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

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CONTENTS

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 ante-
lopes 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: Neotra-
gini) (Estes, 1974; Jarman, 1974; Leuthold, 1977).
These antelopes generally rely on silence and conceal-
ment 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 Dande-
lot, 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 Kho-
mas Hochland through a deep narrow gorge that gra-
dually 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 descrip-
tions (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 glandu-
ligera* occur, and in shallow washes the succulents
Zygophyllum simplex and *Mesembryanthemum gueri-
chianum* 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 sesu-
vioides*. 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 epheme-
rals. *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
sycomorus* 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 klip-
springer 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
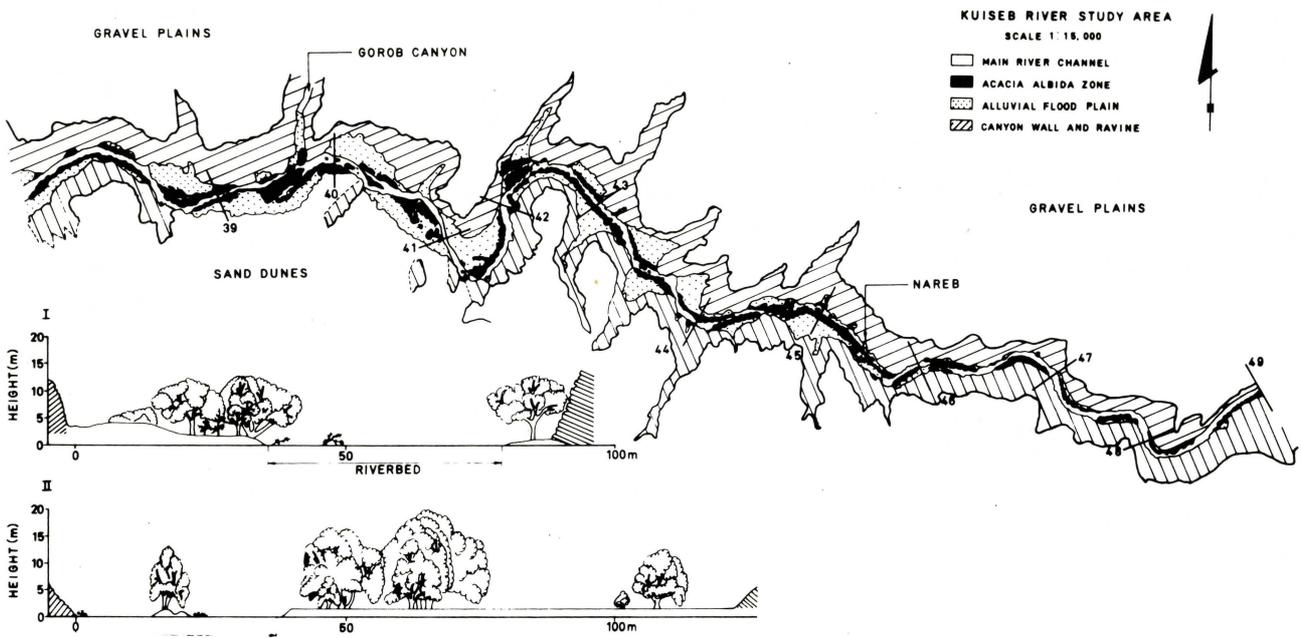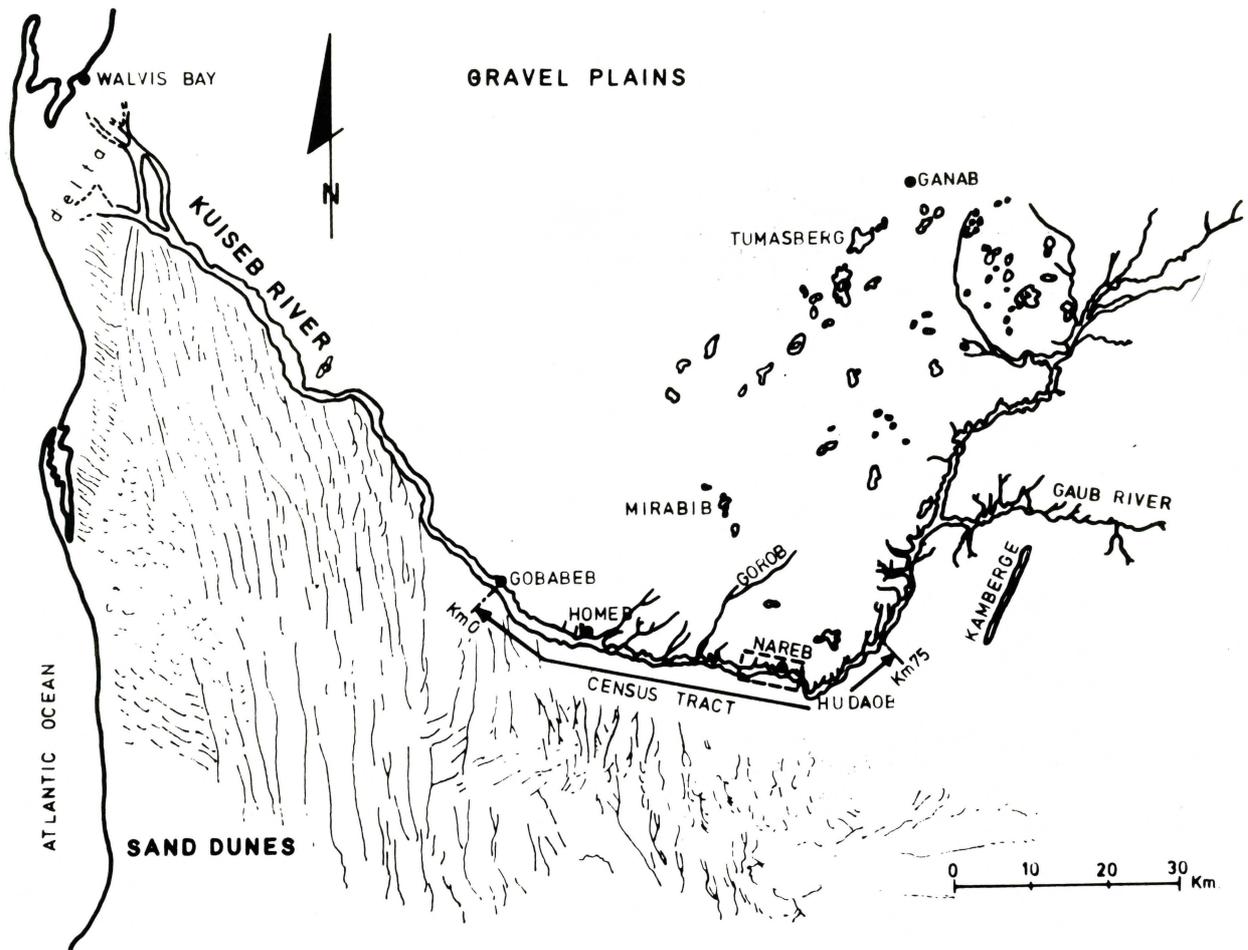
PLATE 2: The acacia dominated riparian forest on the canyon floor.

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 | |
	$\overline{X}$	Range	$\overline{X}$	Range	$\overline{X}$	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 $\overline{X}$	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 ($\overline{X}$ = 10,1 m) than when resting ($\overline{X}$ = 4,6 m) or travelling ($\overline{X}$ = 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
Resting			
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
Feeding			
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
Travelling			
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 (x^2 = 36,05, p<,005) and undisturbed movements (x^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 (%) | | | |
	Male	Female	Juv.	Male-Fem.	Male-Juv.	Fem.-Juv.	(%) Total
Resting							
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

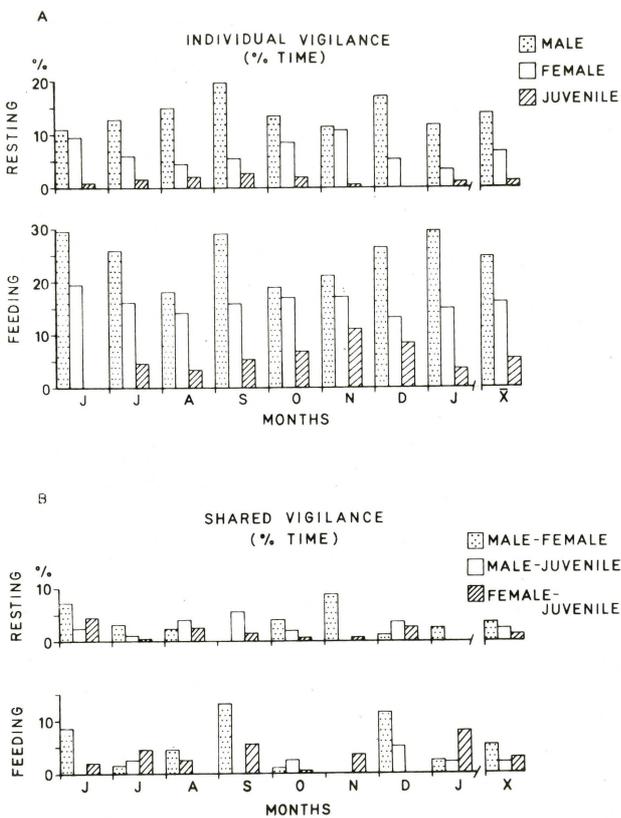| Month	Individual vigilance (%)			Shared vigilance (%)			
	Male	Female	Juv.	Male-Fem.	Male-Juv.	Fem.-Juv.	(%) Total
Feeding							
June	29,4	19,3	0,0	8,4	0,9	1,9	59,9
July	25,8	16,0	4,6	1,6	2,5	4,4	54,9
Aug.	17,9	14,0	3,3	4,6	2,7	0,0	42,5
Sept.	29,0	15,8	5,3	13,2	0,0	5,3	68,4
Oct.	18,8	17,1	6,8	0,8	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

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 rufofuscus*). 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 Blottnitz 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 ($\overline{X}$ 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 (x^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		
	No.	%	Category
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 (x^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.

5 ACKNOWLEDGEMENTS

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