a significantly ( $X^2 = 18,5$ ,  $df = 1$ ,  $p < .001$ ) greater proportion of the encounters (in total 81,2 %) between males and females than of those among adult males (60 %). One-sided "displays I" (occurring in 53 % of the encounters and deciding 51,7 % of them) were significantly ( $X^2 = 23,31$ ,  $df = 1$ ,  $p < .001$ ) more frequent than in encounters of adult males among each other, although they also had been the most frequent form of one-sided displays there. In contrast to the situation in encounters among bulls, the one-sided frontal horn threats were next in frequency (occurring in 20,8 % of the encounters and deciding 19,5 % of them), and the proportion of decisive frontal horn threats was significantly ( $X^2 = 14,58$ ,  $df = 1$ ,  $p < .001$ ) greater than in encounters among bulls.

TABLE 4: Forms of aggression and decisions (or carrying out) of agonistic encounters in adult males (in %)

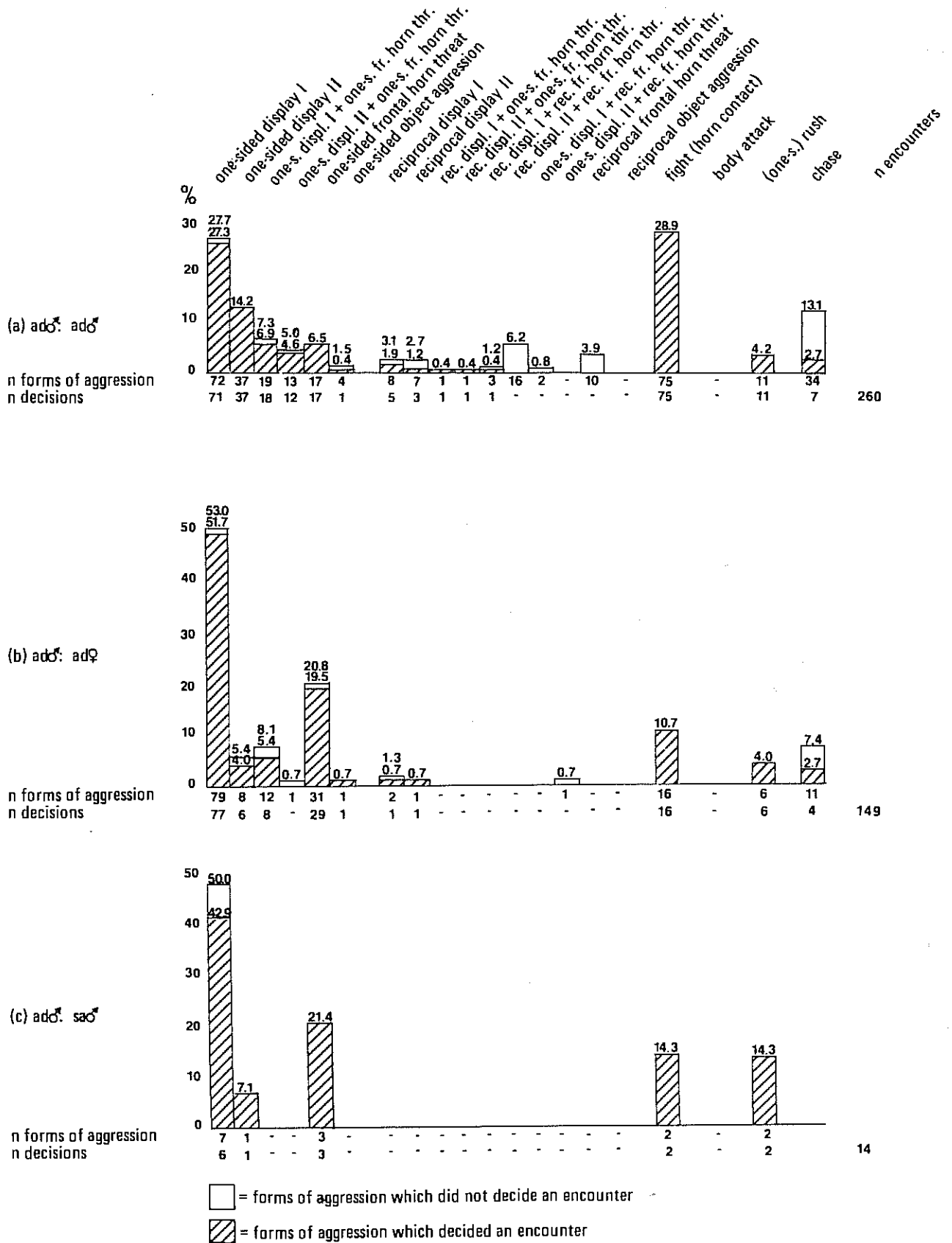


TABLE 5: Forms of aggression and decisions (or carrying out) of agonistic encounters in adult females (in %)

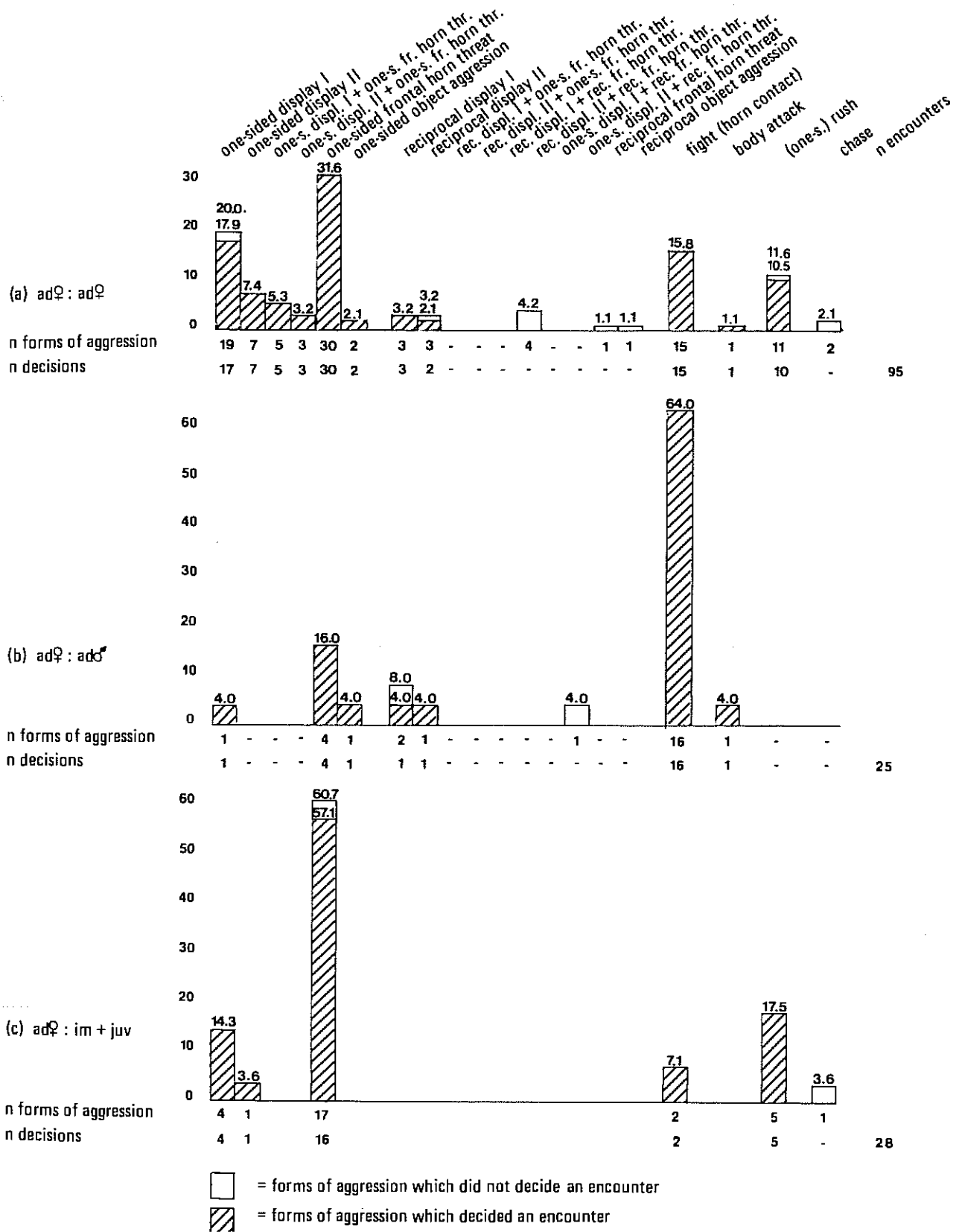
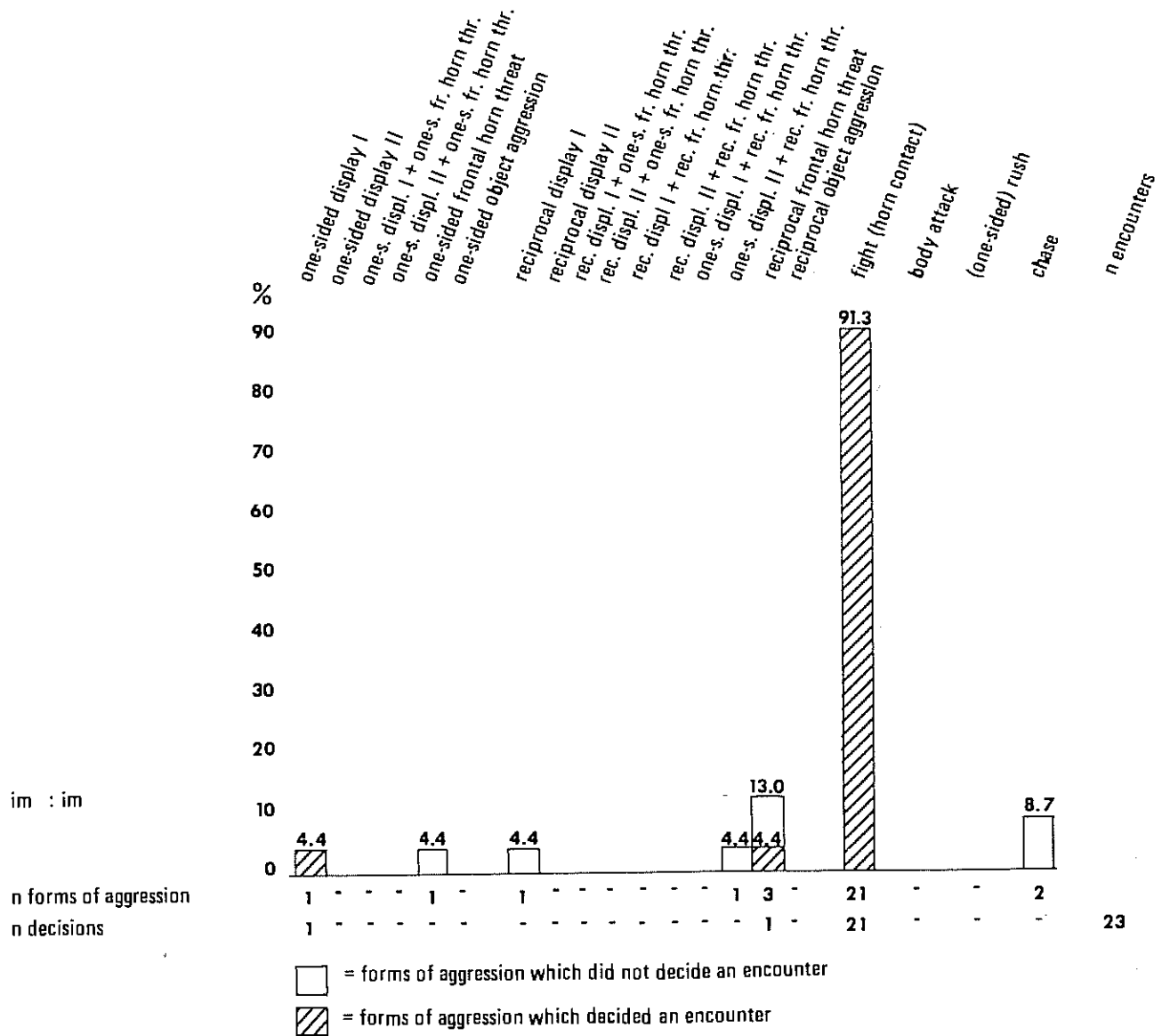


TABLE 6: Forms of aggression and decisions (or carrying out) of agonistic encounters between immature males (in %)



COMMENTS ON TABLES 4 - 6:

With respect to the display categories, Tables 4 - 6 follow Table 3. The other forms of aggression are the same as in Table 2. The formulation "or carrying out" (of agonistic encounters) refers to the few cases without a clear resolution (see Table 2) which are treated as equivalent to decisions in Tables 4 - 6.

The encounters are divided according to sex and age classes in "adult male : adult male", "adult male : adult female", etc. Due to extremely small sample sizes, I did not present the (5) aggressions of adult males toward sub-adult females (2 one-sided erect displays, 2 one-sided frontal horn threats, 1 rush), the (1) fight of a sub-adult male with an adolescent female, the (1) fight of an adolescent male with a calf, and the (1) body attack of a calf toward its mother.

Except when said otherwise, adolescent and sub-adult males are united as immature males (im). In the category "ad ♀ : im + juv", the aggressions of adult females toward immatures of both sexes and toward juveniles (calves) are combined.

Tables 4 - 6 present the forms of aggression, those which did not decide an encounter (open block diagrams), and those which decided the encounters (cross hatched block diagrams) simultaneously in percentages. Reference figure for both are the numbers of encounters. Therefore, the percentages of the mere occurrences of forms of aggression do not add to 100 %, but only the percentages of the decisions do. Thus, e.g., Table 4a reads the following way: "one-sided displays I" occurred in 27,7 % of the (260) encounters among adult bulls, and 27,3 % were decided by them, etc.

When several forms of aggression occurred in the same encounter, the question arises which of them decided the encounter. I considered any encounter in which a fight occurred, to be decided by this fight, and then, displays prior to fighting as well as possibly a chase after the fight, were counted as forms of aggression which did not decide the encounter. When a chase followed after a display or after a rush, the display or the rush were considered to be the decisive forms of aggression. In the very few cases in which it was impossible to make a decision after these simple principles, I decided according to my subjective impression.

In the (14) aggressions of adult males toward sub-adult males (Table 4c), there were a few fights and rushes, but most of the encounters were decided by one-sided displays (in total 71,4 %), mostly by "displays I" (42,9 %) or by frontal horn threats (21,4 %).

In the (95) encounters of adult cows among each other (Table 5a), fights (15,8 %) made a significantly ( $X^2 = 5,59$ ,  $df = 1$ ,  $p < .02$ ) smaller portion as compared to the encounters among bulls (28,9 %). Also the number of chases following fights (2,1 %) was much smaller and decisive chases without prior fighting, rushing or displaying were lacking completely. On the other hand, the proportion of rushes (deciding 10,5 % of the encounters) was significantly greater than that in adult males ( $X^2 = 3,87$ ,  $df = 1$ ,  $p < .05$ ). The total proportion of decisive one-sided displays between adult cows (67,4 %) did not differ significantly ( $X^2 = 1,31$ ,  $df = 1$ ,  $p > .20$ ) from that in interactions among adult males (60 %). However, there were some differences in the frequencies of the single categories of displays. In cows, the proportion of "one-sided display I" (occurring in 20 % of the encounters and deciding 17,9 %) was smaller than that of "one-sided frontal horn threats" (occurring in 31,6 % of the encounters and deciding all of them). In bulls, this was the opposite. When the proportion of "one-sided frontal horn threats" among cows was tested against that in the encounters among adult bulls, the difference was found to be significant ( $X^2 = 35,83$ ,  $df = 1$ ,  $p < .001$ ).

The number of observations (25) on aggressions of females toward males (Table 5b) was considerably smaller than that of bulls toward cows (149). Rushes followed by chases, otherwise so typical of females (see above), were lacking completely. The proportion of one-sided displays (in total 24 %) was considerably below all those previously discussed (ranging between 60,0 and 81,2 %). Thus, the majority of the encounters were reciprocal encounters with an enormous proportional preponderance in the fights (64 %).

In the (28) encounters of adult cows with immature animals of both sexes and with juveniles (Table 5c), rushes decided the encounters (17,9 %) several times and, at least, one chase occurred despite the small sample size. Reciprocal displays were lacking, and the number of fights was small (7,1 %). The majority of the encounters were decided by one-sided displays (in total 75 %) with a strong preponderance of frontal horn threats (57,1 %).

In the (23) encounters of immature males among each other (Table 6), chases as well as one-sided or reciprocal displays showed up in small numbers. The overwhelming majority of the encounters (91,3 %) were fights, most of them without prior displays.

### 3.5.2 Discussion

The encounters of adult bulls among each other were characterised by decisive one-sided displays, and by

fights with or without prior reciprocal displays, sometimes followed by chases. In the one-sided displays, the "display I"-type clearly preponderated.

The great portion of fights and in quite a number of cases (see also Table 3) their initiation by reciprocal displays as well as, on the other hand, the relatively rare occurrence of (one-sided) rushes and decisive chases in the encounters among adult bulls, is indicative of the equal status of the peers and their equally high aggressiveness. That some of these fights were followed by the defeated opponent's flight and the victor's pursuit, speaks for their severity.

The proportion of encounters among adult bulls decided by one-sided threat or dominance displays is also great, and this, of course, is indicative of the unequal status of the opponents. In part, the latter may be due to differences in the individuals' physical or psychological state and/or age. In part, this may be a consequence of social hierarchies within the groups and/or of dominance relationships established in previous encounters. Moreover, sometimes a recipient may simply "obey" (e.g., by walking away) the sender's display when the latter is aiming for an activity which the recipient would have performed on his own in the next moment, for example, to move ahead after the animals have stood for some time (activity change — see below). That "display I" (erect posture with head-sideward inclination, usually in broadside position toward the recipient) was most frequently seen in these one-sided encounters indicates that in many cases, the sender has not to go through the entire display sequence, but that the very first movements of this sequence are sufficient to release a response in a (subordinate) recipient.

The aggressive encounters of adult bulls with adult cows were characterised by one-sided displays (on the part of the bulls) and fights. This is essentially the same as with encounters of bulls among each other. However, there are considerable quantitative differences as the proportion of fights is reduced and the proportion of one-sided displays is enhanced as compared to the encounters of adult bulls among each other. In the displays of bulls toward cows, the "display I" and the "frontal horn threat" play an especially great role.

The rareness of reciprocal displays and the great proportion of one-sided displays is easily explained by the fact that adult bulls usually are physically stronger than cows, and thus, they usually are the dominant partners in intersexual encounters right from the beginning. The situation is similar when the proportional frequency of "displays I" is greater than in encounters between bulls. Of course, this is more likely the more inferior the recipient.

The increase of mere frontal horn threats in the interactions of bulls with cows, as compared to the encoun-

ters of bulls among each other, is not easy to interpret. I feel that it may also be a consequence of the inequality of the partners — at least, when displayed by adult bulls in one-sided encounters (when used by adult cows, it may be somewhat different — see below).

On the whole, it has to be emphasised that oryx bulls principally use the same forms of aggression toward cows which they use among each other, and that fights between bulls and cows definitely occur, though clearly rarer than among bulls. In a species such as Thomson's gazelle, the males only use the chase with considerable frequency toward females, but hardly any other form of aggression. I, particularly, did not witness any fight between an adult tommy male and female in three years (Walther, 1978b), and one may say that tommy males have a different behavioural inventory toward females and toward other males (Walther, 1978c). Clearly, all this is different in oryx. Here, the females are treated as inferior opponents by the males, but they obviously are not as hopelessly inferior to them as the tommy females are to males.

In the aggression of adult males toward sub-adult males (aggressions of adult bulls toward adolescents and juveniles did not occur), about the same picture emerges as in the encounters of adult bulls with adult females. This means that adult bulls treat sub-adult bulls and adult females alike. They both are inferior opponents to an adult male, and the sex of the inferior does not matter much in an agonistic encounter (Walther, 1978b). These results absolutely agree with the corresponding results from quantitative investigations of other ungulate species (e.g., Geist, 1971; Walther, 1978b). The small sample size prevents a discussion whether the adult oryx females may be somewhat less inferior to adult bulls than the sub-adult males are, or vice versa.

The picture of the encounters of adult females among each other generally resembles that of interactions among adult bulls, particularly with respect to the occurrence of a (small) number of reciprocal displays with the peak in the category "display II + frontal horn threat", and most of them continued by other forms of aggression. In the details, however, there are several and apparently rather typical differences when compared to adult males.

The smaller number of interactions in general, as well as the smaller proportions in fights and in chases following fights indicate that the cows are not as aggressive among each other as are bulls. Interesting is the proportional increase in rushes and, above all, in one-sided frontal horn threats, as compared to bulls. In adult bulls, a relative increase in the proportion of one-sided horn threats was found in encounters with inferior opponents (sub-adult males and cows), however, the one-sided "displays I" still outnumbered the one-sided horn threats. In the encounters among cows, it was the

opposite. As discussed above, the frontal horn threats are only slightly ritualised fighting movements, and thus, they are close "at hand" in a hostile encounter, whereas the erect posture with head-sideward inclination in broadside position makes the impression of a much more special and elaborate display, not to speak of its intensification in "display II". Although oryx females have in principle the same display patterns as the males, the less frequent use of the (more elaborate) "display I" as well as the more frequent use of the (more primitive) "frontal horn threats", may indicate that the elaboration and ritualisation of the agonistic displays has not reached the same extent and perfection in the females. Also, the comparatively greater proportion of rushes in females fits this picture since the rush, too, is an only slightly ritualised fighting action, and thus, a rather primitive display.

The aggressions of cows toward adult bulls appear to be typical for a combatant who generally is inferior to the opponent. The few events in which an adult cow displayed against an adult bull and the latter withdrew without counter-display, are probably due to cases of extremely high-ranking cows which can sometimes be observed in oryx (Walther, 1965a, 1978a). On the other hand, when one considers the high portion (81,2 %) of one-sided displays of adult bulls toward cows, it is obvious that it is usually the bull who starts the interaction. Thus, the high proportion of fights in the aggressions of cows toward bulls seems to be largely indicative of cases in which the cows fought back and were forced into these interactions by the bulls.

The situation is very different in aggressive interactions of adult cows with immature and juvenile animals. Here, the adult cows are the superior partners, and thus, the picture is totally opposite (great proportion of one-sided displays, some rushes, but only a few fights).

Under merely quantitative aspects, the aggressions of immature males among each other resemble those of adult cows toward adult bulls (proportionally many fights, but only a few one-sided or reciprocal displays). However, the infrequency of threat and dominance displays of cows toward bulls is due to the superiority of the partner. In encounters among each other, the cows use them quite frequently. In immature males, these displays occur infrequently because generally the youngsters infrequently use them, as was also found in investigations on several other ungulate species (e.g., Geist, 1968, 1971; Walther, 1965b, 1978b). Apparently, this is due to the relatively late maturation of such displays during ontogeny. Thus, in their agonistic interactions, the young males have to fight more often than the adults. Certainly, many of these fights are more or less playful sparring matches, but several very vehement and apparently severe fights were observed among sub-adult males.

### 3.6 Situational motivations of agonistic encounters

#### 3.6.1 Categories and descriptions of situational motivations

The situational motivations are grouped into four superclasses in Tables 7 and 8: Superclass "A" are encounters between strangers. Superclass "B" contains encounters between strangers and encounters among members of the same group. Superclass "C" refers exclusively to interactions between group members. Superclass "D" (only in Table 8) again consists of encounters among group members as well as with strangers.

The term "stranger" means that the individual(s) had not been together with the others in the same group before the encounter took place. In the water-hole situation, the combatants were considered to be strangers when they — singly or within a group — had come from different directions. Furthermore, at the water-holes as well as in other areas, newcomers which showed up after a given herd had been under observation for hours, were also considered to be strangers.

The categories of situational motivations were established empirically with reference to corresponding categories in a study on Thomson's gazelle (Walther, 1978b) with a few modifications for their use in oryx. A few more modifications have been made in Table 8 to meet the special points of interest in the water-hole situation.

These categories of situational motivations are described as follows:

"Meeting strangers when 'hanging around' in the vicinity of a water-hole." Provided that there is no danger of predators or disturbances by other animals (e.g., elephants), oryx may sometimes remain about 50 to 200 m away from the water-hole for up to three or four hours. Usually they stand, sometimes they lie down or graze. This can happen before they have been at the water, or, more commonly, after they have drunk. In this situation, of course, quite frequently a single stranger or a group of strangers may approach the water-hole and meet the animals "hanging around" there.

"Meeting strangers when moving in opposite directions to and from a water-hole." When an individual or a group has drunk, and is now leaving the water-hole, it often follows a well-established trail. Then, it may happen that a newcomer or a group of newcomers encounter the animals leaving the water-hole on the same trail.

"Meeting strangers at the water." This refers to cases in which an individual standing at the water was approached by a newcomer.

"Emphasised dominance toward strangers." One may say that the claim of dominance is a motivating factor in almost all the encounters with strangers and in many of those among group members. In some cases, however, the tendency to dominate the other is extremely emphasised, i.e., it does not occur as a consequence of a more or less accidental meeting, but it obviously is the goal of an aimed approach. Frequently, the subordinate is already stepping aside, withdrawing or even fleeing, but the dominant follows him or even runs after him at a full gallop, passes him, blocks his way in broadside position, and challenges him. In the water-hole situation, the category "emphasised dominance toward strangers" exclusively comprises encounters of this type. In encounters not at water-holes (Table 7), it also includes cases in which a newcomer tried to join a group and was challenged by group members.

"Spontaneous action, contagion, redirected aggression." These are three separate motivations. They are united in Tables 7 and 8, because (a) the samples in each of them were small, and (b) they have something in common: the great spontaneity of aggression. This statement does not imply that there would not be any spontaneity in other agonistic encounters, however, in the category under discussion, spontaneity is the prominent factor. In "spontaneous actions", it appears to be the only one. These are aggressive interactions which start very suddenly and without any recognisable reason. "Contagion" means that two animals fight each other obviously for no other "reason" than that two other combatants are fighting close by. Occasionally, five or even more pairs can be seen fighting at close range. "Redirected aggression" refers here exclusively to those special cases of redirected aggression which Grzimek (1949) termed "*Radfahrer-Reaktion*", i.e. aggressions toward an "innocent" animal, but not toward inanimate objects.

"Taking offense" means that an animal aggressively reacts either to a non-aggressive behaviour (e.g., defecation) of another animal, or to an aggressive action which is not directed at him but to another individual. In oryx, the most common case is that an animal — usually a very heavy adult bull — "takes offense" when two others are fighting. He moves straight toward their interlocked horns, and often his approach is sufficient to make the two combatants interrupt their fight and withdraw. Such cases are not included in the presentation, but only those in which the intervening individual displayed to one or both of the opponents and possibly fought one of them.

"Initiation of sexual behaviour or defense against it." In *Oryx gazella*, the erect posture, sometimes even a frontal horn threat, may initiate the bull's courtship. Thus, this category comprises cases in which the bull's initial (agonistic) display was continued by "Laufschlag" (Walther, 1958) or other sexual behaviour. In some cases, the aggression was on the part of the cow which

defended against the male's sexual approach by displays or (mild) fighting.

The next three classes of situational motivations fall under the super-category "Co-ordination of group activities". All three of them are related to each other, and the mechanism behind them is a special kind of "taking offense" (Walther, 1978b).

"Activity changes within the group" — from lying to standing or grazing, from standing or grazing to moving, and vice versa — can motivate aggressive interactions when some of the group members continue the previous activity while others are already engaged in the new activity. Then, the latter may "take offense" and threaten or fight those which are still resting, or standing, etc.

"Disagreements whether to stop or to move, on march-direction and march-order." Disagreements on march-direction and march-order show up in the beginning of a move when all the members of the group are on their feet and moving, but are still moving in different, frequently even in opposite directions. The aggressions which then show up, are some kind of "voting" and result in a final, mutual march-direction. A — sometimes rather temporary — marching order is established simultaneously. Included in this category are "disagreements whether to stop or to move", which are particularly frequent when a herd is approaching a water-hole. In this situation, the first animals of the file may stop in order to watch for danger, but animals from behind continue marching and come forward. Then, the standing animals may easily chase back the animals coming from behind, or the latter may "push" the standing ones.

"Pushing during moves" refers to cases in which an animal is slowing down or is deviating from the mutual course during a move, and another animal — usually the animal behind it — speeds it up or brings it back into the file by aggressive behaviour.

"Emphasised dominance within the group and keeping the group together." "Emphasised dominance" of course, means essentially the same as in "emphasised dominance toward strangers", but here it is with group members. In some cases, it apparently had something to do with "keeping the group together".

"Maintaining individual distance when grazing" and "when standing". Many animals keep a certain individual distance (Hediger, 1941). This individual distance may vary with sex, activity and orientation of the individuals to each other (Walther, 1977). Its important role in oryx has been beautifully demonstrated by Hamilton *et al.* (1977). In Table 7 and 8, the corresponding categories refer to cases in which the violation of this individual distance gave rise to aggressive interactions, i.e., that two group members simply came too close to each other. In standing and

grazing oryx, this minimum distance ranges between 1 and 5 m, depending on sex and individual relationships (e.g., mother-offspring) of the animals involved, on their orientation toward each other (it is smallest when they stand behind one another, and largest when they are frontally oriented toward each other), and on activity (in grazing frequently larger than in standing). In the observations at water-holes (Table 8), the "standing" category is subdivided into "when standing during a move to or from the water-hole" (see "disagreements on stop or move") and in "when standing at the water".

"Competition over water" refers to those aggressions which occurred when at least one of the two animals involved was drinking or just lowering the head to drink. It is likely that even in some of these cases, not the competition for water *per se*, but the individual distance was the factor which primarily motivated the aggression.

### 3.6.2 Results

In the *animals not at water-holes* (Table 7), the majority of the interactions were among adult bulls (59 out of 87), and many of the encounters (45 out of 87) were carried out and decided by (one-sided) displays. However, the number of fights (39 out of 87) was not far from that.

The proportion of "taking offense" (4,6 % of the total) was relatively small. However, the proportion of "spontaneous action, contagion, redirected aggression" (19,5 % of the total) was quite impressive. Interactions other than fights were rare in this category. In the (34) fights of adult bulls among each other, 38,2 % were spontaneous or due to contagion.

The three categories of "co-ordination of group activities" combined made up 44,8 % in the oryx not at water-holes, and thus, the greatest portion of the (87) encounters. The sub-category "activity changes within the group" (19,9 %) clearly outnumbered "pushing during moves" (3,4 %) and "disagreements on march-direction and march-order" (11,5 %). Also, the greatest portion (together 44,1 %) of the (34) fights among adult bulls were due to co-ordination of group activities.

Encounters over individual distance in grazing and standing made 16,1 % of the (total of) encounters, and encounters due to "emphasised dominance within the group or keeping the group together" were rather rare (3,4 %). With respect to this last category as well as with "pushing during moves", it should be mentioned that no long moves were seen in these herds, i.e., that situation was lacking in which these categories are most likely to occur.

Only the category "emphasised dominance toward strangers" refers to interactions with strangers in Table 7. Encounters belonging to it occurred with moderate frequency (9,2 % of the total). This was due to the



TABLE B: Situational motivations of agonistic encounters at waterholes

Decisive form of aggression	One-s. or rec. display encounters				Fight or body attack				Rush or chase				Total
	<i>ad</i>	<i>ad</i>	<i>ad</i>	others	<i>ad</i>	<i>ad</i>	<i>ad</i>	others	<i>ad</i>	<i>ad</i>	<i>ad</i>	others	
Opponents	<i>ad</i>	<i>ad</i>	<i>ad</i>	others	<i>ad</i>	<i>ad</i>	<i>ad</i>	others	<i>ad</i>	<i>ad</i>	<i>ad</i>	others	
n encounters	142	116	63	34	41	15	15	25	18	10	9	6	494
A. Meeting strangers when "hanging around" in the vicinity of a waterhole	14.1 20	13.8 16	12.7 8	14.7 5	22.0 9		6.7 1	12.0 3					12.6 62
when moving in opposite directions to and from the waterhole	10.6 15	11.2 13	3.2 2	5.9 2	2.4 1	6.7 1	6.7 1					1	7.3 36
at the water	5.6 8	6.0 7	9.5 6	5.9 2	12.2 5							1	6.1 30
Emphasized dominance toward strangers	19.7 28	2.6 3	1.6 1		9.8 4				44.4 8				8.9 44
B. Spontaneous action, contagion, redirected aggression		2.6 3		5.9 2	14.6 6	20.0 3		36.0 9	5.6 1				4.9 24
Taking offense (intervening)	6.3 9	0.9 1	3.2 2	8.8 3	4.9 2			4.0 1					3.6 18
Initiation of sexual behaviour or defense against it		7.6 9											1.8 9
C. Coordination of group activities													
Activity changes within the group	12.0 17	14.7 17	9.5 6	8.8 3	9.8 4	20.0 3	13.3 2	16.0 4	11.1 2			1	11.9 59
Disagreements whether to stop or to move, on march-direction and march-order	4.9 7	12.9 15	20.6 13	20.6 7	2.4 1	33.3 5	13.3 2	4.0 1	16.7 3	20.0 2		2	11.9 59
Pushing during moves	2.8 4	5.2 6	4.8 3	2.9 1	2.4 1	6.7 1							3.2 16
Emphasized dominance within the group and keeping the group together	7.0 10	7.6 9								50.0 5			4.9 24
Maintaining or enlarging individual distance													
when grazing		0.9 1											0.2 1
when standing during a move to or from the waterhole	7.7 11	3.5 4	15.9 10	14.7 5	17.1 7	6.7 1	33.3 5	24.0 6		10.0 1			10.1 50
at the water	6.3 9	5.2 6	6.4 4	8.8 3			20.0 3	4.0 1	11.1 2			2	6.1 30
D. Competition over water	2.8 4	5.2 6	12.7 8	2.9 1	2.4 1	6.7 1	6.7 1		11.1 2	20.0 2		4	6.5 32

Straight figures = absolute numbers

Slanted figures = percentages

Abbreviations: one-s. = one-sided; rec. = reciprocal;

A = encounters between strangers; B and D = encounters among group members or with strangers; C = encounters among group members.

## COMMENTS ON TABLES 7 AND 8:

Tables 7 and 8 present the situations and/or motivations which lead to the agonistic interactions observed. Table 7 shows the encounters in the herds which were not at water-holes, and Table 8 presents those which took place at water-holes and their vicinity (i.e., in a radius of about 300 m around a water-hole). Three of the observed encounters (two horn threats of cows toward calves, and one body attack of a calf toward a cow) are not presented in these tables because they would have required a special category (soliciting milk or defense against it) which is of minor importance to this study.

Tables 7 and 8 are based on the numbers of encounters; however, the encounters are subdivided according to those forms of aggression which decided them. Since the forms of aggression and the frequency in which they occurred have been presented in Tables 2–6, some of these were combined in the interest of a shorter presentation. Thus, in Tables 7 and 8, rushes and chases are united in one class, and the very few body attacks are added to the fights. The most comprehensive class is "one-sided or reciprocal display encounters". It comprises all the displays which have been termed "erect display" and "intensified erect display" or "display I" and "display II" in the previous tables, as well as "frontal horn threats" and "object aggressions". Furthermore, the decisive one-sided and reciprocal displays are combined.

Each of these three classes of forms of aggression is subdivided in four sub-classes according to the opponents involved: "adult male : adult male", "adult male : adult female", "adult female : adult female", and "others" (i.e., adult male : sub-adult male, sub-adult male : sub-adult male, etc.). For the samples in these four sub-classes, Tables 7 and 8 show the proportions which fell into the single categories of situational motivations. These proportions are presented in absolute numbers and in percentages. When the sample size was less than 10, only the absolute numbers are given. Thus, Table 8 (and correspondingly also Table 7) reads the following way: One-sided or reciprocal displays decided 142 encounters among adult males. Of these 142 encounters, 14.1 % (= 20 cases) occurred in the situation "Meeting strangers when 'hanging around' in the vicinity of a water-hole", etc.

relative infrequency in which newcomers joined the herds observed in areas other than at water-holes.

In the (494) interactions of *oryx* at Etosha water-holes (Table 8) the encounters decided by one-sided or reciprocal displays (355) considerably outnumbered the (96) fights. Although encounters between adult bulls (201) were more frequent than those of any other class, their fights (41) made up a significantly ( $X^2 = 29,01$ ,  $df = 1$ ,  $p < .011$ ) smaller portion than the fights (34) among adult bulls in their (59) interactions not at water-holes.

Sexual behaviour was seen on only a few occasions, and the proportion of aggressions linked to it was correspondingly small (1,8 % of the total). "Taking offense" (intervening) was in about the same small range (3,6 %) as in animals not at water-holes. As compared to the latter, however, the proportion of "spontaneous actions and contagion" (4,9 % of the total) was significantly ( $X^2 = 22,12$ ,  $df = 1$ ,  $p < .001$ ) smaller.

"Competition over water" made up only 6,5 % of the encounters at water-holes, but it included relatively many rushes and chases, i.e., rather unritualised forms of aggression. Also, one of the very few body attacks was observed in this situation.

The total of "maintaining and enlarging individual distance" comprised 15,4 % of the (494) encounters at water-holes. This was almost precisely the same as the 16,1 % of encounters apart from water-holes. However, in the areas apart from water-holes, 9,2 % of the (total of) encounters were over grazing distances, but only 0,2 % at water-holes because the animals infrequently grazed in the vicinity of water-holes. Thus, at the water-holes, most of the distance encounters took place while the animals were standing, and the majority of them (10,1 %) during halts on the way to the water-hole.

The three sub-categories of "co-ordination of group activities" together comprise 27 % of the total of encounters. This is significantly ( $X^2 = 10,21$ ,  $df = 1$ ,  $p < .01$ ) less than the 44,8 % of corresponding encounters in areas far from water-holes. In "pushing during moves", there is no difference (3,2 % as compared to 3,5 %). Also, there is no quantitative difference (11,9 % as compared to 11,5 %) in the "disagreement" category. However, in the herds which were not at water-holes, these disagreements were mainly over the march-direction, whereas in the water-hole situation, most of them were over halting or moving on the way to the water. It also should be noted that there were relatively many encounters of males with females in this category. Thus, the major quantitative difference between animals at water-holes and animals not at water-holes was in the "activity changes within the group" (11,9 % as compared to 22,9 %).

"Emphasised dominance within the group and keeping the group together" occurred in an about as small portion (4,9 %) as in animals not at water-holes (3,4 %).

The "emphasised dominance toward strangers", with a total of 8,9 %, occurred in about the same proportional range as in animals not at water-holes (9,2 %). In the latter, however, this category represented the only situational motivation which lead to encounters with strangers. In the water-hole situation, there were three more situations for meeting strangers ("hanging around in the vicinity of a water-hole", "when moving in opposite directions to and from a water-hole", and "at the water"), so that altogether, "meeting strangers" made up 34,8 % of all the encounters observed at water-holes. This is significantly ( $X^2 = 21,46$ ,  $df = 1$ ,  $p < .001$ ) more than the total of interactions (9,2 %) due to meeting strangers in the herds not at water-holes. Furthermore, with 34,8 %, "meeting strangers" played an incomparably greater role in the encounters of *oryx* at Etosha water-holes than the competition over water (6,5 %).

## 3.6.3 Discussion

The total of encounters (87) observed in areas other than at water-holes (Table 7), was considerably smaller than that of encounters (494) at water-holes (Table 8).

This difference, however, was primarily due to the much longer observation time spent at water-holes (see "Material and Methods"), but it does not necessarily suggest that there would be more aggressions at water-holes.

Some of the categories of situational motivations were established especially with respect to the water-hole situation ("competition over water", "standing at the water", etc.). Of course, no cases falling under these categories could possibly occur in areas other than in the vicinity of water-holes. In all the other situational motivations, corresponding cases were observed in animals at water-holes as in animals far away from water-holes. Particularly, when one compares the number of fights among adult males (34) at places other than water-holes to that of fights between adult males (41) at water-holes, and when one takes the much longer observation time at water-holes into account, one may safely say that fights among males are, at least, not rarer outside the water-hole situation.

Spontaneous aggressions and interactions due to contagion were proportionally more frequent in areas other than water-holes. In this category, the absolute numbers of fights outweighed the numbers of (decisive) display encounters. Most of these fights were sparring matches. It fits the picture that 36 % of the (25) fights were between "others" (than ad♂ : ad♂, ad♂ : ad♀, and ad♀ : ad♀), since the "others" were almost exclusively immature males, and sparring matches are typical of immatures. The playful nature of (many of) these fights may also explain their rare occurrence in the vicinity of water-holes. It is generally accepted (Eibl-Eibesfeldt, 1967), that playful interactions predominantly occur in relaxed situations, and the situation around a water-hole relatively often is not relaxed, sometimes due to the danger from predators, sometimes due to the presence of superior species (such as elephants), sometimes because of intraspecific tensions.

Interactions linked with activity changes within the groups were proportionally less frequent in animals at water-holes than in other areas. This was a result to be expected. Changes from lying to another activity, and changes from grazing to another activity were rare at water-holes because the animals infrequently grazed and rested there. Thus, only the changes from standing to moving, and vice versa, remained in the water-hole situation.

Dominance within the group and keeping the group together infrequently motivated aggressive interactions in the Etosha oryx. In the *Oryx beisa* invading Serengeti National Park (Walther, 1978a), one-sided display encounters of alpha-bulls with the subordinate bulls and with cows were frequently linked with emphasising dominance and with keeping the group together. In the *Oryx gazella* in Etosha National Park, the position of an alpha-bull in a herd was not as prominent as in the said herds of *Oryx beisa* and his

activities in preventing members from leaving the group were never as frequent and striking. The most pronounced case of this type occurred when a herd of a few bulls and several cows had come to a water-hole (Okondeka), had drunk there, and then found their way back blocked by a lion pride. They tended to split and to move away in different directions in this situation, but the strongest of the bulls "desperately" tried to keep the group together for about half an hour; however, his efforts were in vain. One animal after the other managed to escape, so that this bull was alone, eventually. In the observations on migratory *Oryx beisa*, the alpha-bulls always succeeded in their frequent herding actions.

In the herds observed at places other than water-holes, aggressions of adult bulls toward cows were infrequent — as they had been in the herds of *Oryx beisa* observed in Serengeti (Walther, 1978a) — most of them were one-sided display encounters and occurred in connection with co-ordination of group activities. In the vicinity of water-holes, the frequency of aggressions of bulls toward cows was considerably increased mainly due to meeting strangers and to disagreements on stop or move. Oryx often stop when approaching a water-hole in order to watch for danger. Cows frequently march in front of a file, and thus, they are the first ones to stop at occasion of such a halt, and then the males may "push" from behind. Or, the animals — males or females — standing in front of the file, may chase back other animals which try to pass them. This may also explain the relatively frequent occurrence of rushes and chases in this situation. Finally, when marching in front of the file, the cows are the first animals to meet strangers.

On the whole, the possibility and the probability to meet strangers is great in the vicinity of a water-hole, and in this study, meeting strangers was the only situation which motivated significantly more agonistic encounters in the vicinity of water-holes than in other areas.

The present material does not allow a conclusion whether oryx truly have more interactions at water-holes. That visitors to the park can see most of the agonistic encounters at water-holes (see Introduction) could simply be due to the tourist situation, i.e., that they predominantly watch animals at water-holes. If, however, the frequency of agonistic encounters should be increased, it can only be due to the more frequent meeting of strangers in the vicinity of the water-holes.

### 3.7 Interactions with other animals

In the same period in which I recorded 584 encounters of oryx among each other, I witnessed only 14 agonistic interactions with other species, and in four of them not the oryx, but the animals of the other species were the aggressors (half-grown elephants, *Loxodonta africana*, and Hartmann's zebra, *Equus zebra hart-*

*mannae*). Of the aggressions of oryx toward other animals, two were against springbok (*Antidorcas marsupialis*), three against warthog (*Phacochoerus aethiopicus*), two against red hartebeest (*Alcelaphus buselaphus caama*), and three against greater kudu (*Tragelaphus strepsiceros*). Fights or body attacks did not occur in these encounters. The oryx used rushes toward the warthog, rushes and frontal horn threats toward springbok and red hartebeest, frontal horn threats, erect posture in broadside position and the symbolic stab over the shoulder against greater kudu. Except for one interaction with a springbok, all these encounters were in the immediate vicinity of water-holes, most of them at Dinteri when (for one day) the water was very low there so that the animals had to step down into the (artificial) water-hole. In red hartebeest and kudu, the addressees were exclusively adult males, but the displaying oryx were not only bulls, but sometimes also cows and in one case even a sub-adult animal. All the recipients withdrew from the displaying oryx.

More important than overt aggression seems to be some kind of biological rank order (Hediger, 1941) among the (non-predatory) species in the water-hole situation. This means that a subordinate species either withdraws from the water-hole when a dominant species arrives, or that the subordinate waits in some distance until the dominant species is through drinking and has left the water-hole. Of course, this biological rank order becomes the more striking (and the more important under certain management aspects), the smaller the water-hole. Among the observed animals, elephant and the two zebra species (*Equus quagga antiquorum* and *Equus zebra hartmannae*) ranked over oryx, and oryx ranked over red hartebeest, kudu, warthog and springbok. Sometimes, this rank order may be "broken" by an old and apparently highly dominant male of an inferior species, e.g., a very strong, adult oryx bull may sometimes approach the water-hole and drink when zebra are still around.

#### 4 SUMMARY

In June and July 1978, data on 584 agonistic encounters of *Oryx gazella* were collected in the Etosha National Park. The majority of the encounters took place among animals of the same sex and age class; encounters between adult bulls and cows also were frequent. The fighting techniques as well as the agonistic displays followed the usual "oryx pattern" (Walther, 1958, 1965a, 1978a; Huth, 1976). Among the displays, however, a "symbolic stab over the shoulder" quite frequently occurred in *Oryx gazella* which had not been noted in *Oryx beisa* or any other bovid species up to now. In the typical case, it was part of a display sequence: erect posture (commonly in broadside position to the adversary) — sideward inclination of the head (away from the opponent) — symbolic stab over the shoulder — sideward angling of the horns (toward the recipient) — frontal presenta-

tion of the horns and/or symbolic butt or forward-downward blow. One-sided displays frequently decided agonistic encounters. Reciprocal displays were usually followed by fights. However, a surprisingly great portion of the fights started without striking prior displays. All the fights were horn-to-horn contacts. Body attacks were rare. Flights of the subordinates infrequently occurred after displays, somewhat more often after fights, but proportionally frequently after one-sided (symbolic) rushes. In interactions among adult bulls, one-sided displays decided many of the encounters. Often the dominant male's erect posture was sufficient to release the subordinate's withdrawal. Next in frequency were fights. One-sided displays also decided most of the encounters of adult bulls with cows. Fights developed mainly when the cow would not or was not fast enough to respond to the bull's display. Aggressive actions of cows toward bulls were much rarer than the opposite. In a very few cases, cows dominated bulls. In encounters among adult cows, rushes were more frequent, but fights were less frequent than among bulls. Most of their interactions were decided by one-sided displays. The cows exhibited the same displays as the bulls; however, they used erect (and related) displays less frequently, but frontal horn threats more often than bulls. In the interactions of adult cows with immature and juvenile animals, reciprocal displays were lacking, and fights were rare. The overwhelming majority of the encounters among immature males were fights without prior displays. The most important categories of situational motivations of agonistic interactions were co-ordination of group activities, maintaining or enlarging the individual distances between group members, meeting strangers, and some more or less spontaneous actions such as sparring matches, contagion, and taking offense (i.e., intervening when others were fighting). These situational motivations were the same at water-holes as away from water-holes, except for direct competition over water which, however, consisted of only a minor portion of the encounters at the Etosha water-holes. Encounters due to maintaining or enlarging the individual distances were proportionally as frequent at water-holes as in other areas. The proportions of spontaneous interactions and of encounters due to the co-ordination of group activities were even greater in the animals far away from water-holes. Encounters due to meeting strangers strongly preponderated in the animals at water-holes over the corresponding proportion in animals in other situations. This category (meeting strangers) also accounted for the more frequent interactions of bulls with cows in the vicinity of water-holes. Thus, the increase in meeting strangers appeared to be the major reason for a possible increase in aggressive interactions of oryx at Etosha water-holes. Interspecific aggression was rare. In the water-hole situation, interspecific avoidance due to a biological rank order among the different game animals appeared to be more important than overt aggression.

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**Klipspringer**  
**(*Oreotragus oreotragus*)**  
**social structure and predator**  
**avoidance in a desert canyon**

by

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ABSTRACT

Klipspringer, *Oreotragus oreotragus*, were observed for 17 months (1976-78) in the Kuiseb River Canyon of the Namib Desert. The typical social group is a monogamously mated adult pair and one to two offspring. Daily activities of the family group are highly synchronised, and individuals maintain spatial proximity throughout the day. Adult females initiate and lead most group travel, including flight from potential danger. Klipspringer avoid predators through frequent vigilance, especially by adult males, and loud duetted alarm calls by the adult pair. Spatial cohesiveness, synchronised activities and persistent vigilance of the family group are adaptations to an open habitat that distinguish klipspringer from cover-dependent Neotragini antelopes.

## 1 INTRODUCTION

The gradation of social organisation in African antelopes from solitary individuals or monogamous pairs to large social groups is correlated with a habitat shift from closed forests and dense bush to open grasslands and savannah (Eisenberg, 1966; Estes, 1974; Jarman, 1974; Leuthold, 1977). Cover-dependent antelopes of forest and bush include the duikers (Cephalophinae) and most of the dwarf antelopes (Antilopinae: Neotragini) (Estes, 1974; Jarman, 1974; Leuthold, 1977). These antelopes generally rely on silence and concealment to avoid predation. This is maximised by group dispersion and solitary habits. One apparent exception is the klipspringer, which occurs on isolated rocky outcrops and steep slopes of mountains and gorges through southern and eastern Africa (Dorst and Dandelot, 1970). In these open areas klipspringer are conspicuous and cannot rely on concealment to avoid predators. Here I describe the structure of klipspringer social groups and its significance to habitat preference and predator avoidance.

## 2 STUDY AREA AND METHODS

### 2.1 The Kuiseb River Canyon

In South West Africa klipspringer are restricted mainly to mountain escarpment and broken plateaus (Joubert and Mostert, 1975), and in the central Namib Desert to the rocky canyons in the upper reaches of the Swakop, Khan and Kuiseb Rivers (Stuart, 1975). The main study population included four klipspringer groups inhabiting the rocky slopes of the Kuiseb River Canyon, 45 km east of Gobabeb (23°34'S, 15°03'E). The Kuiseb is a seasonally dry river stretching about 440 km westward across the Namib, dropping from the Khomas Hochland through a deep narrow gorge that gradually widens and flattens as it approaches the Atlantic Ocean. The river-bed was marked by designating Gobabeb (56 km inland) as kilometre 0, then placing numbered stone markers at one kilometre intervals for 75 km up-river (Fig. 1).

Average annual rainfall at Gobabeb has been 17 mm (1962 – 1972: Seely and Stuart, 1976). For the two years of this study 123 mm of rain fell in 1976 and 15 mm in 1977 (Gobabeb meteorological records). Mean monthly temperatures at Gobabeb vary from 33.3°C to 9.7°C. Although usually dry, the Kuiseb has flooded sometime between December and March every year since 1963 following seasonal rains in the Khomas Hochland and its escarpment that average 100 – 400 mm (Stengal, 1964). Floods may persist for one to three months in the region of this study, and minor flows may continue for another two to three months in the up-river parts. In the dry period between floods, water-pools in the Kuiseb gradually decrease in size and number until open water remains only in the higher reaches of the canyon beyond the study

area, except for a few isolated water-holes in the lower areas that are excavated by gemsbok (*Oryx gazella*) (Hamilton *et al.*, 1977).

### 2.2 Habitat types

The study area encompasses three different habitats: 1) the upper rim of the canyon and adjoining Namib plains, steeply dissected on the north bank and overlain by sand-dunes to the south; 2) the 100 – 170 m high rocky slopes of the canyon walls; and 3) the canyon floor (Plate 1). In 1976, just after the heaviest summer rains in 40 years, the barren gravel plains became covered with grass. The effects of this unusual growth persisted through the following dry year, which are summarised here from more detailed vegetation descriptions (Tilson and Tilson, in prep.).

The plains are dominated by grasses, especially the tuft grass *Stipagrostis ciliata*. Scattered dwarf shrubs, especially *Tephrosia dregeana* and *Euphorbia glanduligera* occur, and in shallow washes the succulents *Zygophyllum simplex* and *Mesembryanthemum guericchianum* are found.

The canyon wall habitat includes sheer cliffs, steep washes and erosion courses and vegetated boulder-strewn slopes. Near the top grasses make up two-thirds of the cover but decrease in importance on the lower slopes, where forbs and shrubs contribute one-half of the cover. The small shrubs *Euphorbia glanduligera*, *Forsskaolea candida*, and *Ruellia diversifolia* are common, and succulents are still well represented, especially *Zygophyllum simplex* and *Sesuvium sesuvioides*. After heavy rains plant cover on broken slopes may be as high as 30 %, but as the dry season begins the annuals die off, and by August coverage by the remaining vegetation drops to an average of 2 %.

The 100 m wide canyon floor (Range = 80 – 300 m) is dominated by a narrow riparian forest. As the flood waters recede and the river dries, the main channel of the sand and cobble river course fills with ephemerals. *Acacia albida* trees line the river-banks, and stoloniferous grasses and many shade-seeking annuals grow in their shade. The near continuous canopy of *A. albida* is broken occasionally by stands of *Tamarix usneoides* and *Ricinus communis*, which are more common down-river. An occasional tree of *Euclea pseudebenus* intrudes, as do the wild figs, *Ficus sycamoros* and *F. cordata*, though the latter grows most commonly from rock crevasses. On the alluvial flood-plains between the riparian forest and canyon walls *Acacia erioloba* trees are interspersed with sprawling clumps of *Salvadora persica* and a sparse cover of other shrubs and grasses (Fig. 1).

### 2.3 Methods

In the study area (km 38 – 48) four groups of klipspringer were observed for four months (June – Sept.



PLATE 1: The Kuiseb River Canyon at Nareb, 45 km up-river from Gobabeb, showing the main habitat types described in the text.

1976) from sites situated on the opposite canyon wall (about 100 – 300 m) with a 40× telescope. After two of these groups were habituated, observations for the next five months (October – February) continued from a vehicle at distances of 20 – 50 m. Floods in the canyon from March – May 1977 precluded travel to the area. In June 1977 observations on the same groups resumed and continued until the canyon flooded again in January 1978. Data presented here are from 215 field days, including over 900 h of systematic observations on a single klipspringer group spread over the last eight-month period.

Activity patterns are derived from continuous observations from 0700 – 1900 hours on a single group six days per month. These are supplemented by discontinuous observations on three different groups that varied from 2 – 4 days per month. The main group was the subject during the first and last period (3 days each) of the month, another during the middle of the month. Every five minutes the activity (lying, standing, walking, running, feeding and social interactions) of each individual of the group was noted, as well as the estimated distance between individuals to the nearest metre. I used the length of a klipspringer's body from nose to tail to approximate one metre (mean length = 90.0 cm: Wilson and Child, 1965). Movements were

sketched roughly and referenced to conspicuous landmarks, then transferred to the field map. Social interactions were noted on prepared check sheets or recorded on tape and later transcribed.

Individual klipspringer were recognised by body scars, horn and hoof shape, and in some cases by ear patterns. These markings were used to distinguish individuals of the four study groups. For censusing I noted the distance in kilometres to the nearest tenth (Landrover odometer) and which side of the canyon the group occupied. This, in conjunction with the age and sex composition of each group, and the differences in coat colour of the adults, permitted relatively consistent identification of 17 other groups in the canyon. The locations of these sightings were transferred onto a 1:1 000 field map drawn from aerial photographs. Censuses of 75 km of canyon were made semi-monthly, each census being a trip up and back along the same route (see Fig. 1).

### 3 RESULTS

#### 3.1 Group size and composition

In the canyon klipspringer are concentrated between km 38 – 65, with a few isolated groups above and



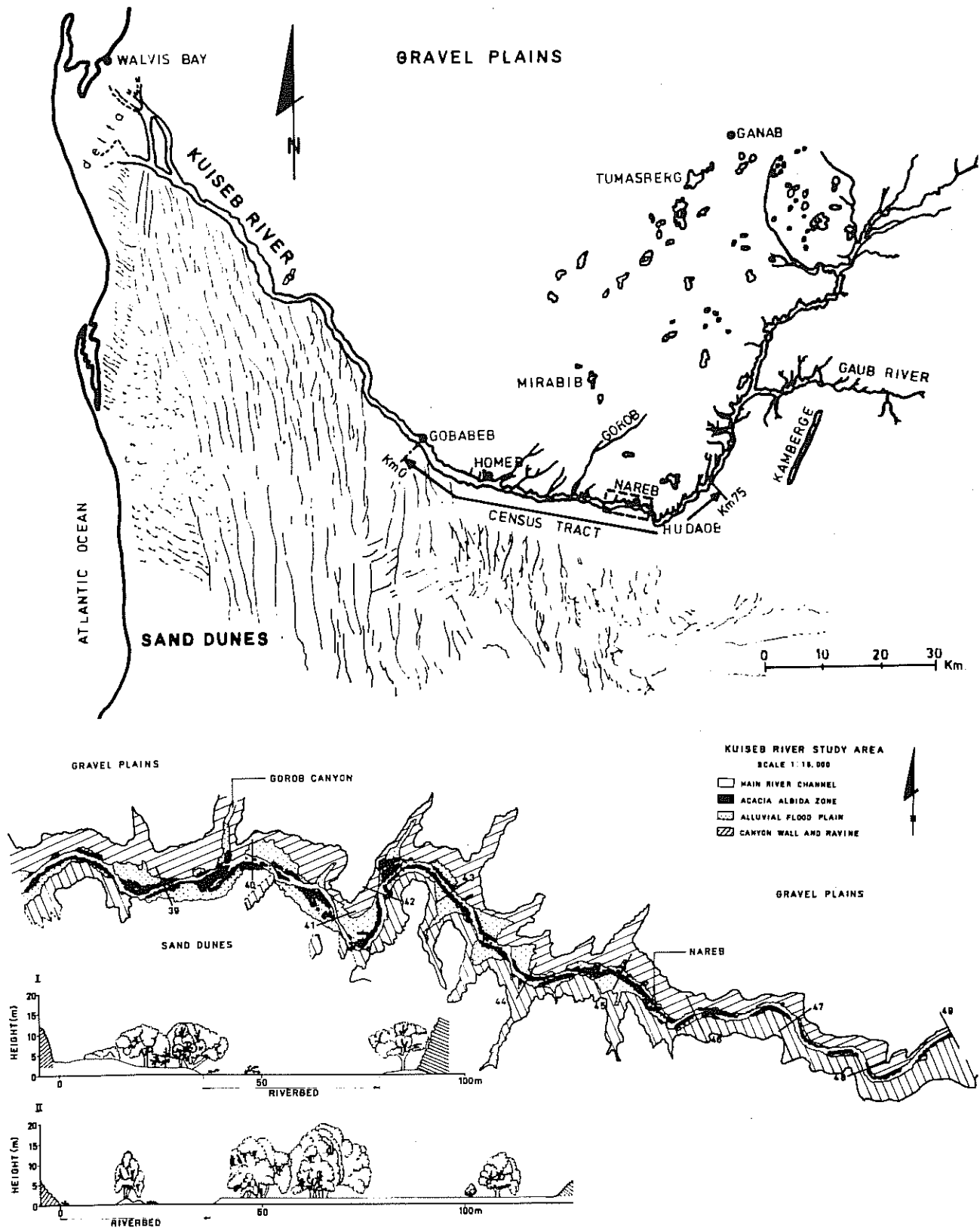


FIGURE 1: A map of the Kuiseb River with an enlargement of the canyon study area (km 37 – 47). The census tract begins at Gobabeb (km 0) and ends 75 km up-river at a massive rock landslide into the canyon's main channel. Vegetation on the canyon floor was drawn from aerial photographs. Profiles of *Acacia albida* forest are based on 5 m wide transects located 1 km (I) and 0,5 km (II) up-river from Nareb. This narrow strip of trees is the principal food resource for klipspringer for most of the year.



PLATE 2: The acacia dominated riparian forest on the canyon floor.

below this area (Fig. 1). The social organisation of four klipspringer groups of known individuals and 17 other groups censused in the canyon is centered around an adult pair with one to two offspring. In the study area one group numbered four animals; the other three groups had three animals. The regularly censused groups ranged from two to four animals per group (Table 1). On the average, these 21 groups included 2,6 (SD 0,5) individuals. Adult pairs remained together for the 17 months of this study and were considered to be monogamously mated.

TABLE 1: Distribution of group sizes for all censuses of klipspringer in the Kuiseb River Canyon.

Group size	1976/77		1977/78	
	Number	Percent	Number	Percent
1	12	7,7	25	8,6
2	59	38,1	157	53,8
3	82	52,9	104	35,6
4	2	1,3	6	2,1

Females bear a single offspring about once every 16 months. For the first two months the infant is hidden among the rocks, after which it accompanies the adults throughout the day. In these early months it closely follows the adult female, but by four months of age it is more independent and associates with either parent. Male and female offspring are difficult to distinguish in the field until the male's horns begin to develop at about six months. By seven months both sexes are close to full adult size (Cuneo, 1965; personal observations) and are capable of breeding (Jantschke, personal communication). At this age, sub-adult females are difficult to distinguish from adult females. The inability to sex young klipspringer or to distinguish adult females from their full-sized offspring may lead to the impression that klipspringer groups are sometimes composed of two or more mature breeding females (see Dunbar and Dunbar, 1974). However, among the 21 groups no more than one offspring was born to a family within a 16-month period. Also, in the family groups where individual identities were established, adult females consistently dominated female offspring; and when a new infant was born, the older left the group soon afterwards.

### 3.2 Habitat preference

The three divisions of the klipspringer range, 1) the relatively flat plains, 2) the rocky slopes of the canyon and its tributaries, and 3) the narrow sandy canyon floor, differ in structure and in diversity of vegetation. Each is associated with particular klipspringer activities. Except when klipspringer are feeding (see below) or moving to another part of their range, they prefer the upper slopes of the canyon wall and spend a majority of the diurnal time in these areas. Klipspringer are generally on the top edge of the canyon walls during the first two to three hours of the morning, alternately standing or lying in the sun. The top of the canyon walls are the highest, or close to the highest, sites in the group's range and offer a commanding view of the top, bottom and opposite sides of the canyon. From similar sites I often observed four groups in view of one another. A majority of their attention is directed towards other groups and is only broken by the movements of other animals (i.e., gemsbok, mountain zebra, chacma baboons) on the canyon floor. Three to four hours after sunrise ambient temperature increases, and klipspringer move to shady areas next to large boulders or under rocky shelves on the canyon wall. Although caves large enough to shelter klipspringer occur, they are not used. Each group had two or three preferred resting sites that it used repeatedly. These sites are situated on the middle slopes and offer an unobstructed view of the lower terrain. From them the klipspringer descend as a group to the canyon floor to feed, then return and rest again.

The riverine forest is visited only for feeding. As each group occupies only one side of the canyon, they seldom traverse the entire canyon floor. The few exceptions occurred when neighbouring males chased

each other during intergroup encounters, when a group was startled while feeding and ran for the nearest slope (which was opposite their own), or when a group occasionally crossed the river-bed to rest in shade on the opposite slope.

The flat plains of the klipspringer range are dissected by a number of side canyons that become more shallow away from the Kuiseb. These channels extend about 1.5 – 2.0 km out onto the plains and define the farthest extension of the klipspringers' range. After seasonal rains klipspringer feed in these areas, but within three to four months the vegetation desiccates and they venture into them only for occasional forays. Most of these forays occur when the group is traversing side canyons with walls too steep to negotiate nearer the main canyon.

### 3.3 Synchrony of activities

During 48 days of systematic observations taken on one group over a period of eight months, group members were engaged in the same activities for 77 % of the time, and for only 3 % of the time were all three individuals engaged in different activities (Table 2). The co-ordination of group activities was consistent between individuals, from month to month, and between seasons. Synchrony between individual activity patterns decreases from dawn, when 89 % of observations showed complete synchrony, to midmorning, when all animals were engaged in the same activity for only about 66 % of the observations. This is associated with activity patterns. Feeding was the least synchronised activity, which typically occurs in midmorning and late afternoon, and resting was the most co-ordinated activity. Most often (79 %) the rest of the group emulated the adult female. The juvenile had the lowest score (Table 2).

TABLE 2: Co-ordination of klipspringer group activities. Percentage time an individual is engaged in a) the same activity as other group members, b) a different activity from either group member, or c) when all individuals are engaged in different activities.

	Group Activity (% time)					
	a) same		b) one different		c) all different	
	$\bar{X}$	Range	$\bar{X}$	Range	$\bar{X}$	Range
Individual						
Female	79	73-82	18	12-26	3	1-9
Male	76	64-84	21	9-24	3	1-9
Juvenile	74	68-80	23	11-28	3	1-9
Month						
June	74	61-79	21	12-30	5	2-7
July	78	68-86	19	14-29	3	1-4
Aug.	77	69-88	21	15-31	2	1-4
Sept.	81	73-85	14	11-27	5	1-9
Oct.	76	68-85	21	14-30	3	1-5
Nov.	79	66-84	19	9-32	2	1-6
Dec.	78	67-85	21	12-27	2	1-4
Jan.	72	61-80	24	18-30	4	1-5
Monthly $\bar{X}$	77		20		3	

3.4 Inter-individual distances

Members of klipspringer family groups maintain spatial proximity throughout the day. For all activities inter-individual distances within the group averaged 6,9 m. Group spread was greater during feeding periods ( $\bar{X} = 10,1$  m) than when resting ( $\bar{X} = 4,6$  m) or travelling ( $\bar{X} = 6,0$  m). This results from one individual standing vigilance at a distance above those that are feeding, as inter-individual distances of feeding klipspringer average only 5,5 m (Table 3). Although an individual may occasionally be separated from the others by as much as 50 – 80 m, it will rejoin the group within a few minutes. The adult male was nearest to the female only when resting; the juvenile stayed closer to her during feeding and travelling. For all activities there was no significant difference in individual distances between seasons (Table 3).

TABLE 3: Seasonal variation of inter-individual distances between klipspringer during resting, feeding and travelling.

Activity	Mean distance (m) between		
	Male—Female	Female—Juvenile	Male—Juvenile
<b>Resting</b>			
June-July	4,2	4,8	4,6
Aug.-Sept.	3,8	3,9	5,5
Oct.-Nov.	3,5	4,8	4,9
Dec.-Jan.	3,7	5,5	5,3
Mean	3,8	4,8	5,1
<b>Feeding</b>			
June-July	11,5	8,8	10,7
Aug.-Sept.	12,0	9,1	12,5
Oct.-Nov.	9,8	7,9	11,1
Dec.-Jan.	8,7	9,5	9,9
Mean	10,5	8,8	11,1
<b>Travelling</b>			
June-July	5,8	4,6	5,4
Aug.-Sept.	7,2	5,8	6,3
Oct.-Nov.	6,1	5,5	7,1
Dec.-Jan.	8,7	9,5	9,9
Mean	6,5	5,5	5,9

3.5 Group movements

When the group moves from one feeding or resting site to another, the adult female usually leads. She also leads the group in flight from potential danger, with the adult male last. Table 4 gives the frequencies of female, male and juvenile initiation and leadership of group movements under disturbed (rapid flight up the slopes) and undisturbed conditions. Of 207 progressions, the adult female initiated significantly more of both disturbed ( $\chi^2 = 36,05$ ,  $p < ,005$ ) and undisturbed movements ( $\chi^2 = 28,07$ ,  $p < ,005$ ) than the male. Juveniles were never observed to lead the group in flight, but they sometimes initiated movements to feeding or

resting sites. This occurred only when the juvenile had attained near adult size (see vigilance behaviour for comparison).

TABLE 4: Initiation of group movement under disturbed and undisturbed conditions.

Individual	Disturbed		Undisturbed	
	No	%	No	%
Adult male	39	34,2	24	25,8
Adult female	75	65,8	60	64,5
Juvenile	0	—	9	9,7

3.6 Vigilance behaviour

Characteristic behaviour of klipspringer is surveillance of the surrounding terrain from a prominent site by an individual while the rest of the group feeds or rests nearby (Dorst and Dandelot, 1974). This sentinel behaviour is distinguished from alert postures temporarily assumed by group members and is termed vigilance here. The vigilant individual usually stands in a higher position than the rest of the group, where it has an unobstructed view of the lower surrounding terrain. At least one individual of the group stands in vigilance during 32 % of the daylight hours. Although all mature group members share vigilance, the adult male assumes the greatest burden. He spends 19 % of the day (2,6 hours) in vigilance and is vigilant significantly more often than the female during both resting and feeding activities ( $t = 4,29$  and  $4,89$ , respectively,  $p < ,01$ ,  $df = 7$ ) (Table 5). The female is vigilant significantly more often than the juvenile during both periods (resting:  $t = 4,94$ ,  $p < ,01$ ,  $df = 6$ ; feeding:  $t = 7,34$ ,  $p < ,001$ ,  $df = 6$ ). Individual vigilance does not vary significantly between months or seasons, except for the increased vigilance shown by maturing juveniles. The relatively uniform scores through the months reflect the unchanging daily activity patterns of the family group (Fig. 2).

TABLE 5: Percentage time klipspringer spent in vigilance behaviour during resting and feeding.

Month	Individual vigilance (%)			Shared vigilance (%)			Total (%)
	Male	Female	Juv.	Male-Fem.	Male-Juv.	Fem.-Juv.	
<b>Resting</b>							
June	10,8	9,4	0,8	7,2	2,2	4,3	34,7
July	12,7	5,9	1,6	3,1	1,0	0,2	24,5
Aug.	15,0	4,5	2,1	2,2	3,9	2,5	30,2
Sept.	19,7	5,6	2,8	0,0	5,6	1,4	35,2
Oct.	13,6	8,6	2,0	4,0	2,0	0,5	30,8
Nov.	11,5	10,9	0,5	8,9	0,0	0,5	32,3
Dec.	17,2	5,2	0,0	0,8	3,4	2,6	29,3
Jan.	11,8	3,2	1,1	2,2	0,0	0,0	18,3
Mean	14,0	6,7	1,4	3,6	2,3	1,5	29,4

Month	Individual vigilance (%)			Shared vigilance (%)			Total (%)
	Male	Female	Juv.	Male-Fem.	Male-Juv.	Fem.-Juv.	
Feeding							
June	29,4	19,3	0,0	8,4	0,9	1,9	59,9
July	25,8	16,0	4,6	1,6	2,5	4,4	54,9
Aug.	17,9	14,0	3,3	4,6	2,7	0,0	42,5
Sept.	29,0	15,8	5,3	13,2	0,0	5,3	68,4
Oct.	18,8	17,1	6,8	0,8	2,6	0,8	47,0
Nov.	21,1	17,1	11,0	0,0	0,0	3,7	53,7
Dec.	26,2	13,1	8,2	11,5	4,9	0,0	63,9
Jan.	29,7	14,8	3,3	2,3	2,3	8,0	60,2
Mean	24,7	15,9	5,3	5,3	2,0	3,0	56,3

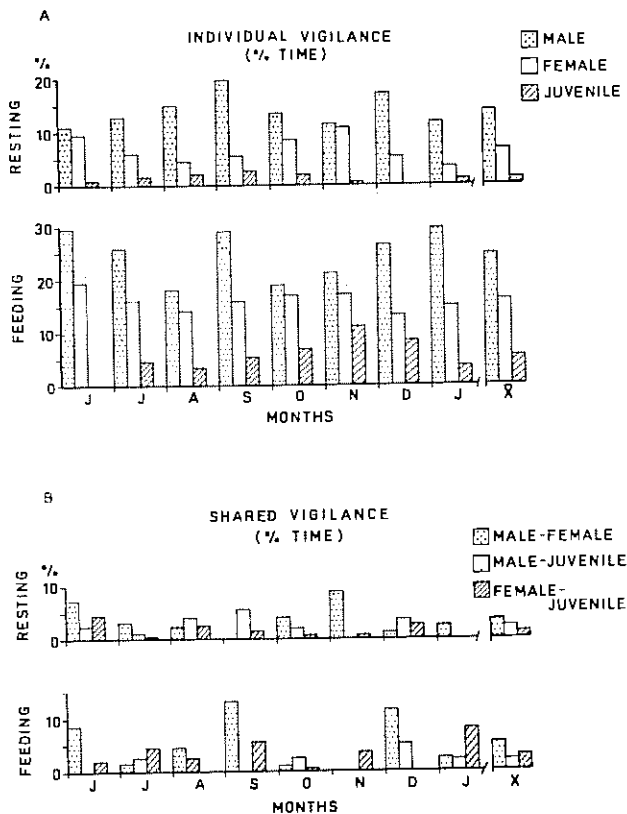


FIGURE 2: Percentage time a family of klipspringer spent in vigilance during resting and feeding activities when A) alone or B) with another member of the family unit.

Vigilance is more often a solitary than a shared activity. An analysis of single versus paired individuals standing vigilance shows that solitary individuals account for 75 % of the total vigilance when others are resting and 82 % when feeding (Table 5). Group members showed no preference as to who they paired with when sharing vigilance. Choices were equally distributed between the three different combinations. The greater reliance on solitary vigilance enables group members to feed and rest alternately without sacrificing predator detection.

Although at least one member of the group is standing in vigilance during 32 % of the day, the proportion

of time spent in vigilance differs with each activity. The doubling of vigilance from 29 % of resting time to 56 % of feeding time (Table 5) can be explained by a combination of factors. Most feeding occurs in the forest at the bottom of the canyon where klipspringer must venture out 25 – 100 m from the safety of the rocky slopes (Fig. 1). The specialised hoofs of the klipspringer sink into the sandy river-bed substrate and slow their ability to flee from potential danger. It is also more difficult for them to detect predators because the dense vegetation obstructs vision. In contrast, resting sites higher up the canyon slopes generally command a clear field of vision for predator detection. From these sites klipspringer can choose among alternate flight routes, some of which cannot be traversed by their terrestrial predators.

### 3.7 Predation and predator avoidance

The predator community of the Kuiseb Canyon is neither abundant nor diverse (Stuart, 1975). Large felids are either absent (lion and cheetah) or rarely encountered (leopard and caracal). Brown hyaena (*Hyaena brunnea*) may occur as transients, but they have not been sighted in the canyon during the course of this study. Birds of prey large enough to capture young klipspringer are the black eagle (*Aquila verreauxi*) and perhaps the jackal buzzard (*Buteo rufufuscus*). Other predators in the canyon include spotted hyaena (*Crocuta crocuta*), black-backed jackal (*Canis mesomelas*), and chacma baboons (*Papio ursinus*).

Twice I observed jackals capture newly born klipspringer lambs hidden in the rocks, and 18 other unsuccessful attacks on adults were seen. Baboons were not observed to prey upon klipspringer, but twice I observed an adult male baboon eating a young steenbok (*Raphicerus campestris*), an antelope of similar size that inhabits the riverine forest. Predation by adult baboons on neonate gazelles is well documented in other parts of Africa (Dart, 1963; Altmann and Altmann, 1970; Harding, 1973). Hence, the alarm response of klipspringer during encounters with baboons is appropriate in my study area, as well as elsewhere. I also found the remains of three adult klipspringer consumed by hyaenas that were presumably captured in the riverbed. An analysis of hyaena predation in the canyon area showed klipspringer accounted for only 1,5 % of their diet (Tilson, von Blotnitz and Henschel, in press).

When potential predators are detected, klipspringer give an immediate attention response (freezing with head towards the alarm source). A series of loud alarm calls may then follow (Dunbar and Dunbar, 1974). Klipspringer give a single call about 64 % of the times that they detect predators (Tilson, 1977). The group then flees 30 to 50 m higher up the canyon slope. After a prominent boulder or ledge is reached they may stop and resume their calling. Measurements from the field map indicate that their calls are audible to about 700 m. Either sex may be the first to call, but after two to four notes the female's call becomes

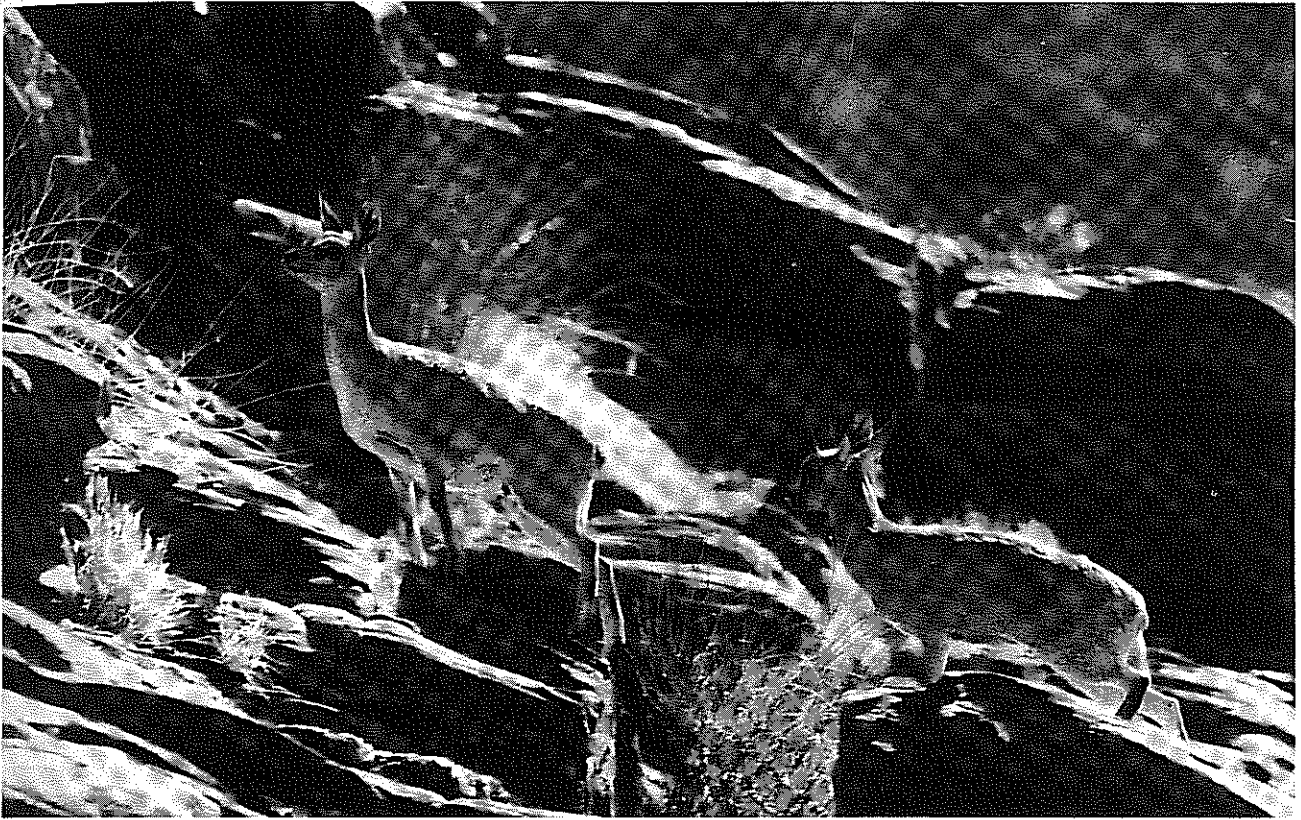


PLATE 3: An adult klipspringer pair with the female in the lead. Note their proximity and lack of sexual dimorphism in body size.



PLATE 4: When klipspringer must cross the river channel to feed they prefer the cobble substrate to the deep sand.

precisely timed to follow that of the male ( $\bar{X}$  interval = 0,03 s, SD 0,02 s, N = 9). Immatures may give a single rendition of the alarm if they are the first to detect danger but do not call with the adults (Tilson, 1977).

Klipspringer in Ethiopia also give alarm calls, but most of these were termed false because no danger to the klipspringers could be determined (Dunbar and Dunbar, 1974). I heard 182 alarm calls elicited in three different situations (Table 6). Potential predators accounted for 120 (66 % of the total). I could detect no apparent danger for 34 (19 %): 19 were in response to gemsbok and mountain zebra (*Equus zebra hartmannae*), 8 to calls of other klipspringer or rock hyrax (*Procavia capensis*), and the remaining 7 seemingly to sudden gusts of wind. Another 28 (15 %) alarm calls were heard at night or from beyond my vision. If this last category is excluded, only 22 % (34 of 154) of the alarm calls could be considered false, a significant deviation from parity ( $\chi^2 = 18,48$ ,  $p < .001$ ). Klipspringer are small antelopes and lack formidable defensive weapons. They avoid predation by rapid flight over steep rocky terrain. They may sense danger through visual, auditory or, especially, olfactory clues that cannot be detected by a human observer. Thus, Dunbar and Dunbar's (1974) higher incidence of false alarms may be a consequence of arbitrary judgements that do not coincide with discriminations made by klipspringer as to what constitutes a dangerous situation.

TABLE 6: Situations evoking klipspringer alarm calls in the Kuiseb River Canyon.

Stimulus	Alarm Calls		Category
	No.	%	
Potential predators			
Spotted hyaena	11		
Black-backed jackal	43		
Chacma baboon	18		
Man (myself)	48		
	120	65,9	(1) Real
Non-predators			
Gemsbok	13		
Mountain zebra	6		
Other animals or wind	15		
	34	18,6	(2) False
Not observed			
Out of view	6		
At night	22		
	28	15,3	(3) Undetermined

In Ethiopia, male klipspringer apparently compensate for most of their false alarms by stopping after 30 – 50 m of flight to re-evaluate the source of danger while the rest of the family waits farther ahead (Dunbar and Dunbar, 1974). In my study area I have observed klipspringer stop after a short flight; but they stop together, and both adults stand near each other, often touching. In flight the female usually runs first, the

juvenile(s) follows, and the male is last ( $\chi^2 = 36,05$ ,  $p = < .005$ , Table 4). Thus, the male keeps himself between his family and the source of danger should it turn out to be genuine, an observation first noted by Dunbar and Dunbar (1974).

The flight pattern of klipspringer can reflect the degree of the alarm situation. An attack by a jackal is evaded by rapid flight up onto nearby boulders. There they stop and may begin to alarm call. Less threatening disturbances, such as passing gemsbok or mountain zebra, also will elicit flight up onto the rocks, but flight distances are shorter and often show a characteristic jumping gait. This is a series of stiff-legged jumps, performed by the entire group in sequential short dashes. Alarm calls are usually not given in these situations, but the group is alert and repeatedly looks down towards the source of disturbance. The impact of their blunt hoofs on rocks produces a sound audible to about 80 – 100 m. I have observed individuals respond to the characteristic noise of these jumps by another group member, even though visual contact was obscured. This specialised bounding is similar to the stiff-legged jumping gait (also called "stotting" or "pronking") described for gazelles (Walther, 1969) and other antelopes (Estes and Goddard, 1967; Leuthold, 1977).

#### 4 DISCUSSION

The diversity of social structures displayed by African ungulates is enormous; and any synthesis of such a diverse spectrum of variation must incorporate a considerable amount of simplification, for many species will not fit any specific set of categories. Despite these constraints, several authors have discerned certain general trends in social structure, especially among the Bovidae. One of these is a gradation of social organisation from solitary individuals or monogamous pairs to large social groups that is correlated with a shift in habitat from closed forests and dense bush to open grasslands and savannah (Eisenberg, 1966; Estes, 1974; Giest, 1974; Jarman, 1974; Leuthold, 1977). A basic dichotomy within this theoretical framework is that small cover-dependent antelopes generally rely on silence and concealment to avoid predation. They enhance their cryptic appearance by group dispersion and solitary habits. In contrast, the larger antelopes of open habitats rely on rapid flight, herd cohesion and, occasionally, individual or group defense to avoid predation (Estes, 1974; Jarman, 1974; Leuthold, 1977).

Klipspringer present an exception to some of the above trends, for they are unusual among the small antelopes (Antilopinae: Neotragini) in being specialised for open habitats and reliance on rocky escarpments rather than dense vegetation for protection. Klipspringer do not rely on stealth or concealment when alarmed. Instead, they rapidly ascend the escarpment to a prominent

boulder or rocky ledge. The family group then stops and turns to inspect the source of alarm. They may begin to call with loud single bursts or duets between the adult pair. After some hesitation they run still higher up the escarpment and repeat the sequence. When pressed, they are capable of phenomenal jumps and have the ability to scale seemingly vertical cliffs. But they always keep the source of danger in view at the expense of being conspicuous themselves. It is this feature that distinguishes klipspringer from other small antelopes and probably accounts for their unusual spatial and social structure.

In most activities klipspringer show some form of vigilance, usually from a site that provides a clear view of the surrounding terrain. Females apparently depend on male vigilance for protection, especially while foraging; and it has been shown that males are vigilant significantly more often than other group members, both in Ethiopia (Dunbar and Dunbar, 1974) and in the Kuiseb River Canyon. But females, and occasionally sub-adult offspring, also are vigilant. This is an important reciprocal advantage for the male, especially during foraging activities in the acacia forest on the canyon floor where klipspringer are most vulnerable. By synchronising group activities, klipspringer can spend the minimum possible time in such dangerous areas. Spatial proximity of group members helps facilitate visual contact and reduces the probability that an individual will be surprised by a predator. Finally, with loud alarm calls klipspringer can immediately warn other group members of nearby danger.

Dunbar and Dunbar (1974) suggest that the formation of a permanent pair-bond in klipspringer may be adaptive in a relatively open habitat because of the advantages females attain through male vigilance. Vigilance is important to the family group, but it should not be considered as the proximal basis of monogamy, for the benefits accrued through male vigilance would not be diminished by the addition of a second or third breeding female. If the detection of predators were the proximal basis for forming social groups, group size should increase beyond the family unit, as the collective senses of a larger group would make them far more difficult to approach undetected than a single animal (Pullian, 1973). Also, by joining part of a pool of potential prey an individual in a group reduces its chances of being selected for capture by a predator (Hamilton, 1971). Klipspringer should benefit from co-operative vigilance, but the advantages must exceed the costs of competition for critical resources on a territory before groups beyond the monogamous pair can evolve (see Wittenberger, 1979). Since klipspringer do not form such groups, the costs of competition must outweigh the benefits of co-operative vigilance.

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# Vegetation polygons in the central Namib Desert near Gobabeb

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## ABSTRACT

In the vicinity of Gobabeb, both north and south of the Kuiseb River, well developed vegetation polygons have been noted. Previous workers have concentrated their efforts on the patterned ground features in the interdune valleys south of the Kuiseb. Two other areas of patterned ground development are described and it is proposed that all three types are genetically similar. Desiccation of gypsum rich sediments in the soil horizons and/or the partially weathered bedrock horizon appears to have produced the polygonal fissure networks.

## 1 INTRODUCTION

During the summer of 1977 – 1978 precipitation in the central Namib Desert was two or three times the long term average. Gobabeb received about 100 mm compared with the earlier long term mean quoted by Schulze (1969) of less than 30 mm. As a result of this the vegetation cover was considerably more extensive than usual, revealing well developed polygonal patterns. These features are the product of large scale soil structures which, although noted by other workers (Goudie, 1972; Ollier and Seely, 1977), have never been fully investigated. Previous studies have concentrated on the patterned ground found in the interdune valleys south of the Kuiseb River, near Gobabeb. This examination will attempt to describe and interpret three distinct types of vegetation polygons, those found on the granite plains near Gobabeb, those associated with gypsum crusts in the vicinity of Swartbankberg, 40 km south-east of Walvis Bay, as well as the interdune patterned ground (Fig. 1).

## 2 GRANITE/GRAVEL PLAINS

The undulating plains to the north of the Kuiseb River are composed of Proterozoic Damara System metamorphic rocks with intrusions of Post-Damara (Khomas and Hakos) Salem Granites. In the vicinity of Gobabeb mica schists with intrusive granite and associated feldspar pegmatite predominate (Martin, 1965). The surface materials in the area are shallow lithosols derived from the weathering of the bedrock though there are also areas of fossil reddish-brown soils and gypsum and gypso-calcareous crusts (Scholz, 1963, 1968 and 1972).

The vegetation polygons in this area are rarely well developed. They consist of lines of grasses which define a net pattern. The lines are generally between 5 and 20 cm wide with the central areas of the polygons being 2 to 5 m in diameter. There are other forms of vegetation patterning in this area, for example, lines of plant growth directly associated with widened joints in the granite bedrock and also rings of vegetation around partially buried granite core boulders which have been weathered by desquamation (Scholz, 1972).

It is possible that the net patterns are also the product of preferential growth of vegetation along joint lines in the bedrock. In most cases, however, the vegetation polygons are found in areas with lithosols over 1 m deep. Though the plant root systems may tap groundwater and soil moisture from great depths in arid zones, here they do not utilise the bedrock joints in exposed rock masses or beneath shallow soil cover as much as they do the polygonal fissure systems on the deeper soils and lithosols. These systems appear to be independent of the larger bedrock networks identifiable on the outcrops. The vegetation grows in cracks filled with sandy material. This sand is a mixture of rounded, iron oxide stained quartz grains and angular quartz

fragments. The polished surfaces and roundness of the former are characteristic of desert dune sand while the iron staining is the same as that on sand grains from the dunes south of the Kuiseb River. Apparently these grains represent Namib dune sand which has been blown across the river. The angular quartz grains show no signs of abrasion or weathering and are probably of recent derivation from the weathering of local bedrock. The sand covers the bulk of the plains near Gobabeb to a depth of 5 to 20 cm but extends to more than 20 cm in the cracks. In the areas with vegetation polygons the sand overlies a silty-clay horizon about 5 to 15 cm thick. This in turn overlies coarse granite fragments which are frequently partially consolidated by calcium carbonate and/or gypsum (figure 2A). Evidently the vegetation grows in the cracks because the roots have easy access to soil moisture below the clay horizon which is relatively impenetrable to the root systems.

The cracks may originate in two ways. Firstly, they may be the result of volume changes in the clay layer caused by wetting and drying cycles. Scholz (1973) stated that attapulgite and halloysite are the main clay minerals associated with the granites but locally montmorillonite may predominate (Rust, 1970). The large volume changes that occur when montmorillonite undergoes wetting and drying could account for the large scale crack patterns (Ollier, 1966). Alternatively the cracking may be related to the materials cementing the granite debris beneath the clay layer. The clay horizon from 5 to 20 cm below the surface has a calcium carbonate content of less than 3 % by weight, while the gypsum content is less than 0.5 %. This compares with a sequence through the underlying weathered granite lithosol showing high calcium carbonate levels at the top but decreasing with depth while the percentage gypsum increases down-profile (table 1).

TABLE 1: Calcium carbonate and gypsum concentrations in a granite lithosol profile from the granite plains north of Gobabeb.

Depth	CaCO <sub>3</sub> %.	CaSO <sub>4</sub> 2H <sub>2</sub> O%.
20 cm	67.14	1.12
30 cm	5.12	50.41
40 cm	trace	63.21
50 cm	17.07	54.35

Similar profiles have been described by Scholz (1972) and are probably the result of leaching of the minerals from surface deposits and precipitation of the less soluble calcium carbonate above the gypsum. This *per descensum* model of soluble salt accumulation has been described by Page (1972) in relation to Tunisian gypsum crusts, while Krupkin (1963) and Yaalon (1964) have examined the mechanisms experimentally and theoretically. Soluble salts deposited at the surface are leached through the soil horizons by rain-water.

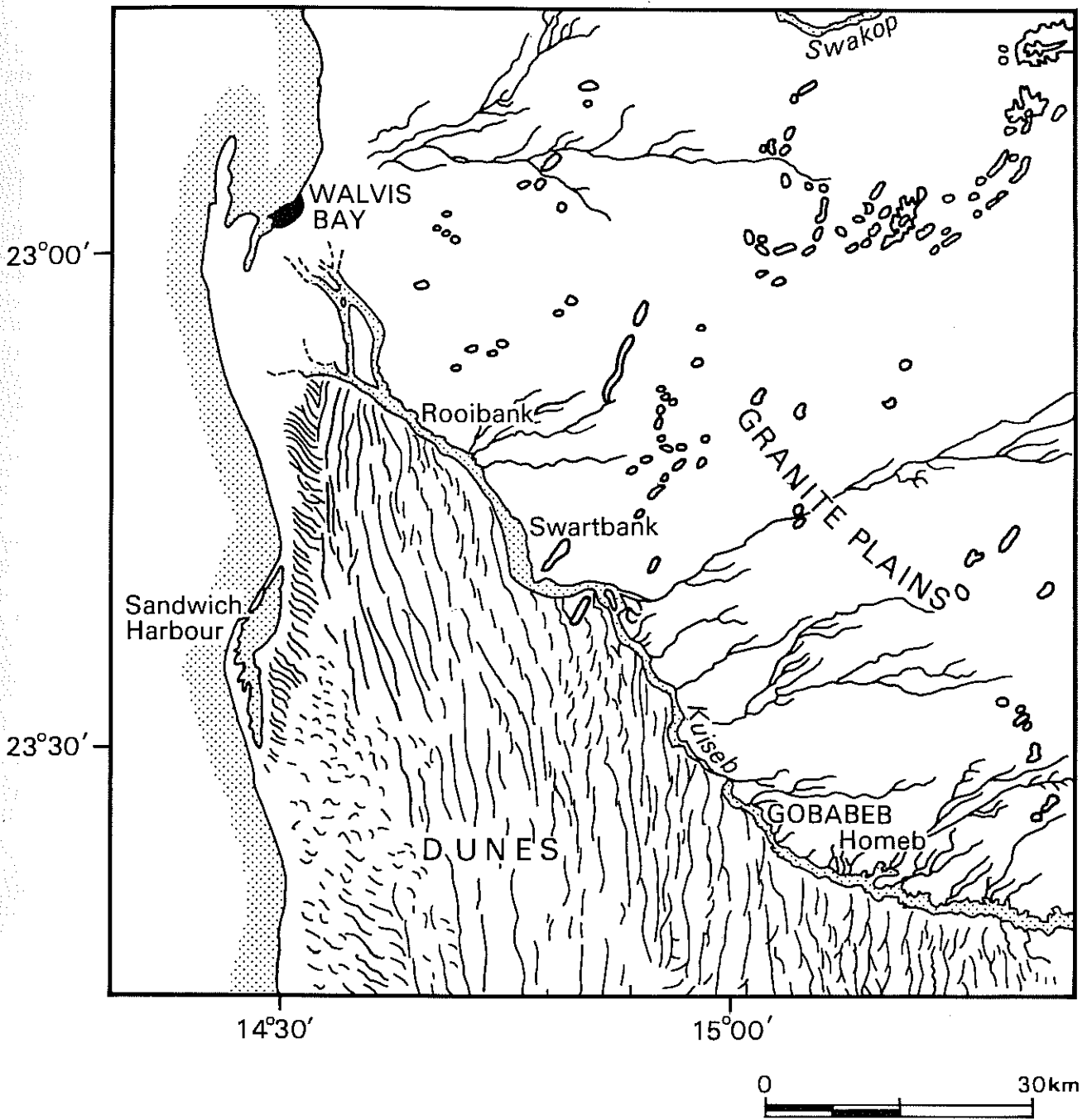


FIGURE 1: The Central Namib Desert near Gobabeb; major dune crests are marked to the south of the Kuiseb River and to the north high ground is encircled.

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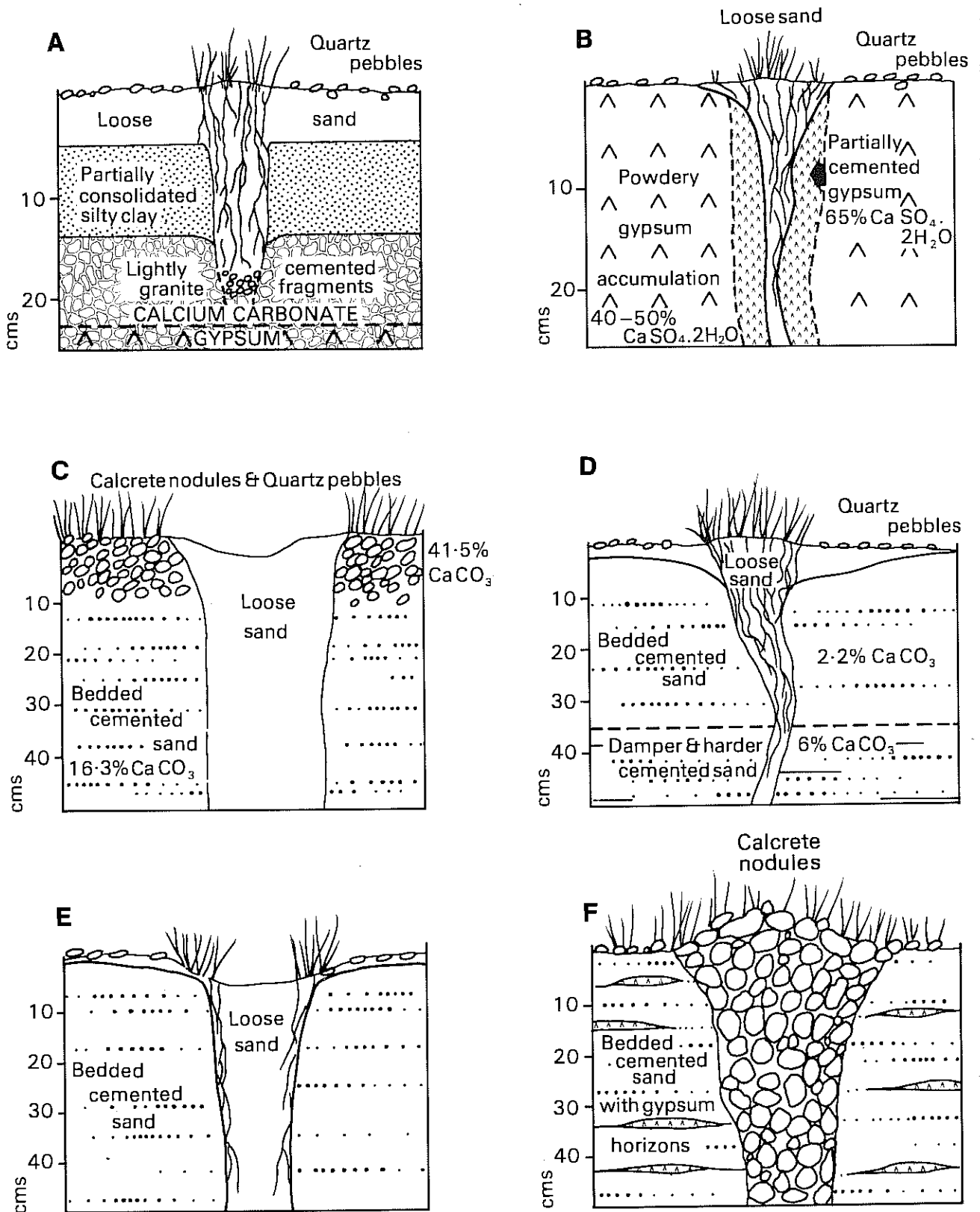


FIGURE 2: Soil profiles across polygon edges: a) Granite/gravel plains north of Gobabeb; b) Gypsum crust area near Swartbankberg; c) Interdune area. Vegetation-free polygon edges; d) Interdune area. Vegetation along fissures; e) Interdune area. Intermediate zone between c and d; f) Interdune area. Polygons with raised edges.

In dry soils the water will replace the soil moisture lost by evaporation during antecedent dry conditions. The salts are precipitated as this soil moisture evaporates during the following dry period. As long as the amount of rain-water available at any one wet phase is insufficient to replace the soil moisture deficit, the salts will not be flushed out of the soil zone. Over a period of several wetting and evaporating cycles the most soluble salts will accumulate at the greatest depth and the least soluble salts nearest the surface. In table 1 the dominance of gypsum beneath a calcium carbonate rich horizon can be explained by the greater solubility in water of calcium sulphate than calcium carbonate, provided the pH does not fall below about 5. The salts required to form these accumulations were probably deposited at the surface as fog moisture evaporated. Walter (1936 and 1937) and Boss (1941) have shown that Namib fogs are capable of depositing up to 100 g/m<sup>2</sup> of soluble salts annually, with an average of 20 g/m<sup>2</sup>.

It is possible that volume changes occur when these soluble mineral accumulations in the soil undergo desiccation. This will be dealt with in the context of the patterned ground associated with gypsum crusts.

### 3 VEGETATION POLYGONS ON GYPSUM CRUSTS

A number of workers (Kaiser, 1929; Kaiser and Neumaier, 1932; Martin, 1963; Scholz, 1963; Besler, 1972; Wieneke and Rust 1973 and 1975; Rust and Wieneke, 1976) have referred to the gypsum crusts of the central Namib Desert but few have described the geomorphic locations, structures or possible origins. There are examples of the three main genetic forms of gypsum crust (Watson, 1979) in the Namib Desert. These are evaporitic crusts, *croûtes de nappe* and surface gypsum crusts. The last of these predominate in South West Africa. They are located on hill tops as well as over large areas of the gravel plains where they underlie a lag of pebbles on the surface. These characteristics suggest that the gypsum crusts are pedogenic features of illuvial origin, their exposure at the surface being the result of deflation of the fine fraction of the original overburden.

Patterned ground associated with gypsum crusts has been described by a number of workers in north Africa (Coque, 1955 and 1962; Butzer and Hansen, 1968; Page, 1972; Vieillefon, 1976) and by Besler (1972) in the central Namib. There are essentially two forms. The first consists of small polygons 0.25 to 1 m in diameter which are associated with large columnar structures in the gypsum crust extending up to 2 m below the surface. This form is rare in the Namib. The second form is found in the central Namib between Rooibank and Swartbankberg. The polygons are between 2 and 6 m in diameter, their edges being defined by lines of grass growth while the rest of the surface is devoid of vegetation. As in the case of the

vegetation polygons on the granite plains the grasses grow in sand filled cracks. The quartz sand has 1 % to 2 % gypsum and 2 % to 3 % calcium carbonate. The rest of the surface is composed of powdery material containing 30 % to 40 % calcium carbonate and 40 % to 50 % gypsum. Occasionally this surface is masked by a layer of sand and pebbles usually less than 5 cm thick. The fissures are 5 cm to 10 cm wide and up to 60 cm deep. They have walls composed of slightly indurated material with a gypsum content of over 65 % and a calcium carbonate content of less than 5 % (figure 2B and plate 1). Evidently the continual movement of moisture down the cracks has resulted in solution and reprecipitation of gypsum on the fissure walls.

These large polygons have never been examined in detail. The clay content of the soil is generally very low, less than 5 % by weight, so volume changes resulting from desiccation effects on clays (Ollier, 1966) would not play a significant role. Large polygonal features have been reported from salt lakes in the western United States (Lang, 1943; Willden and Mabey, 1961; Christiansen, 1963; Neal and Motts, 1967). These are formed by saline water movement and desiccation causing tensional stresses on the rigid salt crust. Tucker (1978) suggested that the columnar structure of some gypsum crusts might be explained by similar desiccation stresses. However, the large ratio of depth to surface diameter of the columns is not in keeping with the salt lake polygons which are up to 300 m in diameter but have fissures the depths of which are generally a tenth of the surface diameter. Alternatively, the volume decrease may be the result of mineralogical changes in the gypsum. Chatterji and Jeffery (1963) and Hunt, Robinson *et al* (1966) have shown that there is a 5 % volume change when gypsum ( $\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$ ) dehydrates to hemihydrate ( $\text{CaSO}_4 \cdot \frac{1}{2}\text{H}_2\text{O}$ ). Under conditions of low relative humidity dehydration can occur when temperatures reach 30°C. The volume reduction of dehydration to anhydrite ( $\gamma$ - or  $\beta$ - $\text{CaSO}_4$ ) would be even greater but the high temperatures required to dehydrate solid phase calcium sulphate probably occur naturally only several hundred metres beneath the earth's surface. It may be necessary to invoke chemical dehydration to explain the columnar structures of some crusts, yet evidence from Tunisia (Page, 1972) suggests that these structures are confined to pedogenic crusts consisting of over 85 % gypsum. It would appear that the development of the structures is closely related to the processes involved in the subsurface accumulation of gypsum by almost total chemical replacement and/or physical displacement of pre-existing materials. The large scale polygonation of the central Namib gypsum crusts seems to be the product of volumetric contraction resulting in fissuring of a semi-cohesive surface layer, the cohesion is caused by gypsum cementation. Volumetric contraction may be attributed to progressive drying of the gypsum crust from the surface downwards. In effect the polygonation is caused by essentially the same processes as those that occur on some

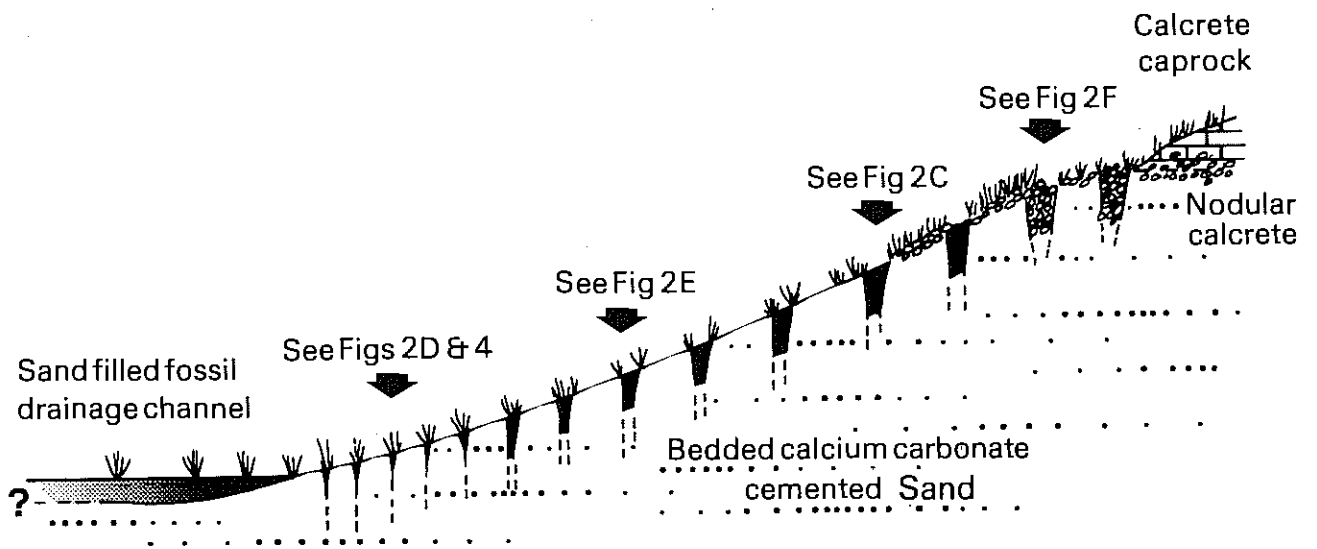


FIGURE 3: Diagrammatic section showing the transition of vegetation characteristics in the interdune valleys.

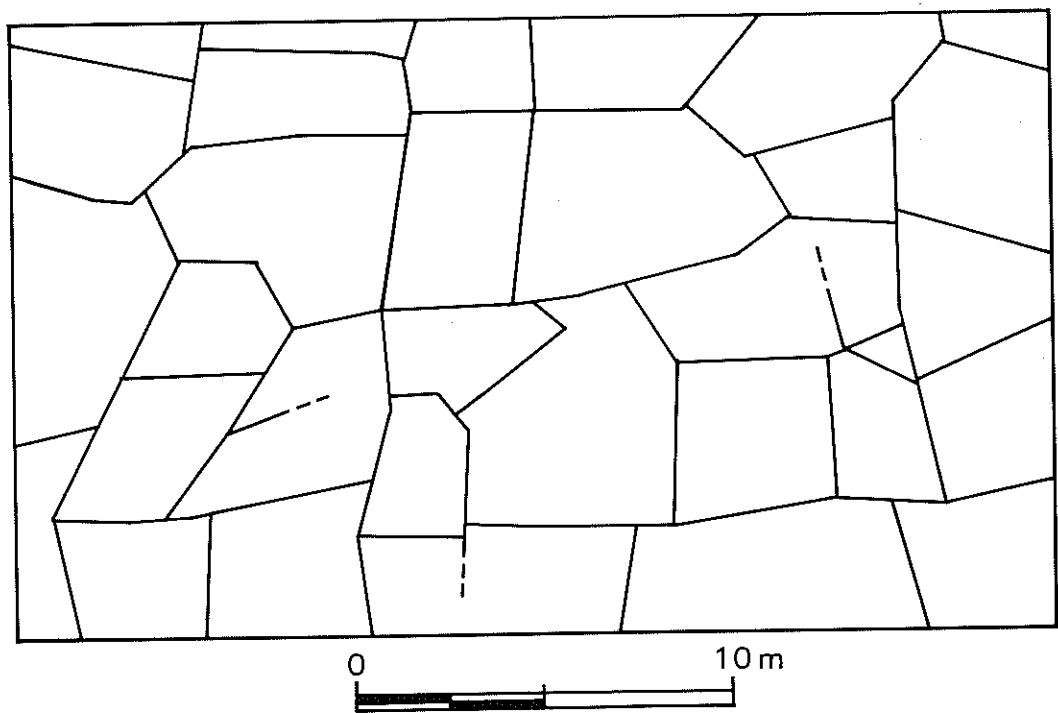


FIGURE 4: Vegetation polygon pattern defined by *Stipagrostis gonatostachys* growing in the fissures, interdune valley south of Gobabeb. Surveyed approximately with tape measure and compass, east is to the top of the diagram.

salt lakes. Furthermore, the ratio of fissure depth to polygon diameter is in keeping with that of salt crust desiccation structures, that is 1:10.

Once the cracks have developed they are maintained through the processes of infilling with wind-blown sand and moisture seepage through this permeable medium.

#### 4 VEGETATION POLYGONS IN INTERDUNE VALLEYS

A number of different forms of patterned ground have been described bordering the Kuiseb River, south of Gobabeb. All the types form random orthogonal nets and rarely achieve pentagonal or hexagonal patterns (plate 2). Goudie (1972) identified three different forms; polygons with raised edges up to 40 cm high and surface diameters up to 20 m; those with raised central portions; and those with depressions marking the edges (plate 3). Ollier and Seely (1977) classified the features according to different vegetational characteristics; those having vegetation along the cracks and a bare surface; those with grasses on the surface and edges free of vegetation; and an intermediate form with complete grass cover but dominant growth along the polygon edges. They interpreted the differences in terms of the characteristics of the surface materials. The polygons with edges defined by vegetation are located on exposures of calcium carbonate cemented dune sand. The grasses root preferentially in the cracks where moisture is available. In the areas where there is what Ollier and Seely (1977) tentatively term an 'alluvial' fill the fissures are too well drained for plant growth but the surface of the polygon can support growth. The subdivision between these two forms cannot easily incorporate the intermediate type which is not explained.

The patterned ground is located on the sides of dry river valleys dissecting the calcrete capped 42 m terrace of the Kuiseb River described by Goudie (1972). The channels incise the calcium carbonate cemented sand which underlies the bulk of the Namib dune field. They appear to represent overflow channels or distributaries of the Kuiseb. The origin of these channels, which may be identified in many areas along the south bank of the Kuiseb River between Homeb and Gobabeb, has not been adequately explained by any of the workers who have examined the geomorphology of the river recently (Wieneke and Rust, 1973; Rust and Wieneke, 1974; Ollier, 1977; Marker, 1977; and Marker and Mueller, 1979). The channels are now overlain locally by longitudinal dunes. It will be shown that the character of the fissures forming the patterned ground is dependent on their position on the sides of these dry channels (figure 3).

The larger polygons, up to 20 m in diameter with cracks 20 to 30 m wide, are found immediately down-slope from the pebbly calcrete caprock of the 42 m terrace. Here the polygon surface is composed of a lag

of pisolithic calcrete overlying the cemented sand, while the fissures are filled in with loose wind-blown sand. Here the grasses, predominantly *Stipagrostis gonatostachys*, can obtain moisture by rooting in the nodular debris but not in the well drained sand in the cracks (figure 2C). Near the floors of the dry valleys, which may be up to 20 m deep and 200 m wide, there is no longer a nodular calcrete lag and the cemented sand is exposed. This material is bedded sub-horizontally and is relatively resistant to plant root penetration, although there is available moisture within 20 cm of the surface. In this area the polygons are only 4 to 8 m in diameter and the sand filled cracks are less than 10 cm across. Here the *Stipagrostis gonatostachys* roots in the cracks which, being narrower than at the top of the slope, are not as well drained (figure 2D, figure 4 and plate 4). Though the density of the network changes the topology remains the same. Between these two extremes is a zone in the middle of the slope where the bedded sandstone again precludes plant growth but the cracks are 10 to 20 cm wide and moderately well drained. Here the grasses grow at the edges of the cracks but not in the centre, thereby utilising optimal conditions of rooting potential and moisture availability at the side of the sandstone block (figure 2E).

The patterned ground with raised edges described by Goudie (1972) is relatively uncommon compared with the aforementioned forms. It occurs at the highest parts of the valley sides and appears to represent fissures in the sandstone which have been filled with purer calcrete nodules derived from the caprock. This indurated material is less prone to weathering and erosion than the sandstone and so forms a ridge (figure 2F).

This phenomenon suggests that the cracks in the sandstone predate the development of the pebbly calcrete caprock. Yet the increase in the density of fissures down-slope indicates that other factors are involved. If they are relic features developed on the old land surface their density would decrease with depth. Hence, the cracks are not relic joint systems in the sandstone. The raised edges have probably developed as differential erosion has exposed the nodular calcrete which found its way into the fissures after the sandstone was exposed. It is feasible that the density of the crack network is a function of the amount of moisture in the material when it was first exposed by fluvial erosion. The sandstone lower down the slope would have been moister than that upslope and hence volume reductions caused by desiccation would have been greater producing the denser network. This is also a feature of patterned ground on salt lakes. The deeper the water table is in any locality the larger are the polygons and the widths and depths of the fissures (Neal and Motts, 1967).

The soluble mineral content of the surface materials also appears to play a significant role. There is a marked decrease in the calcium carbonate concentration down-slope from the calcrete cap. At the lowest points where the sandstone is exposed it contains between 2 % and 5 % calcium carbonate by weight, while at



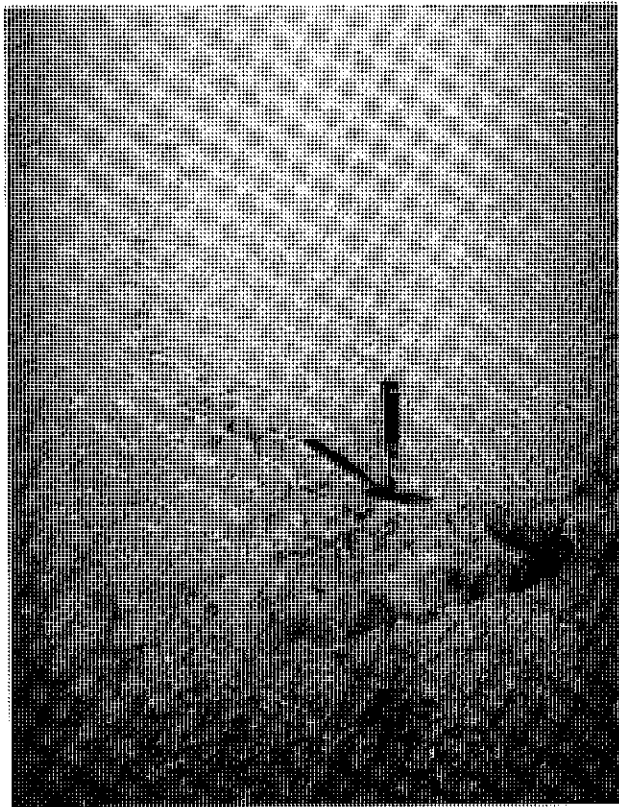


PLATE 1: The edge of a vegetation polygon on a gypsum crust near Swartbankberg.

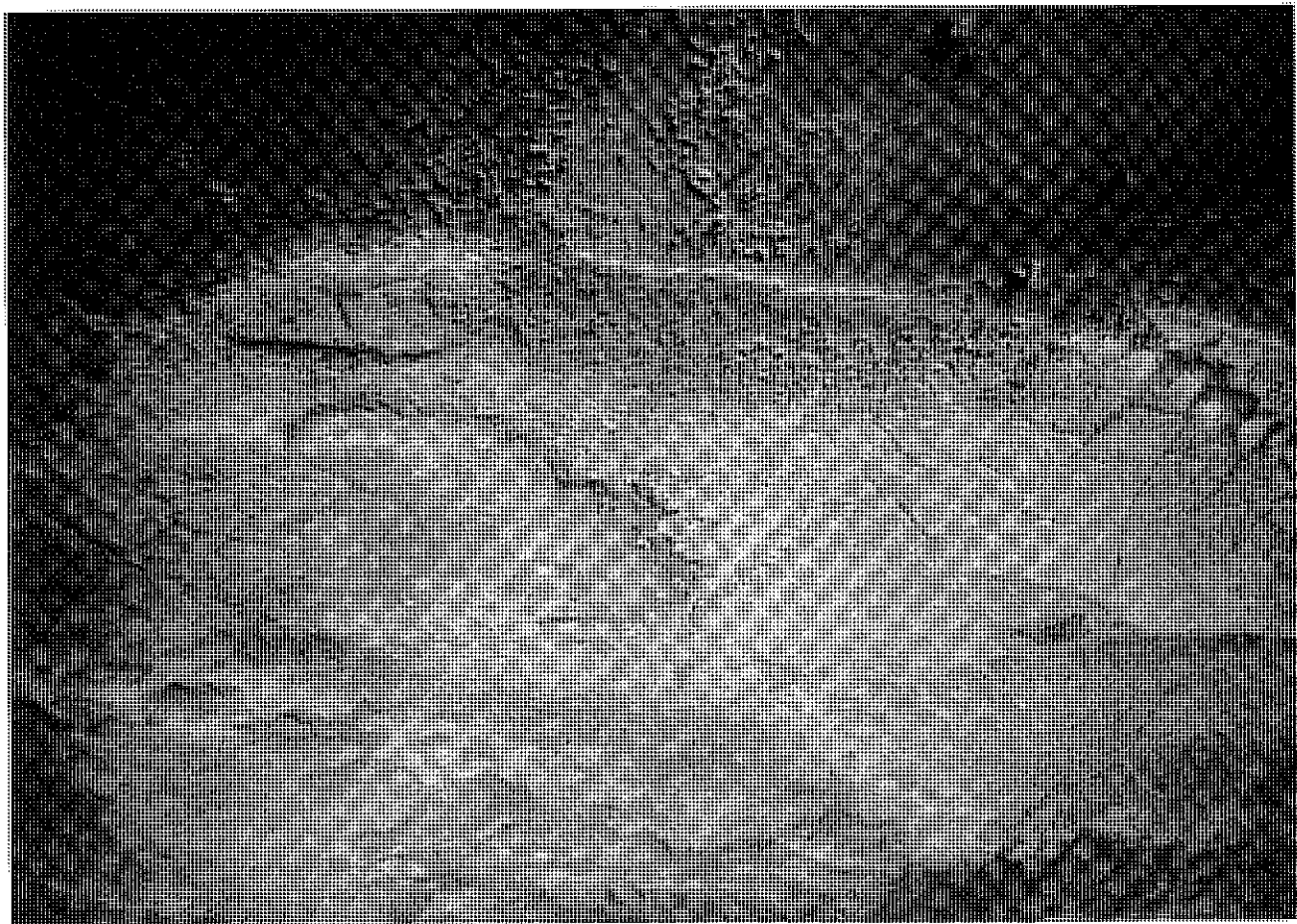
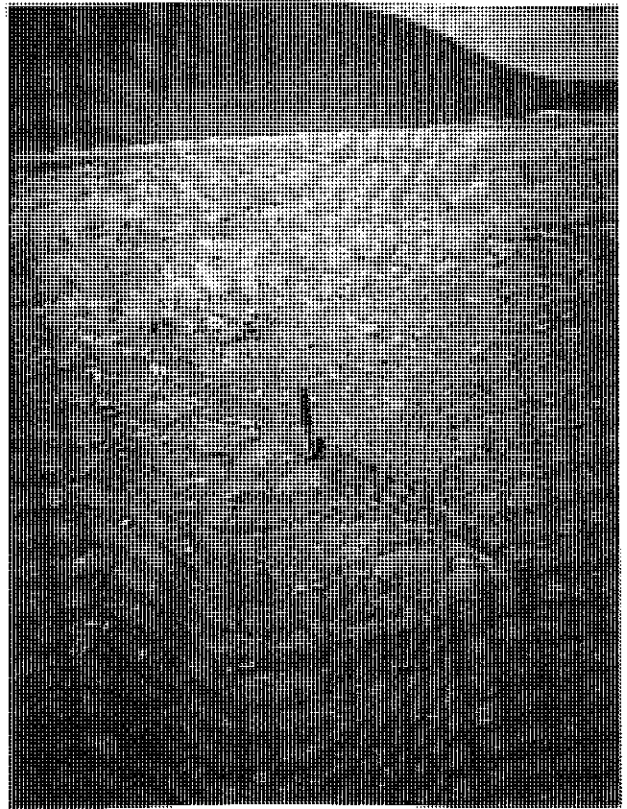


PLATE 2: Aerial view of vegetation polygons in an interdune valley bordering the Kuiseb River near Gobabeb (see vehicle tracks, bottom left, for scale).



ist PLATE 3: Fissured sandstone in the interdune valley south of Gobabeb.



ft. PLATE 4: Interdune vegetation polygons south of Gobabeb.

the highest levels the figure reaches between 20 % and 40 %. The calcrete caprock contains in the region of 60 % to 70 % calcium carbonate and no fissuring is evident. It is possible that the high calcium carbonate concentrations consolidate the sandstone and inhibit fissuring. Both Goudie (1972) and Scholz (1972) pointed out that the soils of the interdune valleys are gypso-calcareous. Analyses of the sandstones and calcretes associated with the patterned ground reveal gypsum contents less than 1 % by weight, though in certain localities 1 to 2 cm thick bands of material with up to 60 % gypsum are found in the bedded sandstone. The increase in gypsum content with depth below calcrete horizons noted on the granite plains north of the Kuiseb is also likely to occur in the interdune valleys. In the latter area, however, the greater permeability of the surface materials will result in the evacuation of the more soluble gypsum to greater depths. This leaching process is also currently reducing the calcium carbonate content of the sandstone surface (figure 2D). Hence the patterned ground may be a product of high gypsum contents at the time of exposure of the sandstone and its desiccation. This interpretation is supported by evidence from identical fossil river channels found in the interdune valleys south of Homeb, 15 km further inland. Here the climate is too wet and/or the area too distant from the coast for gypsum soils to have developed and the vegetation polygons are absent. The only patterned ground in this area consists of sand filled sink-holes in the calcrete caprock. Despite the higher rainfall here the sand is still too permeable to enable plant growth.

## 5 SUMMARY

The vegetation polygons located on the plains north of the Kuiseb River, those on gypsum crusts between Rooibank and Swartbank, and those in the interdune valleys near Gobabeb are all structurally similar. That is, in terms of the topology of the fissure intersections, they are random orthogonal features. On the granite plains the stratigraphy is essentially the same as that described by Ollier (1966) at Coober Pedy in Australia. He attributed the patterned ground formation to volume changes in the montmorillonite layer, not the underlying gypsum. In the Central Namib the fissures extend below the clay horizon and hence the gypsum would seem to play an important role. At Swartbank the patterned ground occurs on materials with very low clay fractions but high gypsum concentrations. In the interdune valleys clays are virtually absent and gypsum horizons are found only locally. Here the bulk of the gypsum has been leached to greater depths since the exposure of the sandstone beds. It is suggested that the main factor in the production of the patterned ground in the central Namib Desert is desiccation of gypsum rich sediments. Variations in gypsum and calcium carbonate concentrations and moisture availability account for different fissure dimensions and network densities.

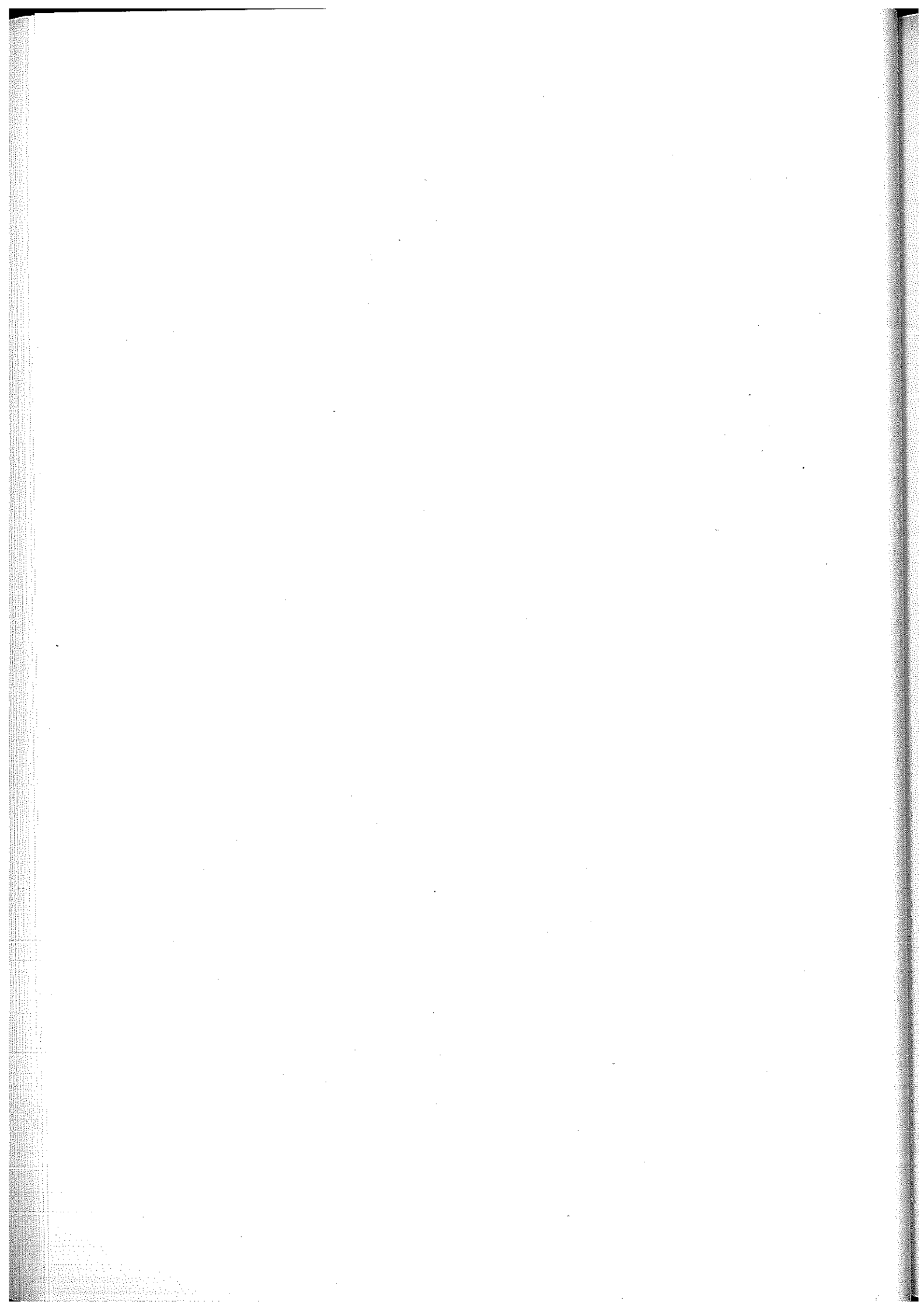
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# Vegetation of the lower Kuiseb River

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Cleared: August 1979

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## ABSTRACT

The withdrawal of water from the lower Kuiseb River for mining and industrial purposes may influence the vegetation along the river. The maintenance of this vegetation is not only essential to the Kuiseb River ecosystem as a whole, but the vegetation acts as a barrier checking the northwards movement of the Namib dune-sea. Physiognomic-structural areas were distinguished on aerial photographs and these areas were investigated in the field for homogeneity and woody species composition. A vegetation map of the area between Nareb and Rooibank was compiled and 14 different communities were distinguished. Some of these communities were subdivided into variations and a total of 40 variations were distinguished. Four additional units, consisting mainly of dead herbaceous species were mapped between Gobabeb and Rooibank.

## UITTREKSEL

Die onttrekking van water uit die laer Kuisebrivier vir myn- en industriële doeleindes kan moontlik die plantegroei langs die rivier beïnvloed. Die instandhouding van hierdie plantegroei is egter nie slegs noodsaaklik vir die Kuisebrivierekosisteem as 'n geheel nie, maar die plantegroei dien ook as 'n hindernis wat die noordwaartse beweging van die Namib duinesee stuit. Fisionomies-strukturele gebiede was op lugfoto's onderskei en in die veld vir homogeniteit en houtagtige spesiesamestelling nagegaan. 'n Plantegroeikaart van die gebied tussen Nareb en Rooibank is saamgestel en 14 verskillende gemeenskappe is onderskei. Sommige van hierdie gemeenskappe is in variasies onderverdeel en in totaal is 40 variasies onderskei. Vier addisionele eenhede, wat hoofsaaklik uit dooie kruidagtige spesies bestaan het, is tussen Gobabeb en Rooibank uitgekarteer.

## 1 INTRODUCTION

The Kuiseb River rises in the Khomas Hochland, near Windhoek, and with the relatively high rainfall in its catchment area it is the largest river in the coastal belt between the Orange and the Kunene (Myburgh, 1967). For the first 230 km the course of the Kuiseb is south-westerly until it reaches the foot of the escarpment (Gamsberg) where the Kuiseb River Canyon begins. For the next 130 km the river has carved its way deeply into the schist formations and follows a narrow, winding path until approximately 45 km upstream from Gobabeb at Nareb (Fig. 1). From Nareb the river gradually widens and sand-banks and/or flood-plains occur on one or both sides of the river-bed. Down-stream from Gobabeb the river-bed widens still further (Plate 1) and meanders between the Namib dune-sea on its southern side (Plate 2) and the Namib gravel plains on its northern side (Fig. 2). Down-stream from Gobabeb, about 27 km from the coast, the river forks into two main branches and ends in the so-called Kuiseb Delta, which is cut off from the sea by sand-dunes.

The Kuiseb River flows infrequently as this depends on the seasonal rainfall of the catchment area. Floods do not reach the lower Kuiseb River annually and are insufficient to maintain an open outlet to the sea (Robinson, 1976). Since 1837 floods have reached the sea only 15 times even though the river flows past Gobabeb for periods of a few days to several months (three months in 1974) in most years (Robinson, 1976). Down-stream from Gobabeb the river flows relatively slowly and plants are seldom uprooted and carried along in the flood, with the result that the river-bed is almost entirely overgrown with *Eragrostis spinosa* down-stream from the Narra Valley outcrops. Although the water from these floods is important to the vegetation along the river, especially to the herbaceous species, it is probably the large quantity of underground water that is essential for maintaining the vegetation along the river.

The mean annual rainfall at Gobabeb in the Namib Desert Park is 18,7 mm and thus the run-off from the gravel plains does not contribute much to the water supply of the lower Kuiseb River. Smaller rivers and streams from the gravel plains, however, probably carry large amounts of soluble salts into the Kuiseb.

Large amounts of water are at present being pumped from the lower Kuiseb between Swartbank and Rooibank. This water is used for town, industrial and mining development. To what extent this withdrawal of water will influence the vegetation along the river is still an open question. The maintenance of the vegetation is, however, not only essential to the Kuiseb River ecosystem as a whole but possibly also acts as a barrier which checks the northwards movement of the Namib dune-sea.

The objectives of this study were to distinguish and map the plant communities so as to provide a basis for

future monitoring of vegetational changes in relation to changes in the water status.

## 2 THE STUDY AREA

The part of the Kuiseb River that was studied stretches from Nareb in the east to Rooibank in the west (Fig. 1 and 4). The largest part of this area is situated in the Namib Desert Park (South West Africa/Namibia) but a small section reaches into the Walvis Bay area (Republic of South Africa).

An overall picture of the climate of Gobabeb over a period of 10 years (1962 to 1972) is given in the climatic diagram in Fig. 2 (Robinson, 1976). The climatic data for Gobabeb (Schulze, 1965; Seely and Stuart, 1976; Robinson, 1976) indicate the general climatic conditions of the area but do not exactly represent conditions that are experienced along the river.

The average annual cloud cover for Gobabeb is 3,3 octas at 08h00 contrasted to 1,3 octas at 14h00 and 1,4 octas at 20h00. Maximum cloud cover occurs during January and February and for the longest part of the year (214 days) the sunshine periods cover 80 % to 90 % of the possible duration.

During the ten years (1962 to 1972) the absolute maximum temperature recorded at Gobabeb was 42,3°C and the absolute minimum temperature 2,1°C (Fig. 5). March is usually the hottest month with a mean temperature of 24,8°C whereas July is the coldest with a mean temperature of 18,4°C. The mean annual aperiodic range (maximum minus minimum) for Gobabeb is 17,3°C.

Rainfall over the entire Namib Desert is very irregular. The mean annual rainfall for Gobabeb is 18,7 mm with the highest monthly mean (5,6 mm) during March. Fog is an important factor in the study area as the fog penetrates 30 to 40 km inland. Incidence of fog decreases eastwards and Walvis Bay experiences 60 days of fog per year (3 year observation period) whereas Gobabeb experiences 38,7 days of fog per year (10 year observation period).

During the summer months Gobabeb receives wind mainly from the north, north-west, west and south-west at mean velocities of 18 km per hour. In winter the predominant direction is east or south-east and wind velocities are, on average, higher. At Gobabeb sandstorms occur throughout the year (on average 7,7 days per year) although they appear to be more common between May and November.

According to the Köppen index (Schulze, 1947) the Namib is a hot desert with a BWh-climate. Thornthwaite classifies the area as a mesothermic region with a water shortage in all seasons (EB'd) (Schulze, 1947).

Although the vegetation is certainly influenced by prevailing climatic conditions, the availability of underground water probably has the most pronounced effect

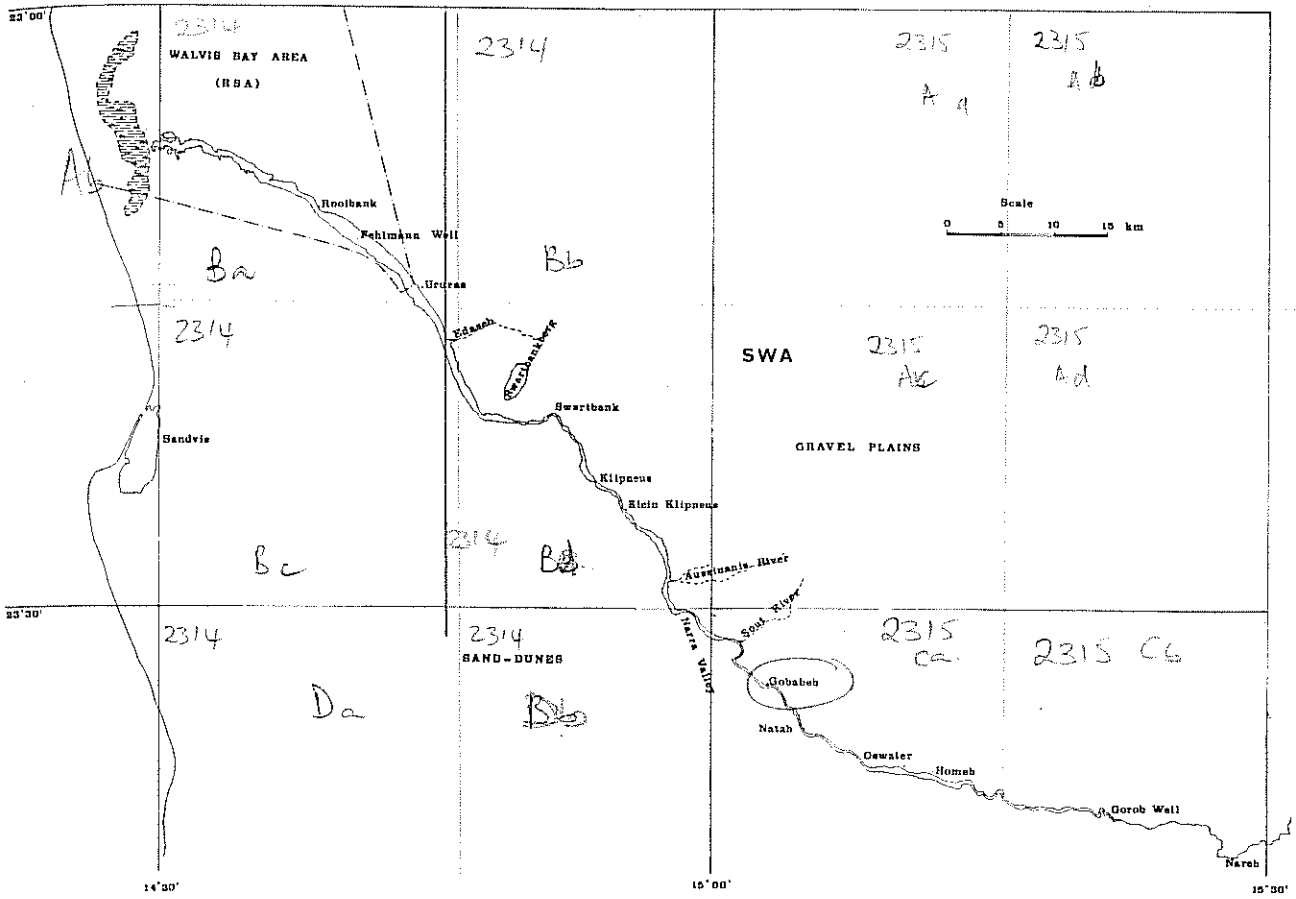


FIGURE 1: Map of the lower Kuiseb River.

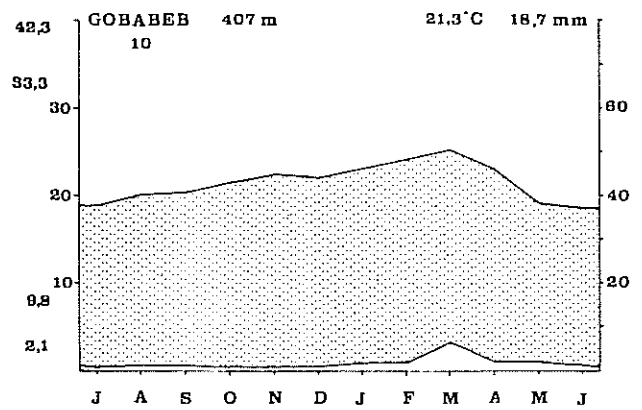


FIGURE 2: Climatic diagram for Gobabeb (Robinson, 1976).



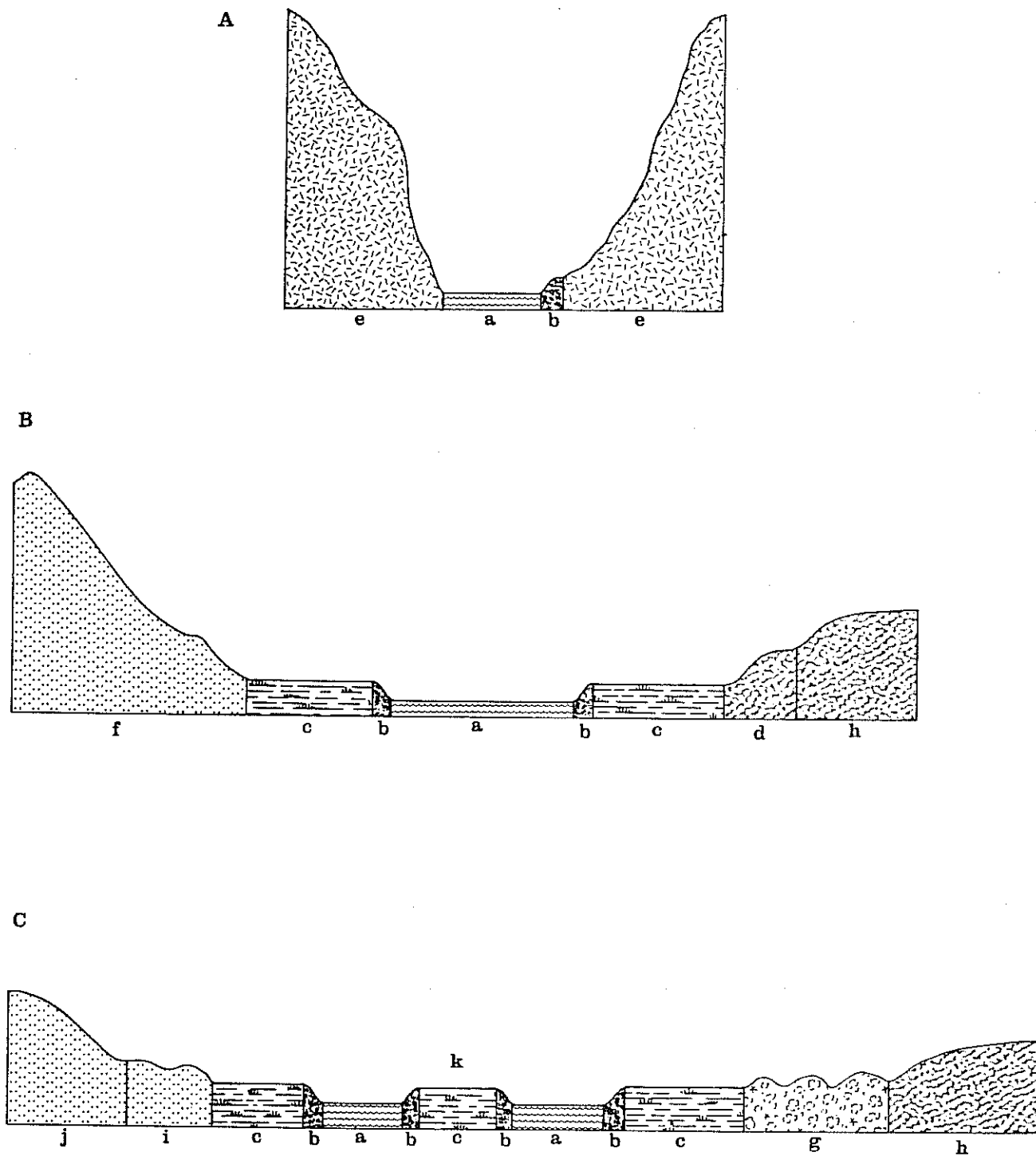


FIGURE 3: Diagrammatic presentation of cross-sections through the Kuiseb River: A = Nareb to Homeb; B = Homeb to Swartbank; C = Swartbank to Rooibank. a = river-bed; b = embankment; c = flood plain; d = terrace; e = cliffs/outcrops; f = steep, high dune; g = knob dunes; h = gravel plains; i = small dunes; j = less steep, high dune; k = island.

on the habitat of the different plant species along the river.

The sandy river-bed varies in width and is fringed by silt and sand-banks. From Nareb down to Homeb (Fig. 3 and Plate 4) the river-bed is relatively narrow and the flood-plains are often absent on one or both sides of the river. In some places the river-bank can be exceedingly steep and in these cases there is an abrupt transition from the river-bed to the steep high sand-dunes, cliffs or rocky outcrops.

From Homeb down to Swartbank (Fig. 3) the river-bed gradually widens and the flood-plains usually occur on both sides of the river. Between Swartbank and Rooibank the river-bed is at its widest and small or large islands occur. In the case of the larger islands a central flood-plain can be distinguished (Fig. 3). In the area down-stream from Swartbank a zone of knob dunes ("knopduine") or small dunes can be distinguished between the flood-plains and high sand-dunes on the southern side. On the northern side of the river the zone of knob dunes occurs between the flood-plains and the gravel plains.

### 3 METHOD

Physiognomic-structural areas were distinguished on aerial photographs of October 1976. These areas were investigated in the field for homogeneity and woody species composition. Units with the same structure and species composition formed a variation and several variations were grouped into a community. With the exception of a few herbaceous species e.g. *Eragrostis spinosa*, *Stipagrostis sabulicola*, *Odysea paucinervis* and *Zygophyllum simplex*, only woody species were used for the characterisation of the vegetation units.

## 4 RESULTS AND DISCUSSION

A vegetation map of the area between Nareb and Rooibank (Fig. 4) was compiled and 14 different communities were distinguished. Some of the communities were subdivided into variations and a total of 40 variations were distinguished (Table 1). Four additional units, consisting mainly of dead herbaceous species were mapped between Gobabeb and Rooibank (Fig. 4).

### 4.1 *Acacia albida* community

This community, characterised mainly by large trees, occupies the river-banks (Plate 5), although a number of large *Acacia albida* individuals often occur in the river-bed (Plate 6). The *Acacia albida* community is well-developed between Nareb and Swartbank (Plate 5), whereas from Swartbank to Rooibank, *Acacia albida* often occurs as solitary individuals (Plate 6). In the vicinity of the Fehlmann Well, along the southern bank, relatively young individuals form a dense stand. Many of these plants have a low vitality and are dying.

Dense stands of *Suaeda plumosa* and *Cyperus marginatus* in this area also show signs of a lowered vitality. The deterioration of the vegetation in this area can possibly be attributed to a lowering of the water table.

The *Acacia albida* variation, consisting of virtually pure stands of *A. albida*, is well-represented up-stream of the Narra Valley outcrops. In the vicinity of Homeb trees often reach 21 m in height. The *Acacia albida* – *Salvadora persica* variation is mainly found between Nareb and Natab where the flood-plains are very narrow or absent. The *Acacia albida* – *Tamarix usneoides* variation (Plate 7) is more conspicuous up-stream from Gobabeb where it occurs in narrow outstretched strips along the river-bank. Down-stream from Gobabeb this variation consists mainly of young individuals of both species. These often occur up-stream of rocky outcrops or water barriers across the river-bed. The other variations of the *Acacia albida* community are mainly found down-stream from Gobabeb. Although some of these variations such as the *Acacia albida* – *Pechuel-loeschea leubnitziae* variation and the *Acacia albida* – *Eragrostis spinosa* – *Pechuel-loeschea leubnitziae* variation appear as clearly distinguishable units on the aerial photographs, they are not always so clearly delineated in the field and should perhaps be grouped together.

### 4.2 *Acacia erioloba* community

The *Acacia erioloba* community is a characteristic of the silt flood-plains but also occurs in the central area on the larger islands (Plate 8). This community is represented by only a few individuals in the Nareb area, whereas down-stream from the Gorob Well, where the flood-plains become wider, more extensive stands of this community occur. From Homeb down-stream to the Narra Valley outcrops, the community is represented primarily by large old trees. In this area the number of large dead *A. erioloba* trees is very conspicuous. The explanation for this is not clear but it is doubtful whether the withdrawal of water from the river-bed can be the cause. Down-stream from Swartbank relatively young plants of *A. erioloba* form dense stands.

According to Fig. 4 the *Acacia albida* community is the predominant type of vegetation in the upper part of the study area where the flood-plains are very narrow. Further down-stream where the flood-plains become progressively broader the *Acacia erioloba* community predominates as vegetation type.

As in the case of the *Acacia albida* community all the variations within the *Acacia erioloba* community between Swartbank and Rooibank are not clearly delineated in the field, nevertheless they show up as distinct physiognomic-structural units on aerial photographs.

*Acacia erioloba* is not confined to the flood-plains, but is also found on the dunes on the southern side of the river (Plate 9) as well as on the knob dunes



PLATE 1: The gravel plains on the left and the Namib dune-sea on the right side of the Kuiseb River.



PLATE 2: The Namib dune-sea on the southern side of the Kuiseb River.

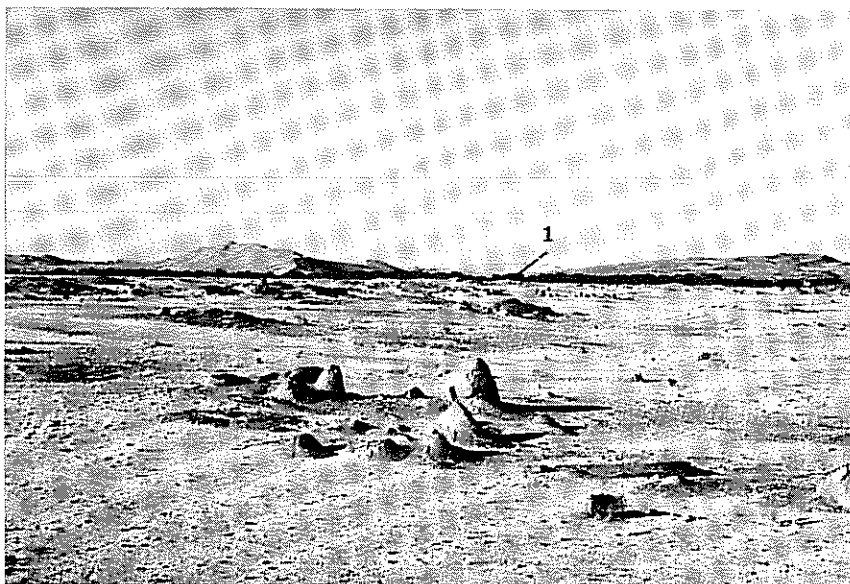


PLATE 3: In the foreground the Namib gravel plains on the northern side of the Kuiseb River (1) and the Namib dune-sea on the horizon.

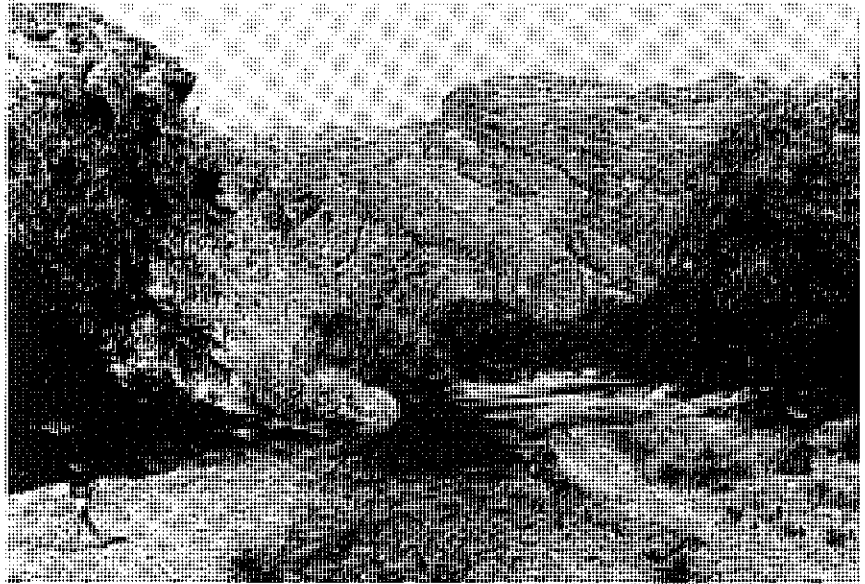


PLATE 4: The Kuiseb River near Nareb with *Acacia albida* on the embankment along the canyon walls.

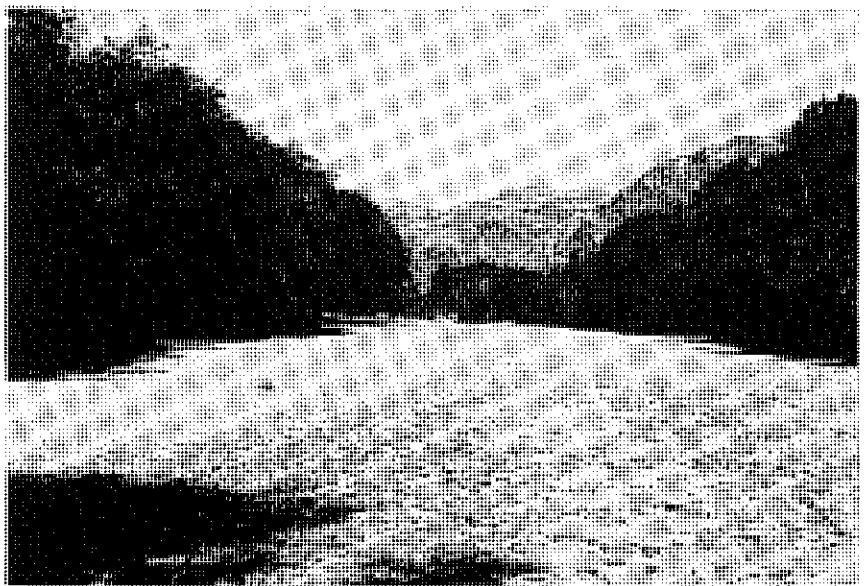


PLATE 5: The *Acacia albida* community along the river-bed near Homeb.

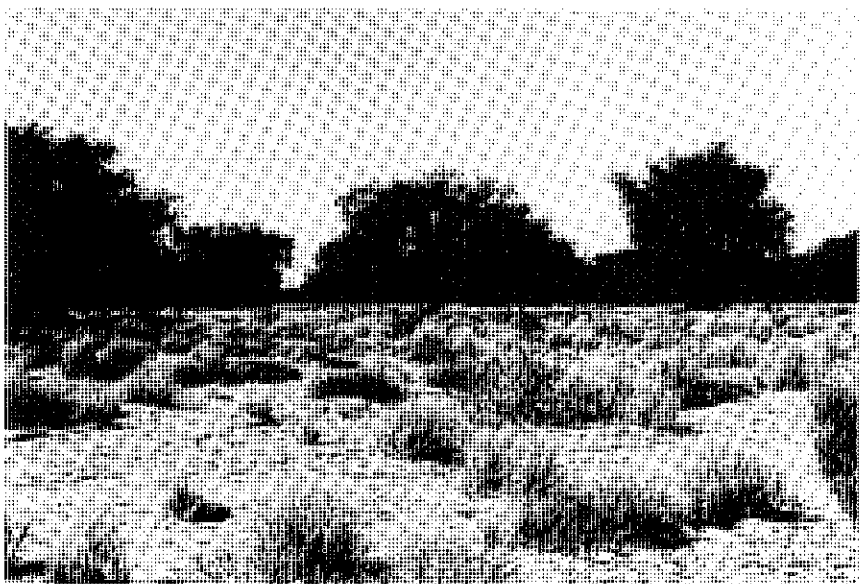


PLATE 6: Large *Acacia albida* individuals with the dominant grass *Eragrostis spinosa* in the river-bed near Swartbank.

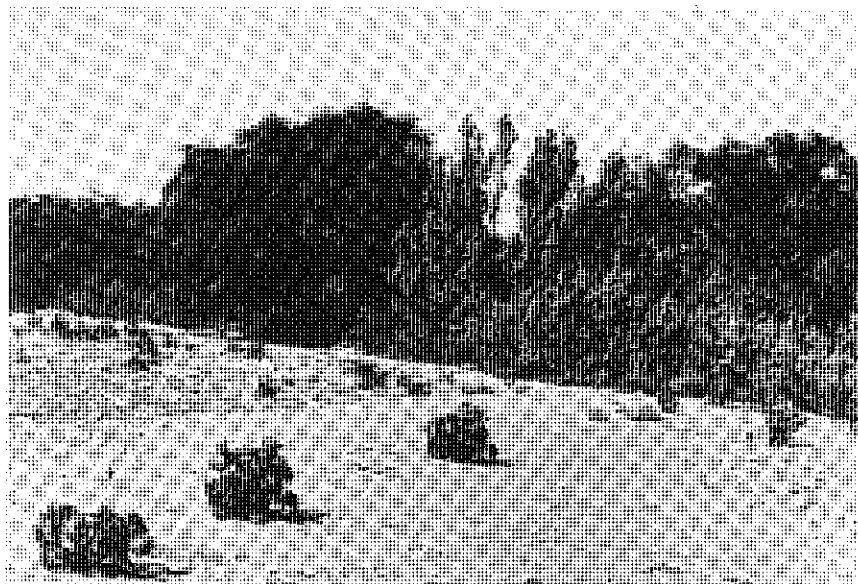


PLATE 7: The *Acacia albida* — *Tamarix usneoides* variation on the embankment near Gobabeb.

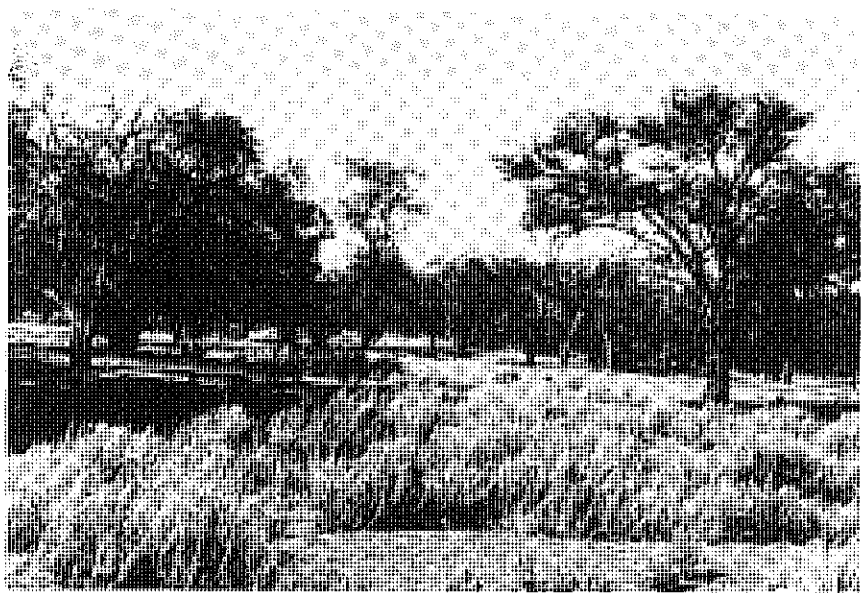


PLATE 8: The *Acacia erioloba* community with *Eragrostis spinosa* in the foreground.



PLATE 9: The *Salvadora persica* — *Acacia erioloba* (1) — *Tamarix usneoides* — *Euclea pseudebenus* (2) dune community near Gobabeb with *Stipagrostis sabulicola* in the foreground.

PLATE 10: The knob dune ("knopduin") community near Swartbank with *Acacia erioloba* on the dunes and *Eragrostis spinosa* and *Stipagrostis sabulicola* in the foreground.

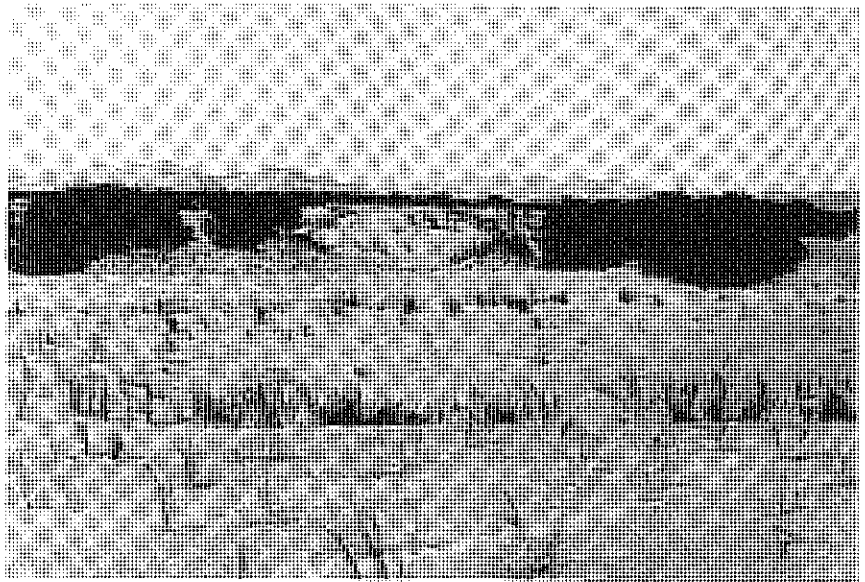


PLATE 11: A dense stand of *Suaeda plumosa* (1) with *Acacia erioloba* and *A. albida* in the background.

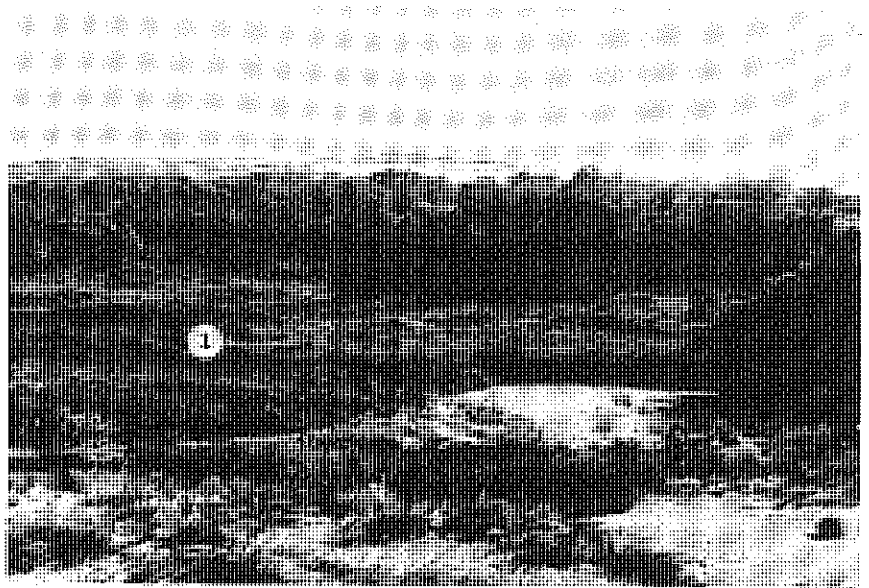
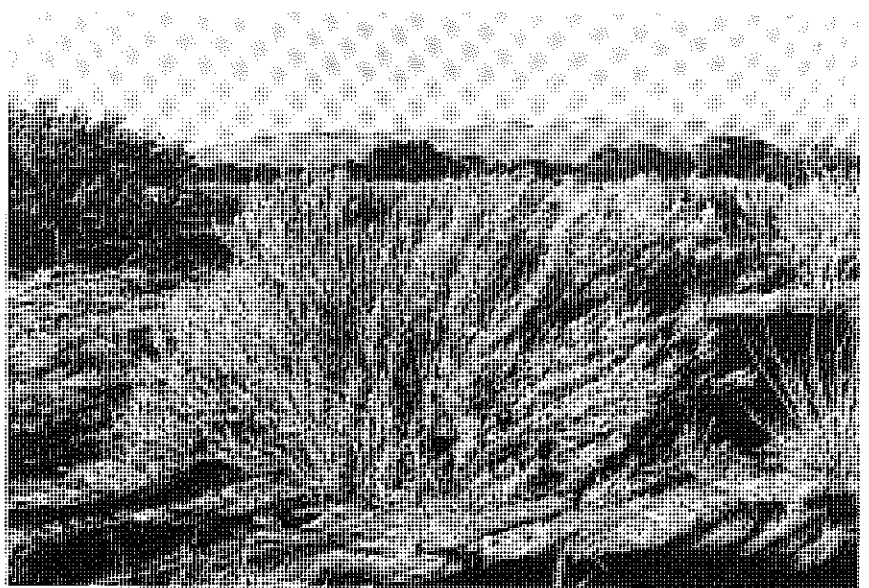


PLATE 12: *Pechuel-oeschea leubnitziae* in the *P. leubnitziae* community on the outstretched flood-plains near Fehlmann Well.



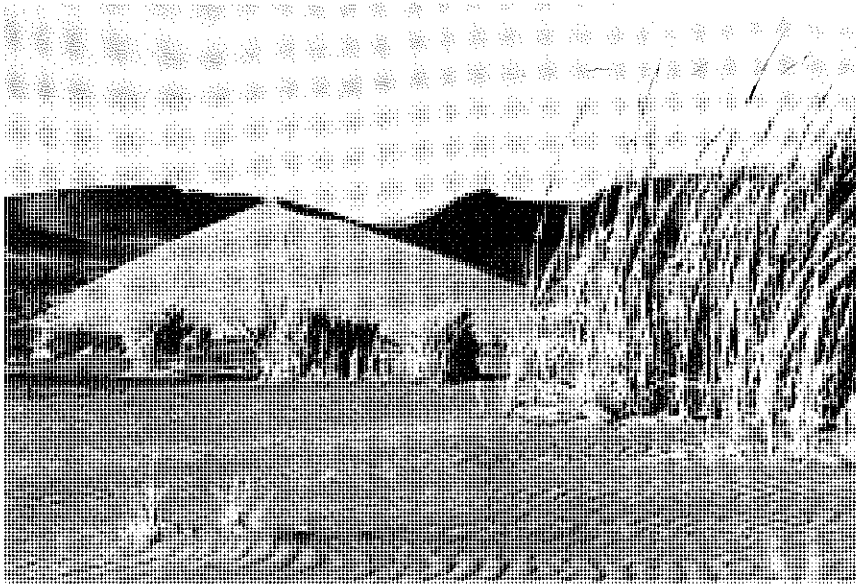


PLATE 13: *Stipagrostis sabulicola* on the sand-dunes south of the Kuiseb River.

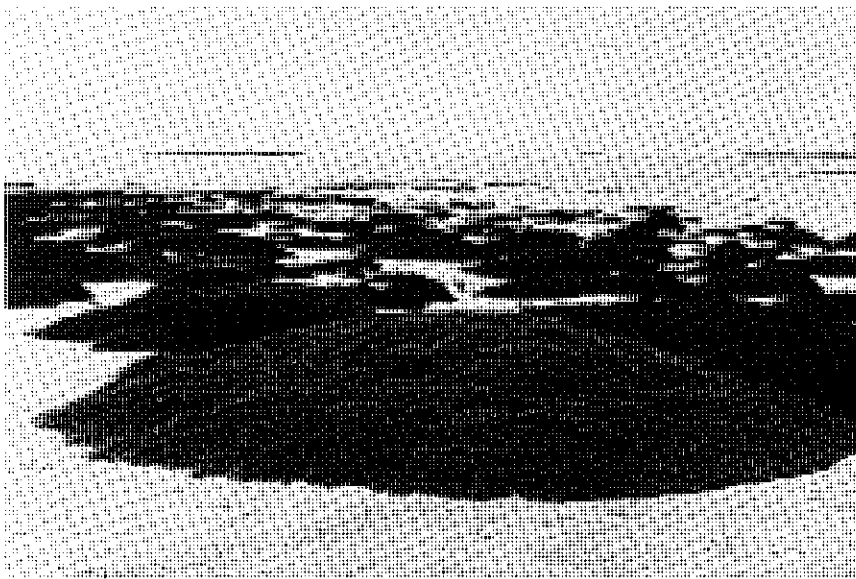


PLATE 14: *Psilocalon* sp. cf. *salicornioides* in the bed of the Soutrivier.

(Plate 10) on both sides of the river in the Rooibank area.

In spite of the reasonably good rains during 1976 to 1978, seedlings of *A. erioloba* are almost absent. The lack of these seedlings can possibly be ascribed to the large numbers of livestock kept by the local Topnaar population.

#### 4.3 *Tamarix usneoides* community

Besides the two above-mentioned communities the *Tamarix usneoides* community is among the most striking of the lower Kuiseb River and occurs on the river-banks (compare Plate 7), flood-plains as well as the foot of the dunes. Immediately above the outcrops jutting out into the river, dense stands of relatively young plants of *Tamarix usneoides* are found in the river-bed. On the flood-plains *T. usneoides* appears as individual plants or as dense impenetrable stands. Big old plants of *T. usneoides* are found on the knob dunes and also at the foot of large sand-dunes.

Between Gobabeb and Swartbank groups of young *Tamarix usneoides* plants grow directly down-stream of *Acacia albida* individuals in the river-bed. Silt accumulation between these dense stands of *T. usneoides* gradually leads to the formation of an island.

Seedlings of *Tamarix usneoides* are found in large numbers in the river-bed and it appears that they are dependant for establishment on the moist conditions inherent in the river-bed. If this is so, the older individuals and thickets of *T. usneoides* occupying the flood-plains possibly indicate an earlier course of the river.

#### 4.4 *Salvadora persica* community

Although this community is seldom present as extensive stands, *Salvadora persica* forms localised mats. The community consists of pure stands of *S. persica* which occur on the steep dunes between Nareb and Gobabeb and in isolated patches down to Swartbank. It is also found on the flood-plains, outcrops and occasionally on the knob dunes on the northern side of the river.

#### 4.5 *Salvadora persica* – *Acacia erioloba* – *Tamarix usneoides* – *Euclea pseudeben* dune community

This community occurs mainly on the southern side of the river, on the sand-dunes (Plate 9). The individual plants are widely spaced and each plant usually forms a large clump with numerous stems. All the above-mentioned species do not occur in each of the mapped units of this community – sometimes only two of these species occur within a unit.

#### 4.6 *Suaeda plumosa* community

The *Suaeda plumosa* community occurs down-stream from Homeb and is especially well-represented in the vicinity of the Aussinans River, Klipneus, Swartbank and up-stream of the Fehlmann Well. The community consists of almost impenetrable thickets of *Suaeda plumosa* (Plate 11) reaching 2 m in height. However, in more open patches *Cyperus marginatus* and *Pechuel-loeschea luebnitziae* are frequently found in association with *Suaeda plumosa*. The *Suaeda plumosa* community is often found where brackish conditions exist and small rivers or streams from the gravel plains join the Kuiseb River. In the Fehlmann Well area, stands of this community are dying and in some places 80 % to 90 % of the plants have died. The deterioration of the vegetation is probably attributable to a lowering of the water table.

#### 4.7 *Eragrostis spinosa* community

This community covers the river-bed from the Narra Valley outcrops to Rooibank (compare Plate 6). In this area the flood-water is apparently not strong enough to sweep the plants away. Other species that are locally conspicuous in this community are *Psoralea obtusifolia* and *Heliotropium ovalifolium*.

#### 4.8 *Pechuel-loeschea luebnitziae* community

This community occurs on the flood-plains especially between the Klipneus area and Rooibank. Although *P. luebnitziae* (Plate 12) can form pure stands it usually grows in association with *Eragrostis spinosa* and/or *Blumea gariepina*. Where this community borders on the knob dune community *Stipagrostis sabulicola* is frequently found among the other species. The species in this community are probably associated with a high-water table and it was noted that plants of *P. luebnitziae* have a higher vitality in the Klipneus area than further down-stream near Rooibank.

#### 4.9 Knob dune (“knopduin”) community:

*Stipagrostis sabulicola*, *Acanthosicyos horrida*, *Acacia erioloba*, *Adenolobus gariepensis*, *Lycium tetrandrum*

This group of plants occurs mainly between Swartbank and Rooibank on the knob dunes (Plate 10) on both sides of the river. The community is characterised by *Stipagrostis sabulicola*, *Acanthosicyos horrida*, *Acacia erioloba*, *Adenolobus gariepensis* and *Lycium tetrandrum*, occurring individually or in groups on a knob dune. Between these dunes *Stipagrostis sabulicola* and *Eragrostis spinosa* are frequently found.

#### 4.10 *Acanthosicyos horrida* community

Strictly speaking this community does not form part of the river communities, but can be regarded as a pure



dune community (Robinson, 1976). The possibility does, however, exist that the roots of *A. horrida* reach the underground water reserves of the river. The community occurs on the dunes on the southern side of the river, occasionally on the knob dunes on both sides of the river as well as in the dune streets at Narra Valley and also opposite Ururas. *Acanthosicyos horrida* is important as a sand binder and occurs on its own or in association with *Stipagrostis sabulicola*. In certain areas *S. sabulicola* predominates (Plate 13) but these units were not mapped as separate units or variations.

#### 4.11 *Psilocalon* sp. cf. *salicornioides* community

This community, consisting of pure stands of *Psilocalon* sp. cf. *salicornioides* (Plate 14) has a limited distribution and is found mainly in the river-bed of the Aussanis River as well as in the area up-stream from Ururas. This community, like the *Suaeda plumosa* one, favours brackish conditions. The existence of this community probably depends on local rainfall to provide a run-off from the gravel plains.

#### 4.12 *Zygophyllum simplex* and *Zygophyllum stapfii* communities

Both communities are found between Ururas and Rooibank along the border of the knob dunes and the gravel plains. They depend largely on the run-off from the gravel plains.

#### 4.13 *Odysea paucinervis* community

This community occurs on the northern side of the river in the Ururas area and is found sporadically down stream to Rooibank. According to Robinson (1976) *O. paucinervis* is associated with marshy conditions. In certain areas it appears that this community indicates previous moist conditions. In areas rich in silt, *Suaeda plumosa* occurs together with *O. paucinervis*, whereas *Lycium tetrandrum* is found with *O. paucinervis* on small sand heaps.

#### 4.14 Dead plant areas

Such areas occur on the flood-plains and in the river-bed and are characterised by the remains of species such as *Datura* spp., *Ricinus communis*, *Nicotiana glauca*, *Eragrostis spinosa* and *Cynodon dactylon*.

### 5 GENERAL

Although this was not a quantitative study, the different communities and variations were easily distinguishable on the basis of their floristic composition, because of the very limited number of species involved. In most cases the variations consist only of the species included

under the name of the variation. Some of the variations are closely related to one another but differ only in the relative dominance of the different species. These variations are nevertheless all clearly distinguishable on aerial photographs.

The large number of variations distinguished can possibly aid the monitoring of vegetational changes to assess the influence of the withdrawal of water for other purposes from the lower Kuseb River.

### 6 ACKNOWLEDGEMENTS

The authors have pleasure in thanking the CSIR, the Division of Nature Conservation and Tourism of the SWA Administration as well as the staff and botany students of the Botany Department of the University of Pretoria for their help during this project.

### 7 SUMMARY

The Kuseb River rises in the Khomas Hochland and with the relatively high rainfall in its catchment area it is the largest river in the coastal belt between the Orange and the Kunene. The river flows infrequently as this depends on the seasonal rainfall in the catchment area. Floods do not reach the lower Kuseb River annually and are insufficient to maintain an open outlet to the sea.

The mean annual rainfall at Gobabeb in the Namib Desert Park is 18,7 mm and this rainfall is very irregular. Fog is an important factor in the study area as it penetrates 30 km to 40 km inland.

The part of the Kuseb River that was studied stretches from Nareb in the east to Rooibank in the west. The withdrawal of large amounts of water from the Lower Kuseb River for town, mining and industrial purposes may have an influence on the vegetation. The maintenance of the vegetation is essential to the Kuseb River ecosystem as a whole, but the vegetation possibly also acts as a barrier which checks the northwards movement of the Namib dune-sea.

Physiognomic-structural areas were distinguished on aerial photographs and these areas were investigated in the field for homogeneity and woody species composition. Units with the same structure and species composition formed a variation and several variations were grouped together in a community. A vegetation map of the area between Nareb and Rooibank was compiled and 14 different communities were distinguished with the *Acacia albida* and *Acacia erioloba* communities as the most important. A total of 40 variations were distinguished. Four additional units, consisting mainly of dead herbaceous species, were mapped between Gobabeb and Rooibank.

The large number of variations distinguished can possibly aid the monitoring of vegetational changes to assess the influence of the withdrawal of water from the lower Kuseb River.

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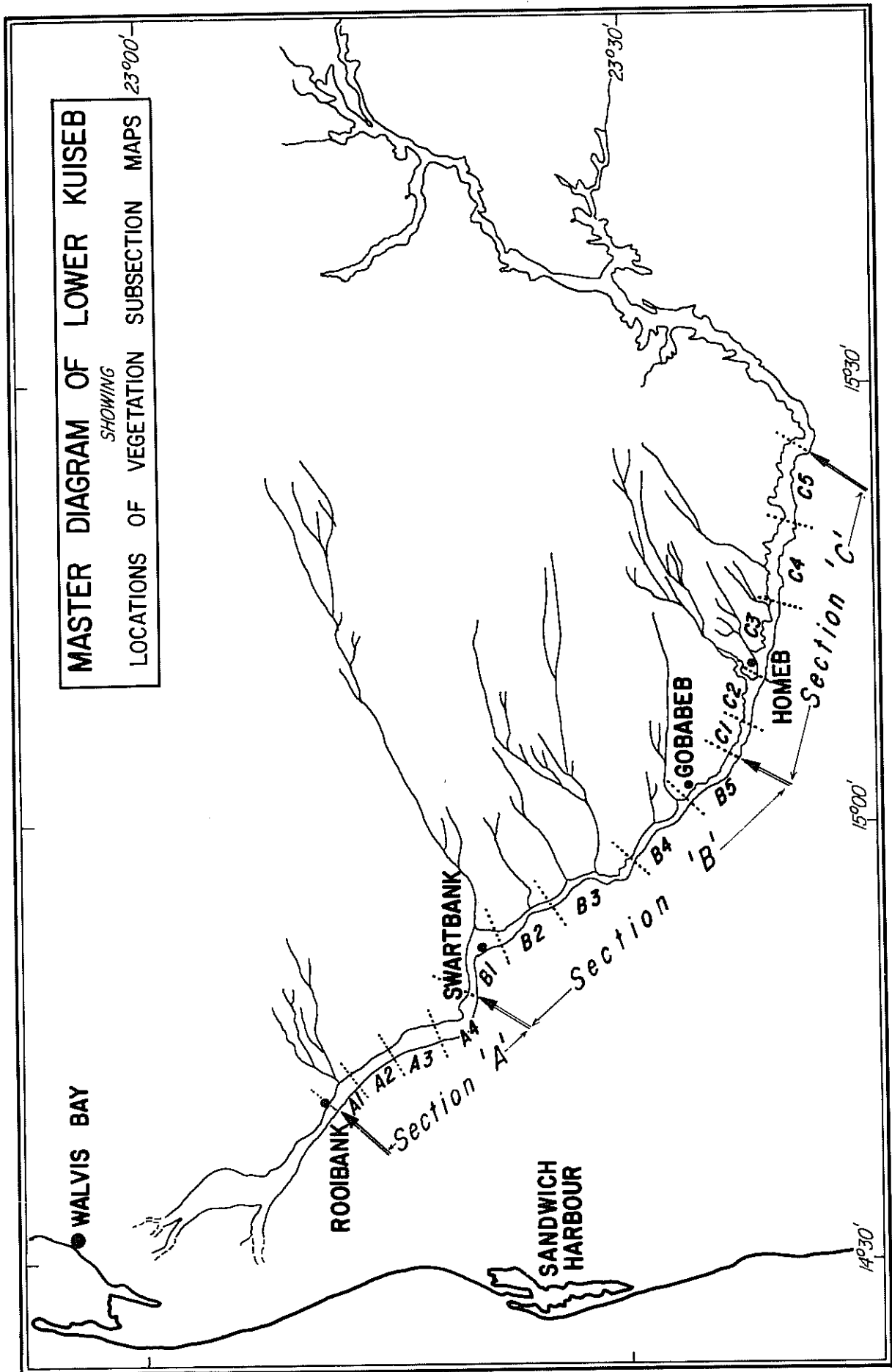
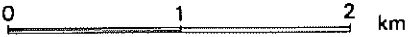


FIGURE 4.

# VEGETATION MAP LOWER KUISEB RIVER

Scale Skaal



- BEACON      BAKEN ●
- WELL        PUT ○

## Subsection A1

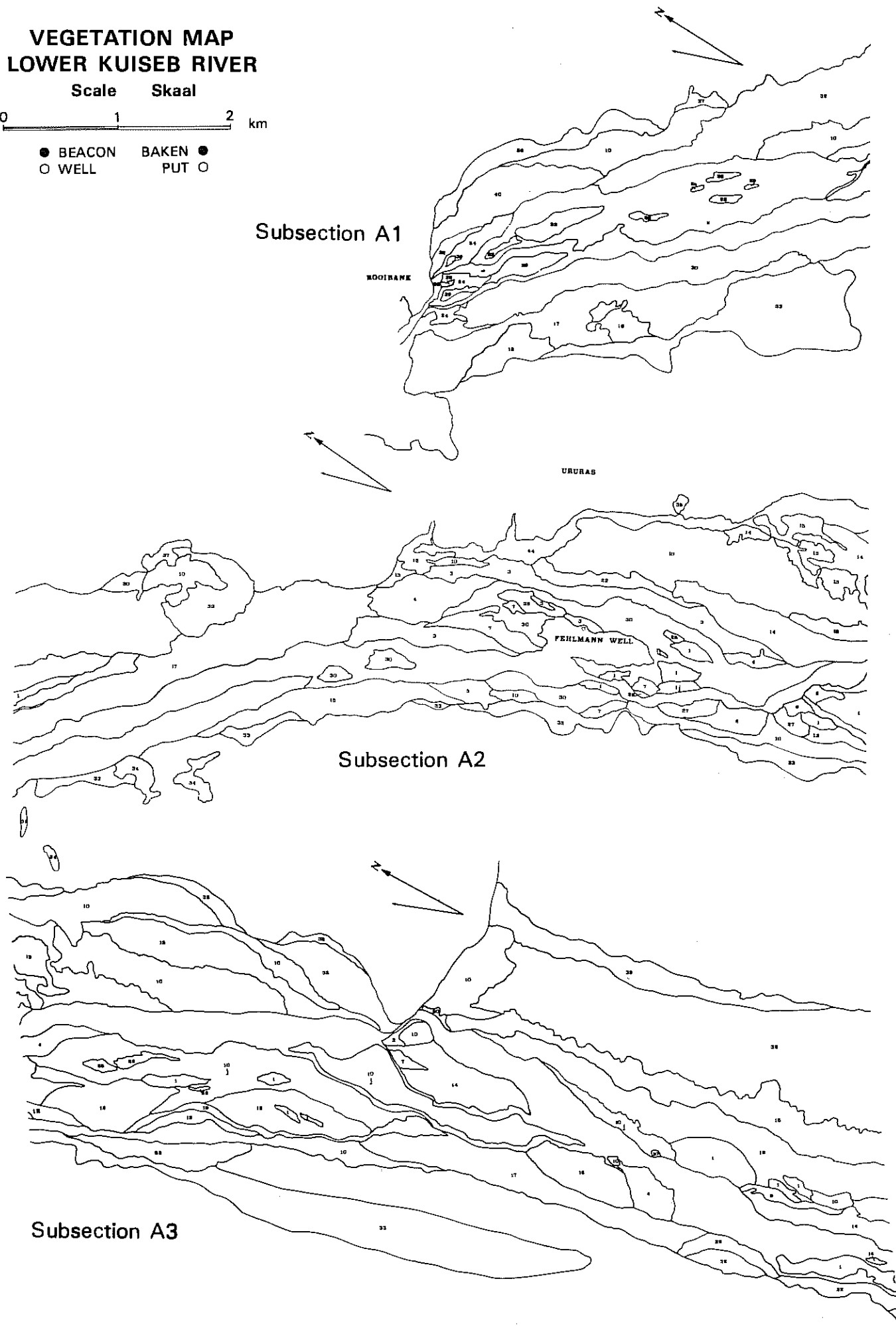
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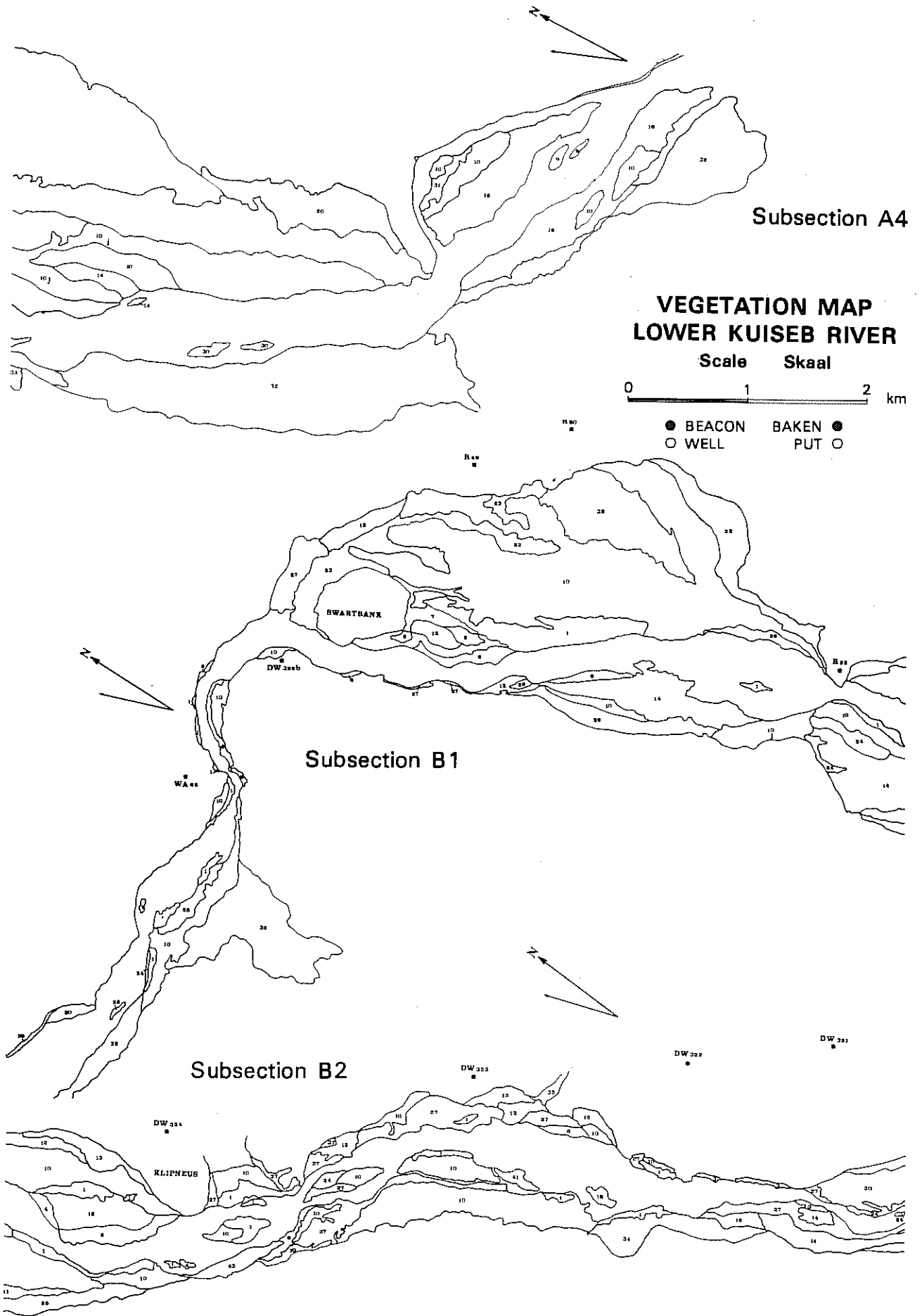
URURAS

FEHLMANN WELL

## Subsection A2

## Subsection A3

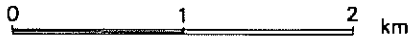






# VEGETATION MAP LOWER KUISEB RIVER

Scale Skaal



- BEACON    ● BAKEN
- WELL      ○ PUT

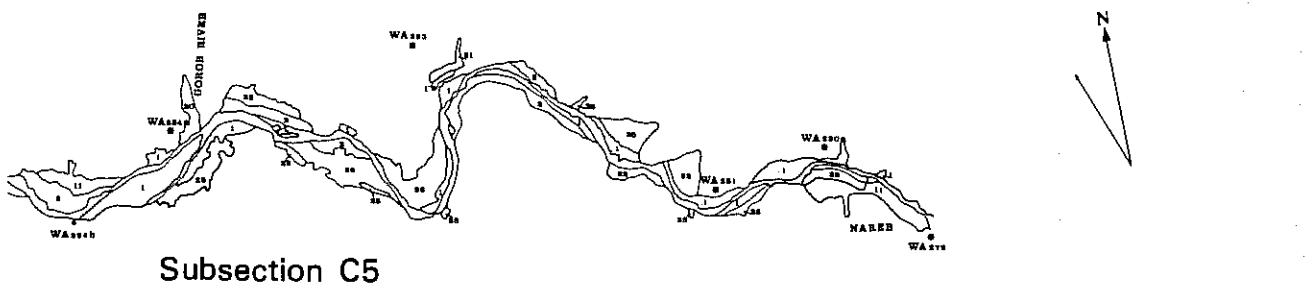
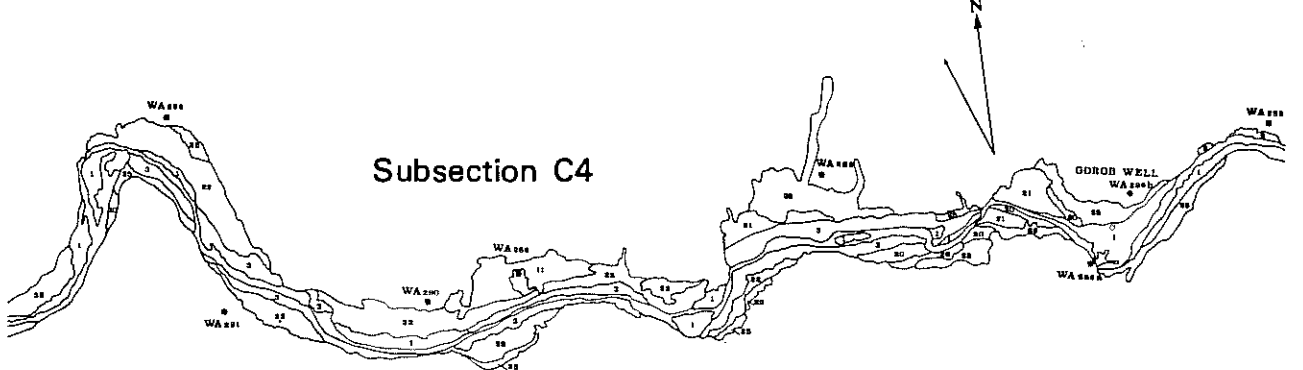
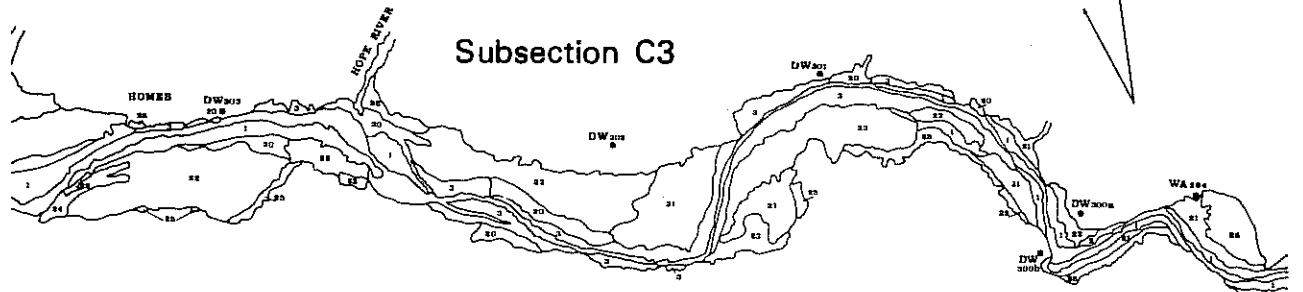
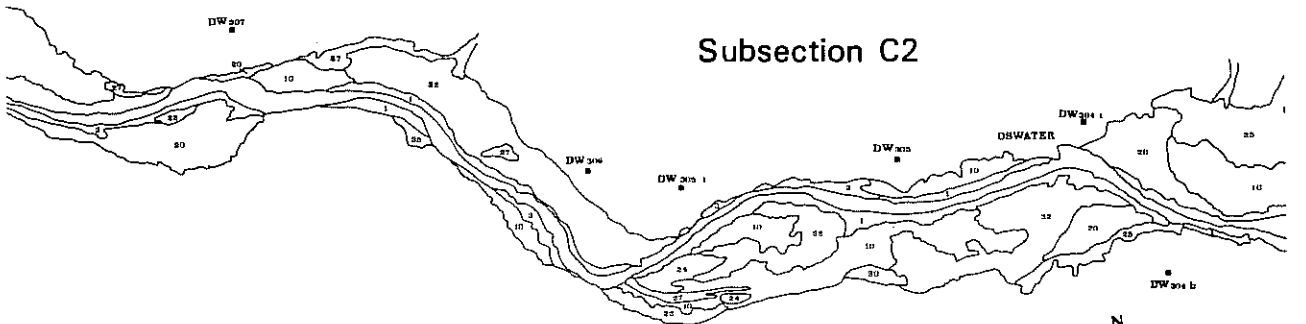
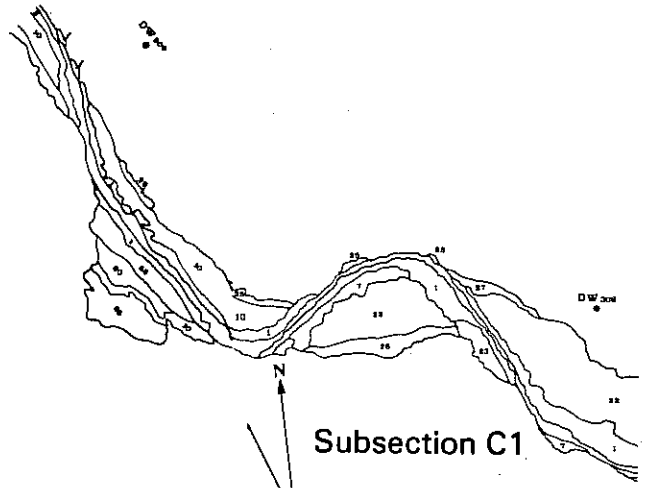
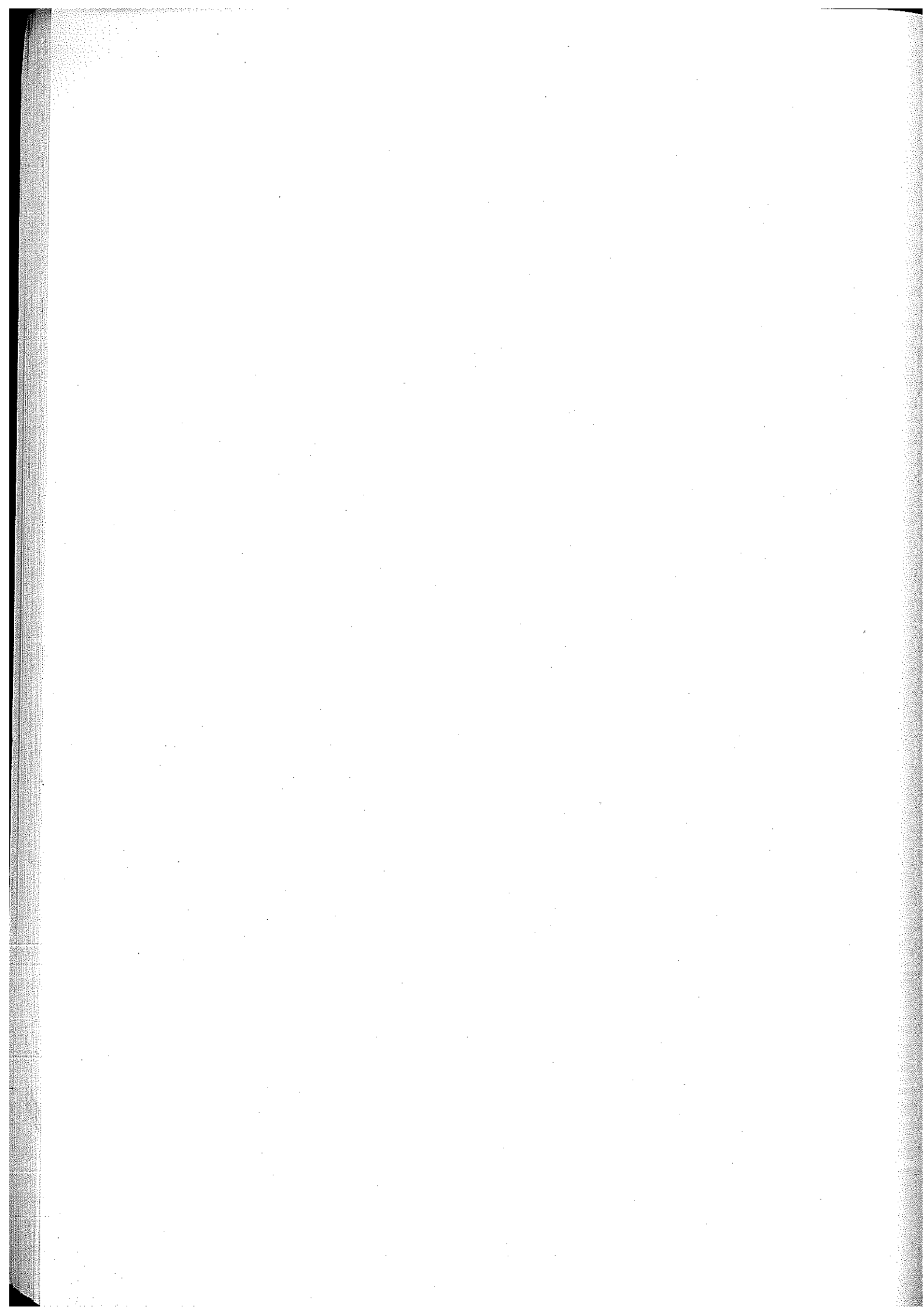


TABLE 1: (Legend to Fig. 4) Plant communities of the lower Kuseb River.

- 
- ACACIA ALBIDA COMMUNITY**
1. *Acacia albida* variation
  2. *Acacia albida* – *Salvadora persica* variation
  3. *Acacia albida* – *Tomarix usneoides* variation
  4. *Acacia albida* – *Eragrostis spinosa* variation
  5. *Acacia albida* – *Stipagrostis sabulicola* variation
  6. *Acacia albida* – *Suaeda plumosa* variation
  7. *Acacia albida* – *Tamarix usneoides* – *Acacia erioloba* variation (sometimes with *Eragrostis spinosa* or *Suaeda plumosa*)
  8. *Acacia albida* – *Eragrostis spinosa* – *Pechuel-loeschea leubnitziae* variation
  9. *Acacia albida* – *Pechuel-loeschea leubnitziae* variation
- ACACIA ERIOLOBA COMMUNITY**
10. *Acacia erioloba* variation
  11. *Acacia erioloba* – *Salvadora persica* variation
  12. *Acacia erioloba* – *Suaeda plumosa* variation
  13. *Acacia erioloba* – *Suaeda plumosa* – *Pechuel-loeschea leubnitziae* variation
  14. *Acacia erioloba* – *Pechuel-loeschea leubnitziae* variation
  15. *Acacia erioloba* – *Stipagrostis sabulicola* variation
  16. *Acacia erioloba* – *Eragrostis spinosa* – *Pechuel-loeschea leubnitziae* variation
  17. *Acacia erioloba* – *Acacia albida* – *Pechuel-loeschea leubnitziae* variation
  18. *Acacia erioloba* – *Acacia albida* variation
  19. *Acacia erioloba* – *Eragrostis spinosa* variation
- TAMARIX USNEOIDES COMMUNITY**
20. *Tamarix usneoides* variation
  21. *Tamarix usneoides* – *Salvadora persica* variation
  22. *Tamarix usneoides* – *Acacia erioloba* variation
  23. *Tamarix usneoides* – *Acacia erioloba* – *Salvadora persica* variation
  24. *Tamarix usneoides* – *Suaeda plumosa* variation
- SALVADORA PERSICA COMMUNITY**
26. *SALVADORA PERSICA* – *ACACIA ERIOLOBA* – *TAMARIX USNEOIDES* – *EUCLEA PSEUDEBENUS* DUNE COMMUNITY
- SUAEDA PLUMOSA COMMUNITY**
27. *SUAEDA PLUMOSA* COMMUNITY
- ERAGROSTIS SPINOSA COMMUNITY**
28. *ERAGROSTIS SPINOSA* COMMUNITY
- PECHUEL-LOESCHEA LEUBNITZIAE COMMUNITY**
29. *Pechuel-loeschea leubnitziae* variation
  30. *Pechuel-loeschea leubnitziae* – *Eragrostis spinosa* variation
  31. *Pechuel-loeschea leubnitziae* – *Eragrostis spinosa* – *Stipagrostis sabulicola* variation
- 32. KNOB DUNE COMMUNITY: STIPAGROSTIS SABULICOLA, ACANTHOSICYOS HORRIDA, ACACIA ERIOLOBA, ADENOLOBUS GARIEPENSIS, LYCIUM TETRANDRUM**
- ACANTHOSICYOS HORRIDA DUNE COMMUNITY**
33. *Acanthosicyos horrida* variation
  34. *Acanthosicyos horrida* – *Stipagrostis sabulicola* variation
- 35. PSILOCAULON sp. cf. SALICORNIOIDES COMMUNITY**
- 36. ZYGOPHYLLUM STAPFII COMMUNITY**
- 37. ZYGOPHYLLUM SIMPLEX COMMUNITY**
- ODYSSEA PAUCINERVIS COMMUNITY**
38. *Odyssea paucinervis* variation
  39. *Odyssea paucinervis* – *Suaeda plumosa* variation
  40. *Odyssea paucinervis* – *Lycium tetrandrum* variation
- DEAD PLANT AREAS**
41. *Eragrostis spinosa*, *Datura* spp., *Nicotiana glauca*, *Ricinus communis*
  42. Dead *Eragrostis spinosa* with living *Acacia erioloba*
  43. Dead *Eragrostis spinosa* with living *Acacia albida*
  44. *Eragrostis spinosa*, *Zygophyllum simplex*, *Suaeda plumosa*
-





## SHORT NOTE

Habitat ecology of black storks  
in the Kuiseb River

by

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Bloemfontein

Received: 22 January 1979

As an adjunct to a study on the ecology of water-pools in the Kuiseb River Canyon of South West Africa we noted the presence of a small, and perhaps resident, population of black storks, *Ciconia nigra*, wading in pools that were being monitored on a monthly basis. The extension of the black stork's distribution into this desert canyon is attributed to the seasonal decline in size of water-pools and corresponding concentration of fish and amphibians living in them. Other contributing factors include the lack of competition for these resources, the isolation from human disturbance, and the abundance of suitable roosting and nesting sites on canyon walls.

The black stork is a common Palaearctic migrant to parts of northern and eastern Africa, but in southern Africa it is a relatively uncommon year-round resident that is widely dispersed throughout its range (Siegfried, 1967; Moreau, 1972). The estimated 100 black storks resident in southern Africa apparently only breed in isolated mountainous regions of the subcontinent where permanent water is available, namely the Drakensberg escarpment of South Africa and the rocky hills and mountains of central Rhodesia (Siegfried, *op. cit.*; Siegfried *et al.*, 1976). In South West Africa only a few isolated observations of black storks have been reported in the last two decades, most of these being of solitary birds (Table 1). Given the unconfirmed reports of black storks breeding in the Kuiseb River Canyon (Siegfried, *op. cit.*; Tuer, 1977), we present here our notes on black storks in the canyon between 1976 - 1978.

TABLE 1: Observations of black storks in South West Africa.

Date	Site	No.	Source
Jan. 1950	Ai Ais (Fish River)	3	MacDonald 1957
Feb. 1950	Voigtsgrund Dam	3	MacDonald 1957
— 1970	Daan Viljoen	1	C. Clinning, pers. comm.
Oct. 1970	Daan Viljoen	1	C. Clinning, pers. comm.
Dec. 1975	Etosha National Park	1	C. Clinning, pers. comm.
Mar. 1976	Farm Sandmodder (Karas Mountains)	1	C. Clinning, pers. comm.
May 1977	Bullspoort (Naukluft Escarpment)	1	C. Clinning, pers. comm.
—	Waterberg	—	Winterbottom 1971

The Kuiseb River, with its origins in the Khomas Hochland, has incised a deep narrow canyon of about 75 km in length on its westward flow through the Namib Desert to the Atlantic Ocean. In the canyon, which starts about 40 km east of Gobabeb (23°34'S, 15°03'E), there is virtually no vegetation, but the sandy canyon floor has a number of small, isolated water-pools. Although usually dry, the Kuiseb floods almost every year following seasonal rains in the

escarpment between December and March. Floods past Gobabeb may last from 1 – 102 days ( $\bar{X} = 33$ , S.D. 29 days, 1962 – 1976), but minor flows continue for several more months in the canyon area. After the floods recede the water table gradually drops, confining accessible water to isolated and irregularly spaced pools. Water-pools in the lower parts of the river near Gobabeb dry more rapidly than those farther up-river, and those in the canyon persist throughout the year (Table 2).

TABLE 2: The decline in number and approximate size of water pools in the Kuiseb River Canyon through the dry season. Locations of pools are clumped into four separate regions, defined by their distance (km) up-river from Gobabeb: V = Kuiseb River Valley (Km 0 – 35); L = Lower Kuiseb Canyon (Km 36 – 75); M = Middle Kuiseb Canyon (Km 76 – 120); U = Upper Kuiseb Canyon (Km 121 – 155). The narrow, inner canyon (M) was censused twice on foot. The canyon flooded on 27 January 1978 and the flood-waters reached Gobabeb on 9 February 1978.

Date	Number of water pools				Surface area (m <sup>2</sup> )			
	V	L	M	U	V	L	M	U
1977								
Aug.	11	62	—	50	92	4,025	—	1,694
Sep.	12	64	—	36	48	562	—	1,016
Oct.	10	63	—	22	11	473	—	656
Nov.	9	39	334	18	5	185	6,446	413
Dec.	7	23	—	17	<1	119	—	334
1978								
Jan.	4	23	163	8	<1	31	4,182	185

Individual black storks have been observed as far down-river as Gobabeb in August (1977) and May (1978), but their general distribution is confined to the canyon areas 45 – 140 km up-river. Except for the flood period (March – May) when the canyon is inaccessible for censusing, black storks have been observed in every month (1976 – 1978). Whether they remain in the canyon during the floods or move elsewhere is unknown, but the generally sporadic records of individual birds observed in other parts of South West Africa during these periods suggest that adults do not disperse, although one or two young birds may (Table 1). Single birds or small groups, apparently family units, are the rule, with a mean of  $2.0 \pm 1.2$ ,  $N = 132$  (Table 3). From our census data, gathered by two observers censusing the upper 35 km and lower 75 km of the Kuiseb River on the same day, we estimate there are at least 13 black storks inhabiting the canyon. If the census data for other parts of southern Africa are correct (Siegfried, 1967), this represents about 12 % of the entire black stork population in the subcontinent.

In November 1977 a newly fledged stork, distinguished by its yellow bill, dull brown plumage and slightly smaller size, was observed accompanying two adult storks, presumably its parents. This immature bird could only fly short distances of 75 – 100 m before settling again, suggesting it had just left its nest.

This indicates a breeding date of June – July, which corresponds well with breeding dates of black storks elsewhere in the subcontinent (Siegfried, 1967). In July 1978 two pairs of adults were observed courting, but their nesting sites were not found. Another breeding record in the Maltahöhe district noted that four eggs were laid in September (C. Clinning, personal communication).

TABLE 3: Flock size of black storks in the Kuiseb River Canyon.

Number	Frequency	Percent
1	60	45,4
2	34	25,8
3	25	18,9
4	7	5,3
5	5	3,8
6	—	—
7	—	—
8	1	0,8

The presence of black storks in the Kuiseb River Canyon is almost certainly linked to the gradual decrease in size of water-pools and the availability of fish and amphibians living in them. Three species of fish (*Sarotherodon mossambicus*, *Cyprinus carpio* and *Barbus anoplus*) and at least three amphibians (*Xenopus laevis*, *Bufo vertebralis* and *Tomopterna delalandi*) are found in the pools. The most abundant of the above, and the most important food item for black storks, is *S. mossambicus*. In November 1977 all fish were removed from five different pools. *S. mossambicus* accounted for 89,1 %, *C. carpio* 9,3 % and *B. anoplus* 1,7 % of the total 758 fish captured (specimens smaller than 2 cm were excluded). In two of the pools *X. laevis* tadpoles were noted but not counted; the other three pools had no large vertebrate species other than fish. In a separate count of a sixth pool measuring 18 × 10 m, 863 fish, all of them *S. mossambicus*, were netted, measured to the nearest mm, then replaced. One month later (January 1978) the pool, then measuring 15 × 9 m, was recensused. About half the fish were missing, especially the larger size classes (120 – 280 mm), suggesting that selective predation by black storks may be operating (Fig. 1). During the same period, the number of *X. laevis* adults sampled decreased from 29 to 5. Elsewhere (Tilson and Kok, in preparation) we show that there is a significant decline in the size of water-pools in the Kuiseb River as the dry season progresses, but the area most preferred by black storks (the inner canyon) is where most of the small permanent water-pools are located (Table 2).

Black storks are restricted in their breeding and post-breeding dispersal to suitable aquatic food resources. Siegfried (1967) pointed out that in spite of the abundant mountainous terrain and permanent streams of the south-western Cape, which would seemingly be an ideal nesting habitat, black storks do not breed there because

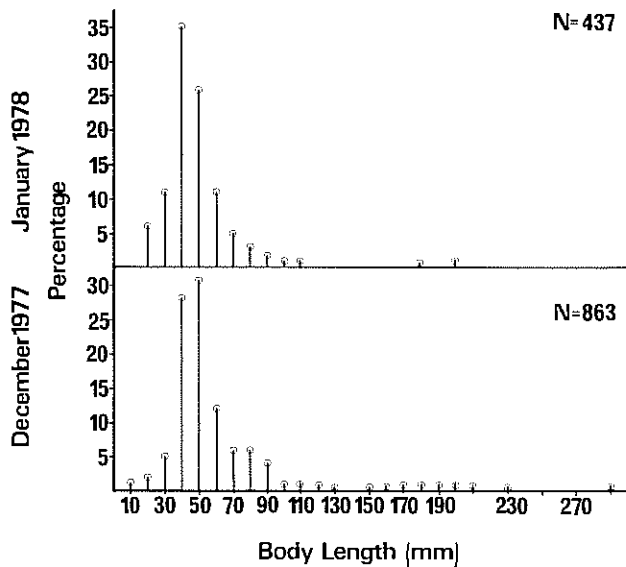


FIGURE 1: The decline in number and size classes of *Sarotherodon mossambicus* in a Kuiseb River Canyon water pool.

at the time the young need to be fed the rivers and vleis are swollen and the fish dispersed. Elsewhere Kahl (1964) has shown that declining water levels, and a corresponding increase in the availability of food items, is the proximal basis for breeding in wood storks, *Mycteria americana*, and that post-breeding dispersal coincides with periods of high-water levels. This is precisely the relationship between black storks and water-pools in the Kuiseb River Canyon. Our censuses show that there are year-round pools in the Kuiseb (except during floods) that contain an abundant, though species poor, population of fish-fauna, notably *S. mossambicus*. These pools are situated in a relatively isolated and undisturbed section of the canyon, close to steep rocky walls that provide ideal nesting sites. The seasonal floods do not occur until after January, long after the time young birds have fledged.

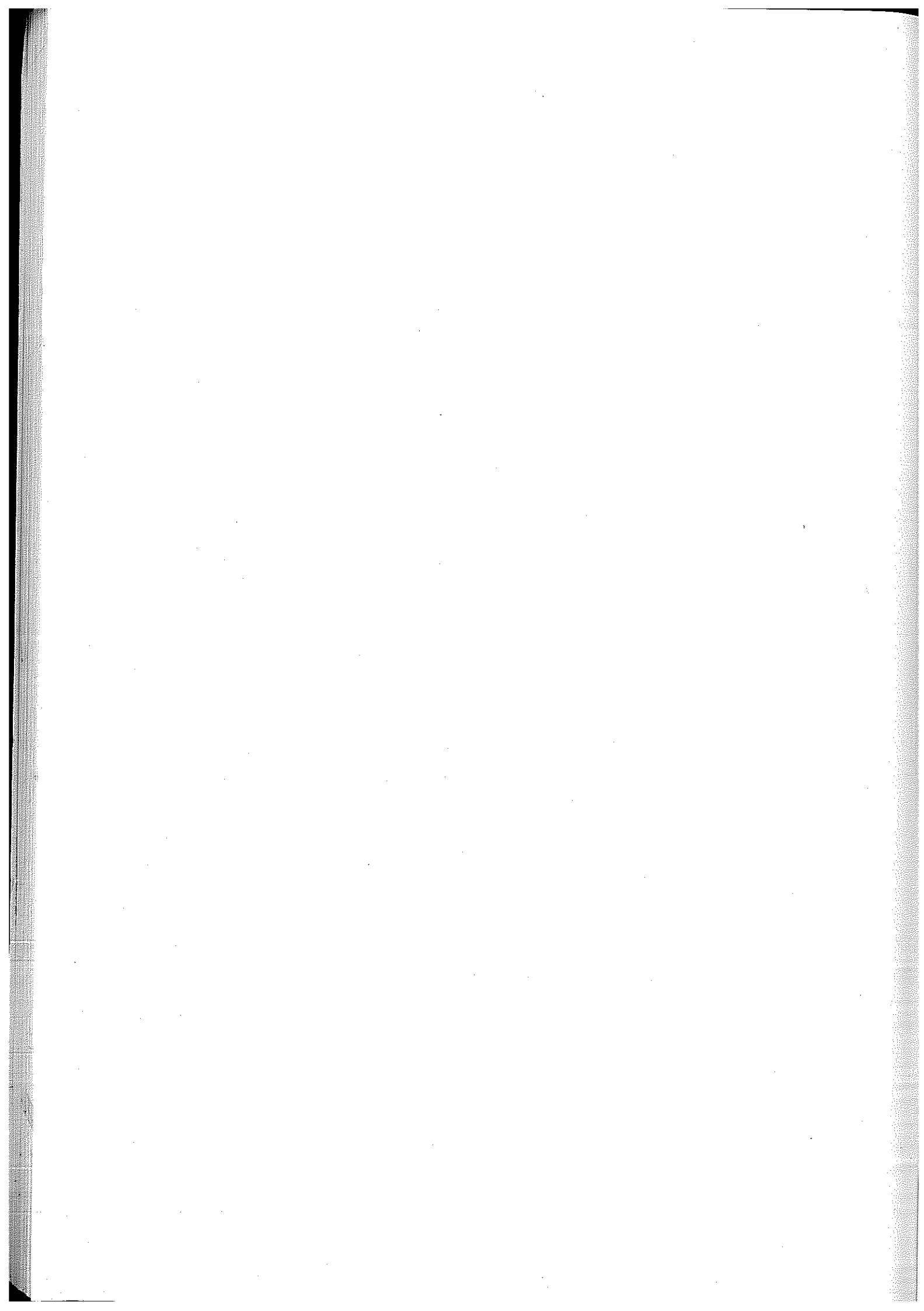
Prior to this is a period when food resources become easily accessible and sufficiently abundant to support this small population of black storks.

#### ACKNOWLEDGEMENTS

We thank Pieter Koornhof, Dirk Mostert, Flip Schoeman, Janet Tilson, Savvas Vrahimis and Pat and Philip Withers for their help in our water-pool censusing, and Charles Clinning for providing the observations of black storks from the files of the Nature Conservation and Tourism Division. The CSIR, Transvaal Museum and University of the Orange Free State are thanked for financial assistance and the Nature Conservation and Tourism Division of South West Africa for facilities and permission to work in the Namib Desert Park.

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## SHORT NOTE

The occurrence of the  
Cape eagle owl  
in South West Africa

by

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Division of Nature Conservation and Tourism  
Windhoek

Received: 4 March 1979

The Cape eagle owl *Bubo capensis* is restricted in its distribution to montane areas in eastern and southern Africa (Benson and Irwin, 1967; Steyn and Tredgold, 1977; McLachlan and Liversidge, 1978). There are no published records of the species from South West Africa (above references and Winterbottom, 1971).

Plate 1 illustrates an adult Cape eagle owl photographed near Lorelei in the lower Orange River valley (28°S 17°E) by Mr H. Walter in October 1956. Mr Walter had until recently been unaware of the identity of the bird. The nearest localities to Lorelei from which *Bubo capensis* has been previously recorded are the Clanwilliam district 32°10'S, 18°52'E (R. Jensen pers. comm.) and Kimberley 28°45'S, 24°46'E (Benson and Irwin, 1967).

The bird recorded from Lorelei may have been a vagrant, a possibility supported by the lack of any more recent records. There are unsubstantiated records of Cape eagle owl from the Fish River Canyon.

Benson and Irwin (1967) point out that the species would probably have been more widespread in the last wet phase of the pleistocene and that its present distribution comprises a series of relict isolates. Possibly a relict population exists in the less arid areas of southern South West Africa. For example the lower Orange and Fish River drainage systems and the Naukluft mountains. Geological evidence indicates however, that even during the wettest periods of the pleistocene South West Africa remained arid (Verdcourt, 1969).

## ACKNOWLEDGEMENTS

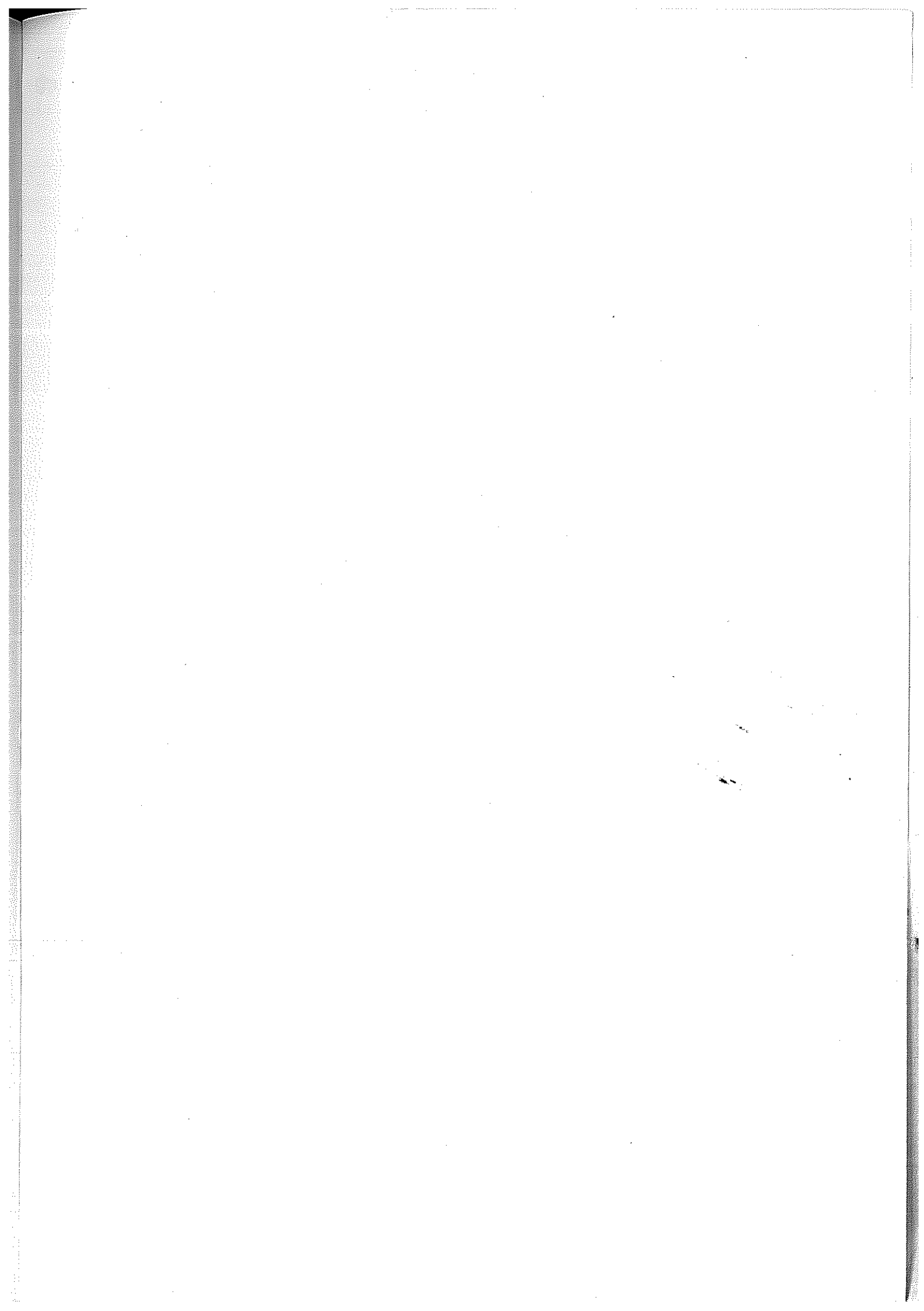
Thanks are due to Mr H. Walter for making his photographs available and to Dr R. A. C. Jensen for confirming the identity of the bird.

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1971: *A preliminary checklist of the birds of South West Africa*. SWA Scientific Society, Windhoek.



PLATE 1: An adult Cape eagle owl photographed near Lorelei in the lower Orange River valley. (Photograph: H. Walter).





## INSTRUCTIONS TO AUTHORS

1. MADOQUA publishes papers on original, basic and applied research concerning nature conservation and the deserts in South West Africa.
2. Papers submitted for publication should be sent to the: Director, Nature Conservation Directorate, Private Bag 13186, Windhoek, 9000, South West Africa.

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1. Papers submitted should be ready for the press.
2. The manuscript should be typed in double spacing throughout, on one side of A4-size (297 × 210 mm) paper, with a left-hand margin of 4 cm.
3. The original and two copies of the manuscript should be submitted.
4. Title page should contain:
  - (a) complete title of paper — which should be concise yet clear as to the contents of the paper;
  - (b) author's or authors' name/s;
  - (c) institution/s from which the paper emanates;
  - (d) present address if different from (c) will appear as a footnote;
  - (e) abbreviated title (running headline);
  - (f) address to which proofs are to be sent.(Note that the name of a new genus or species should not be included in the title).
5. An abstract should be given of not more than 100 words.
6. A list of CONTENTS should give the headings of individual sections and if appropriate also sub-sections.
7. The text should ideally consist of the following, in this order:
  - Introduction
  - Material and methods
  - Results
  - Discussion
  - Conclusions
  - Summary
  - Acknowledgements
  - References
  - Legends to maps, figures, plates and tables.
8. Number all pages consecutively, including tables, literature and legends.
9. English is preferred for purposes of international circulation. Manuscripts in German, French or any other language, are occasionally acceptable, provided they are supplied with a complete summary in English.
10. The system advocated in "Council of Biology, Editors Style Manual, Washington: American Institute of Biological Sciences, 1972" is recommended.
11. The names of species and foreign words must be underlined (for italic print). Vernacular names should be accompanied by the appropriate scientific names the first time each is mentioned.
12. The metric system is the standard unit of measurement accepted.
13. The approximate position of illustrations in the text should be indicated by the author in the manuscript.
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1953: *Southern African mammals: A reclassification*. London. Trustees British Museum (Nat. Hist.)

HANKS, J.

1972: Aspects of dentition of the African elephant, *Loxodonta africana*. *Arnoldia* (Rhod.), (36): 1 — 8.

KELLAS, L. M.

1955: Observations on the reproductive activities, measurements, and growth rate of the dikdik (*Rhynchotragus kirki thomasi* Neumann). *Proc. zool. Soc. London*, 124: 751 — 784.

SHORTRIDGE, G. C.

1931: Field notes on two little known antelopes: The Damara-land dikdik (*Rhynchotragus damarensis*) and the Angolan impala (*Aepyceros petersi*). *S. Afr. J. Sci.* 28: 412 — 417.

1934: *The mammals of South West Africa*. 2 Vols. London: Heinemann.

15. Journals should be abbreviated in accordance with the World list of scientific periodicals 4th edition London: Butterworths, 1963.

16. Legends for figures, plates and tables should be numbered consecutively, type-written on separate sheets, and must follow the references. Figures and tables should not duplicate information or repeat information given in the text.

Figure legends are written: (to appear below the figure).

FIGURE 1: ...

Plate legends are written: (to appear below the plate).

PLATE 1: ...

17. For the general outlay of the manuscript follow the articles in this Madoqua.

Table legends are written: (to appear above the table).

TABLE 1: ...

### Plates and figures

1. Glossy photographs not less than 14 × 20 cm in size, and line drawings in black (waterproof) india ink on white paper must be submitted together with the manuscript. The line drawings should be about the size of reproduction. An indication should be given of the proposed size of reproduction, i.e. full page or one column.

2. The reverse side of illustrations should be marked lightly in pencil with the title of the illustration, author's name and title of article.

3. Scales could be drawn in or photographed so that they form part of the illustration.

### Short notes

1. No headings if possible.

2. Text immediately follows the title.

3. References should be cited as with long manuscript — see 14 above.

### Proof

1. Galley proofs will be sent to the author, who accepts final responsibility for their complete correction, and should be returned promptly.

3. The size of the printing surface of the pages is 24,7 cm × 16,8 cm.

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