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CHAPTER EIGHT

SPATIAL AND SOCIAL ORGANISATION

8.1 INTRODUCTION

Ever since man first pursued animals he has been a student of animal behaviour (Cowan 1974) and today there can be little doubt that intensive ethological research is indispensable to wildlife management (Leuthold 1970b; Geist 1971b; Cowan 1974; Geist and Walther 1974; Jarman 1974; Leuthold 1977). The extent to which animals select certain habitats depends largely on the area they choose, or are obliged to live in which in turn may be influenced by interactions between individuals, families or groups. Furthermore, any behaviour which limits an animal to a particular area, whether this be territorial behaviour or other forms of spacing behaviour (e.g. home range selection) is likely to affect performance to some extent. Hence, it affects population dynamics through reproductive success (e.g. competing males) while dominance hierarchies give a greater chance of survival to the dominant individuals (Mitchell et al. 1977). The ways in which limitations on distribution by social behaviour affect performance are largely influenced by proximal factors, particularly nutrition, but "social stress" factors operating more directly on the animals themselves may also be important (see Watson and Moss (1970).

Performance may also be influenced by inadequate management that fails to consider the importance of certain individuals in the social structure of a population (e.g. see Leuthold 1977; Anderson 1978) as well as by man-made disturbances (Leuthold 1970b; Geist 1971b, 1978). Clearly the successful management of any population depends on a knowledge of the effects on, and the behaviour responses shown by, that population to such management practices as culling, live removals, translocations, and other human activities that result in some form of disturbance to specific individuals; any or all of these may lead to the

disruption of foraging patterns and a subsequent decline in physiological condition, alterations in the normal activity cycles of the animals, movements away from the areas of disturbance etc.

In addition to its affect on performance, spatial and social interactions may have a limiting effect on population density (e.g. Wynne-Edwards 1962; Joubert 1974a; Spinage 1982). Failure to appreciate this fact might render any attempts to increase population density by providing additional food or other habitat requirements largely unsuccessful (e.g. see Mitchell et al. 1977).

Finally, several specific behavioural characteristics have to be taken into account in any successful research or management programme. In particular, the feasibility and/or accuracy of censuses may be affected by certain behavioural features exhibited by ungulates; these include habitat selection (influencing visibility), differential distribution on sex/age groups, daily activity patterns and hiding behaviour of neonates. Knowledge and exploitation of these behaviours will also facilitate capture and marking efforts.

8.1.1 Previous Studies of Bushbuck and Duiker Spatial and Social Organisation

Compared to the more readily observable plains antelope, there have been comparatively few studies on the spatial and social organisation of the Tragelaphines, primarily because of the difficulties in observing these species in their natural habitats (Leuthold 1974, 1979; Waser 1975a; Anderson 1978; Allen-Rowlandson 1980; Owen-Smith 1984). Nevertheless, the bushbuck has probably received more attention than other Tragelaphus spp. and although earlier accounts were somewhat general, anecdotal or speculative (Shaw 1947; Jackson 1955; Verheyen 1955; Bainbridge 1973), several detailed studies on spatial and social interactions have been completed during the last decade or so (e.g. Allsopp 1970, 1978; Elder and Elder 1970; Jacobsen 1974; Waser 1975a, 1975b; Odendaal and

Bigalke 1979a; Okiria 1980). While the majority of these detailed studies indicate that the bushbuck is primarily a solitary species, there is a lack of agreement concerning the interpretation of spatial relationships and social interactions exhibited by this antelope; these aspects will not be detailed here as they are reviewed and considered in some detail below (see section 8.4).

Much less attention has been given to the social behaviour of duiker, and although Sikes (1958) and Hopkins (1966) recorded some behavioural observations of captive animals, only Dunbar and Dunbar (1979) have studied a wild population. Their study was conducted in Ethiopia for a period of less than six months and Dunbar and Dunbar (1979) concluded from sightings of known animals that individuals occupied ranges that overlapped only to a limited extent with the ranges of other individuals of the same sex. Scent marking and agonistic encounters indicated that males defended their territories against neighbouring males, while both sexes were most frequently seen alone; 86% of all groups and 75% of all animals seen consisted of solitary duiker (Dunbar and Dunbar 1979).

8.2 METHODS

The techniques used to capture, mark and monitor marked animals have been detailed in Chapter Seven and Appendix D. Data analysis was similar to that used in habitat utilization assessments in that all sightings of marked and unmarked animals and bearings obtained from radio tracking were plotted on individual 1:12 000 maps of the Intensive Study areas. Home ranges were calculated by connecting all the outermost points and measuring the resultant convex polygon with a digital planimeter. Separate home ranges were plotted and calculated for sighting and radio tracking data and a composite or "total" home range was prepared by superimposing all the localities obtained by both methods for any one individual. Unless otherwise specified, home ranges refer to those determined from resighting and telemetry data.

Area-observation curves (Odum and Kuenzler 1955 cited in Bowen 1982) were constructed to assess sampling adequacy in the evaluation of home range size (also see Allen-Rowlandson 1980; Laundre and Keller 1984).

Because the minimum convex polygon method (Mohr 1947) or periphery method (Leuthold and Leuthold 1978; B. Leuthold 1979; Leuthold 1979) of determining home range size does not illustrate any spatial differences in range utilization, the geometric, two dimensional (x, y co-ordinates) mean of all locations was calculated and considered as the centre of home range activity (Hayne 1949; Murray 1982).

Assessments of individual movements were based on radio tracking data (simultaneous bearings) where individual animals were sequentially relocated at given time intervals (the sequential method of Laundre and Keller 1984). Distances travelled were measured as the linear distances between successive locations. Summaries of male movements excluded those of subadult males because of the potential influences of dispersal (see below) but female movements included subadults as several of these were sexually and socially mature.

In addition to locality records, the time and date of the observation or location were also noted, and all sightings were accompanied with records of group size and structure, associations with known individuals and the immediate activity of the observed subject. Activity categories included lying, standing, walking, running, feeding and other (courtship and aggressive behaviour). Bushbuck activity patterns were determined solely from the marked population, but inadequate sightings of marked duiker necessitated the inclusion of unmarked animals.

All solitary animals were treated as groups and animals within 20 m of each other were considered to be in the same group provided that their activities were generally co-ordinated (e.g. in flight). Highly skewed group size distributions indicated that typical group size (T.G.S.),

which expresses the size of the group in which the average animal finds itself (Jarman 1974), would be more biologically meaningful than mean group size (M.G.S.). However, M.G.S. values favour comparisons between different sets of data (Leuthold and Leuthold 1975b); consequently both mean and typical group sizes were calculated. Similarly, the proportion of groups of differing composition were calculated to illustrate actual grouping patterns, but the proportions of animals occurring in groups of certain sizes and composition were also determined as these proportions are more meaningful at the population level (Leuthold 1979). Group stability was examined by calculating indices of association between known (collared) individuals using the formula:

$$a = 2N/n_1 + n_2$$

where a = index of association, n_1 and n_2 = the numbers of sightings of two individuals during the time in which their periods of observation overlapped and N = the number of times they were seen together (Schaller 1972; B. Leuthold 1979; Leuthold 1979; Bearder and Martin 1980). An index of 0,49 or more was considered as indicating a close relationship between the animals concerned.

8.3. RESULTS

8.3.1 Spatial Organisation

8.3.1.1 Bushbuck

8.3.1.1.1 Home range size

Adult male home range sizes determined from animals with 10 to 20 locations (sightings and radio tracking) were significantly smaller than those based on individuals with more than 20 locations ($t = 2,49$; d.f. = 21; $p < 0,05$). Similar comparisons could not be made between adult females and all subadults due to inadequate sample sizes, but all

animals with less than 20 locations were excluded from all other analyses, with the exception of seasonal comparison when the minimum number of locations required for inclusion was 10. Data from 38 of the 74 marked bushbuck (51,4%) including 18 adult and 3 subadult males, and 11 adult and 6 subadult females, were therefore used to determine mean home range sizes (Table 8.1). Distinction was also made between home range sizes determined from sightings and from radio tracking, and although the only significant difference in mean range sizes computed from these two methods occurred with data from adult females, mean range sizes determined from radio tracking were consistently larger than those obtained from field observations (Table 8.1). Area-observation (AO) curves were constructed to evaluate sampling adequacy in individual home range size determination, and although asymptotes were obtained from several bushbuck after 20 to 30 locations, these were not always evident in the two most frequently monitored individuals from each sex and age class (Table 8.2). These results indicated that the intensity of

TABLE 8.1 Bushbuck mean home range sizes (ha) determined from field sightings, radio tracking and both of these methods.

		Sightings	Radio Tracked	t value(p)	Overall
Adult males	n	18	13		18
	$\bar{x}$	84,28	123,49	1,84	128,58
	S.D.	53,77	64,64	(n.s.)	69,84
Subadult Males	n	3	2		3
	$\bar{x}$	47,83	141,15	N/A	118,27
	S.D.	42,29	-		72,16
Adult Females	n	9	7		11
	$\bar{x}$	23,49	60,41	3,19	56,51
	S.D.	18,71	27,51	(p<0,01)	30,92
Subadult Females	n	6	6		6
	$\bar{x}$	41,67	74,97	1,69	90,12
	S.D.	31,36	36,54	(n.s.)	29,79

TABLE 8.2 A summary of the relationship between the number of locations and the proportions of the area of the "final" home range mapped for the eight most frequently monitored bushbuck at Weza.

Sex and Age Class	Total No. of locations	Area of 'final' home range (ha)	No. of locations that constituted 70%, 90% & 100% of the 'final' home range		
			70%	90%	100%
Adult Male No. 7	252	260,0	139	227	227
Adult Male No. 28	206	234,6	115	173	173
Subadult Male No. 67	105	162,6	78	78	105
Subadult Male No. 59	126	157,2	99	111	122
Adult Female No. 34	244	102,1	92	115	244
Adult Female No. 36	102	52,7	61	72	102
Subadult Female No. 21	210	110,4	151	159	159
Subadult Female No. 66	186	75,4	126	169	186

sampling was inadequate for the reliable determination of home range sizes. To examine this aspect further, frequency distributions of home range sizes were plotted for two levels of sampling (Table 8.3). From these distributions it appeared that male ranges were generally larger when based on samples of 50 or more locations, but that female range sizes were generally less affected by sample size. Correlations between individual home range size and a) the number of locations and b) the length of the monitoring period confirmed these trends. Adult male range sizes were positively correlated with both frequency of locations and duration of monitoring period whether ranges were based on resighting data, radio tracking positions or a combination of these two methods (Table 8.4). In contrast, the relationships between range size and both location frequency and duration of monitoring was significant only when female ranges were determined from visual contacts (Table 8.4). Insufficient data precluded similar analyses for subadult

TABLE 8.3 Frequency distribution of individual bushbuck home range sizes in relation to sampling intensity.

Sex and Age Class	Method of Monitoring	Frequency Class of recorded Locations	Home Range Size Class (ha)					Total No. of Individ.
			0-49	50-99	100-149	150-199	200-249	
Adult Male	Sightings (S)	20-49	6	2	5	-	-	13
		50+	1	1	2	1	-	5
	R/Tracking (R.T.)	20-49	2	2	1	2	-	7
		50+	-	2	1	1	2	6
	Combined (S + R.T.)	20-49	2	3	3	-	-	8
		50+	-	2	2	2	4	10
Subadult Male	Sightings (S)	20-49	1	1	-	-	-	2
		50+	-	1	-	-	-	1
	R/Tracking (R.T.)	20-49	-	-	1	-	-	1
		50+	-	-	1	-	-	1
	Combined (S + R.T.)	20-49	1	-	-	-	-	1
		50+	-	-	-	2	-	2
Adult Female	Sightings (S)	20-49	5	-	-	-	-	5
		50+	3	1	-	-	-	4
	R/Tracking (R.T.)	20-49	3	1	-	-	-	4
		50+	-	3	-	-	-	3
	Combined (S + R.T.)	20-49	2	2	-	-	-	4
		50+	2	4	1	-	-	7
Subadult Female	Sightings (S)	20-49	1	-	-	-	-	1
		50+	4	1	-	-	-	5
	R/Tracking (R.T.)	20-49	1	-	-	-	-	1
		50+	1	2	2	-	-	5
	Combined (S + R.T.)	50+	1	3	2	-	-	6

males, but subadult female range estimates appeared to be unaffected by the sampling procedures adopted in this study. All adult male ranges and those adult female ranges based on resighting data may therefore have been underestimated and should consequently be interpreted accordingly.

Only two of the seven most frequently monitored adults males had ranges, based on sightings, larger than those determined from radio tracking, while both subadult males had larger ranges as determined by telemetry. When these two ranges were superimposed for each individual, the extent of

TABLE 8.4 Correlation coefficients (r) of home range size with number of locations and duration of monitoring period.

	Method of Monitoring	n	$\bar{x}$ No. of locations(+S.D.)	r	$\bar{x}$ no. of months monitored (+S.D.)	r
Adult Males	Sightings	18	39,2 $\pm$ 34,4	0,526*	14,9 $\pm$ 8,7	0,566**
	Radiotracking	13	54,4 $\pm$ 36,4	0,598*	13,2 $\pm$ 8,6	0,774***
	Combined	18	78,3 $\pm$ 67,4	0,674***	14,9 $\pm$ 8,7	0,700***
Subadult Males	Sightings	3	47,7 $\pm$ 32,0	-	10,7 $\pm$ 7,0	-
	Radiotracking	2	52,0	-	15,0	-
	Combined	3	85,0 $\pm$ 53,9	-	11,3 $\pm$ 7,0	-
Adult Females	Sightings	9	49,4 $\pm$ 27,2	0,796**	17,0 $\pm$ 6,5	0,829***
	Radiotracking	7	56,3 $\pm$ 43,3	0,706	13,1 $\pm$ 7,9	0,451
	Combined	11	78,6 $\pm$ 67,2	0,579	15,5 $\pm$ 6,7	0,399
Subadult Females	Sightings	6	70,7 $\pm$ 29,5	0,235	24,8 $\pm$ 7,7	0,407
	Radiotracking	6	79,2 $\pm$ 32,1	0,595	16,5 $\pm$ 8,5	0,481
	Combined	6	149,8 $\pm$ 54,8	0,086	24,8 $\pm$ 7,7	0,019

* $p < 0,05$; ** $p < 0,02$; *** $p < 0,01$.

overlap, expressed as a percentage of the total (or combined) home range varied from 19,1% to 69,6% (Fig. 8.1). Neither of the home ranges determined from sightings or radio tracking fell entirely within the boundaries of the largest range; consequently these superimposed areas invariably resulted in an increase to the total home range size (Fig. 8.1). Ranges based on radio tracking data reflected a greater proportion of diurnal movements while sightings were largely, but not exclusively, based on nocturnal positions. Individual female ranges showed less variation in overlap when sighting and radio tracking data were superimposed (33,0% - 57,9%), and two subadult female ranges determined from sightings or radio tracking were completely encompassed by ranges calculated from the alternative method (Fig. 8.2). Only two ranges based on sightings were larger than those determined by radio tracking (Fig. 8.2).

Mean home range sizes of adult male bushbuck were consistently larger than those of adult females (Table 8.1) whether ranges were determined from sightings ($t = 3,27$; d.f. = 25; $p < 0,01$) from radio tracking ($t = 2,44$; d.f. = 18;

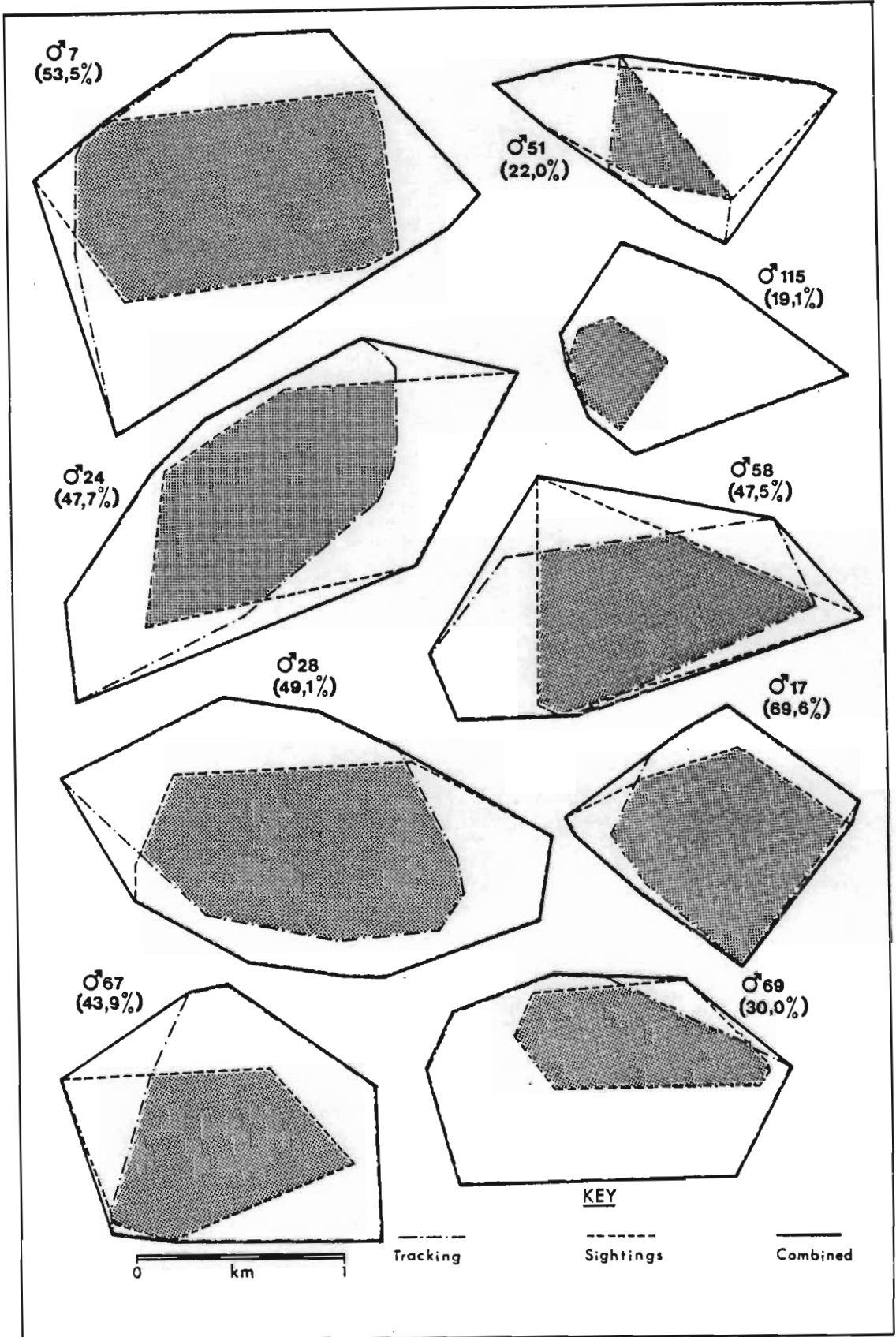


FIGURE 8.1 Male bushbuck home ranges determined from field sightings, radio tracking and from both methods. The extent of home range overlap is expressed as a % of the total range. Each range was determined from a minimum of 20 locations while the total range was based on a minimum of 70 positions. (With the exceptions of subadult males Nos.67 and 69, all males were adult).

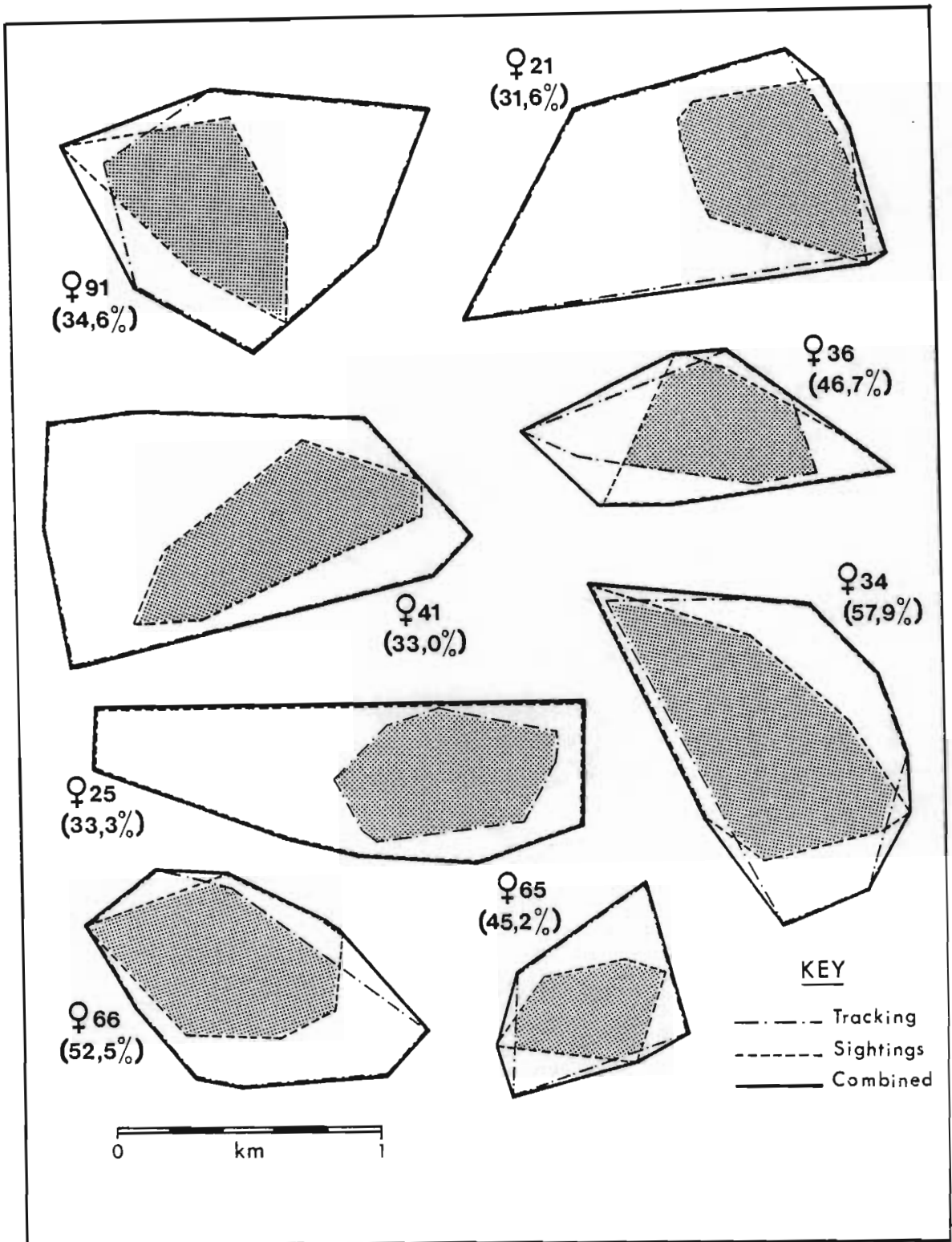


FIGURE 8.2 Female bushbuck home ranges determined from field sightings, radio tracking and from both methods. The extent of home range overlap is expressed as a % of the total range. Each range was determined from a minimum of 20 locations while the total range was based on a minimum of 100 positions. (Numbers 34, 36 and 91 were adults, the remainder were subadult females).

$p < 0,05$) or from a combination of both these methods ($t = 3,22$; d.f. = 27; $p < 0,01$). Subadult females had significantly larger ranges than adult females ($t = 2,17$; d.f. = 15; $p < 0,05$) when mean range sizes determined from combined sighting and radio tracking data were compared. All other sex and age differences in mean range size (calculated from comparable data) were not significant. Male ranges showed considerable overlap with those of other subadult and adult males (Figs. 8.3 - 8.5) as well as with those of females of all ages (Fig. 8.6 and 8.7) within the intensive study area. Four other males ranges (three adults, one subadult) and three female ranges (two adults, one subadult), all of which were determined from a minimum of 20 locations, extended into the centre of the study area but have been omitted from these figures for the sake of clarity.

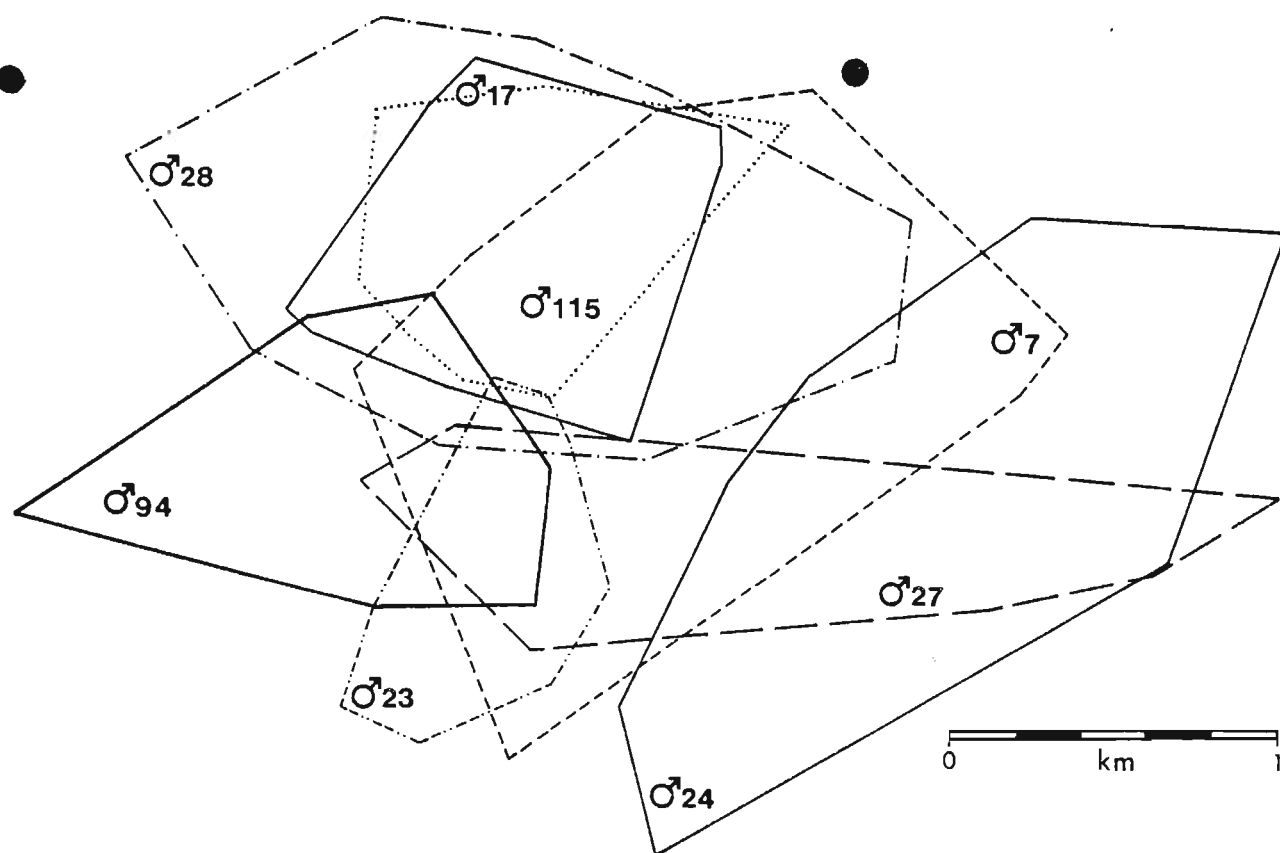


FIGURE 8.3 Home ranges of eight adult male bushbuck each located on a minimum of 20 occasions. (Closed circles indicate known reference points to facilitate comparisons with Figs. 8.4 to 8.7).

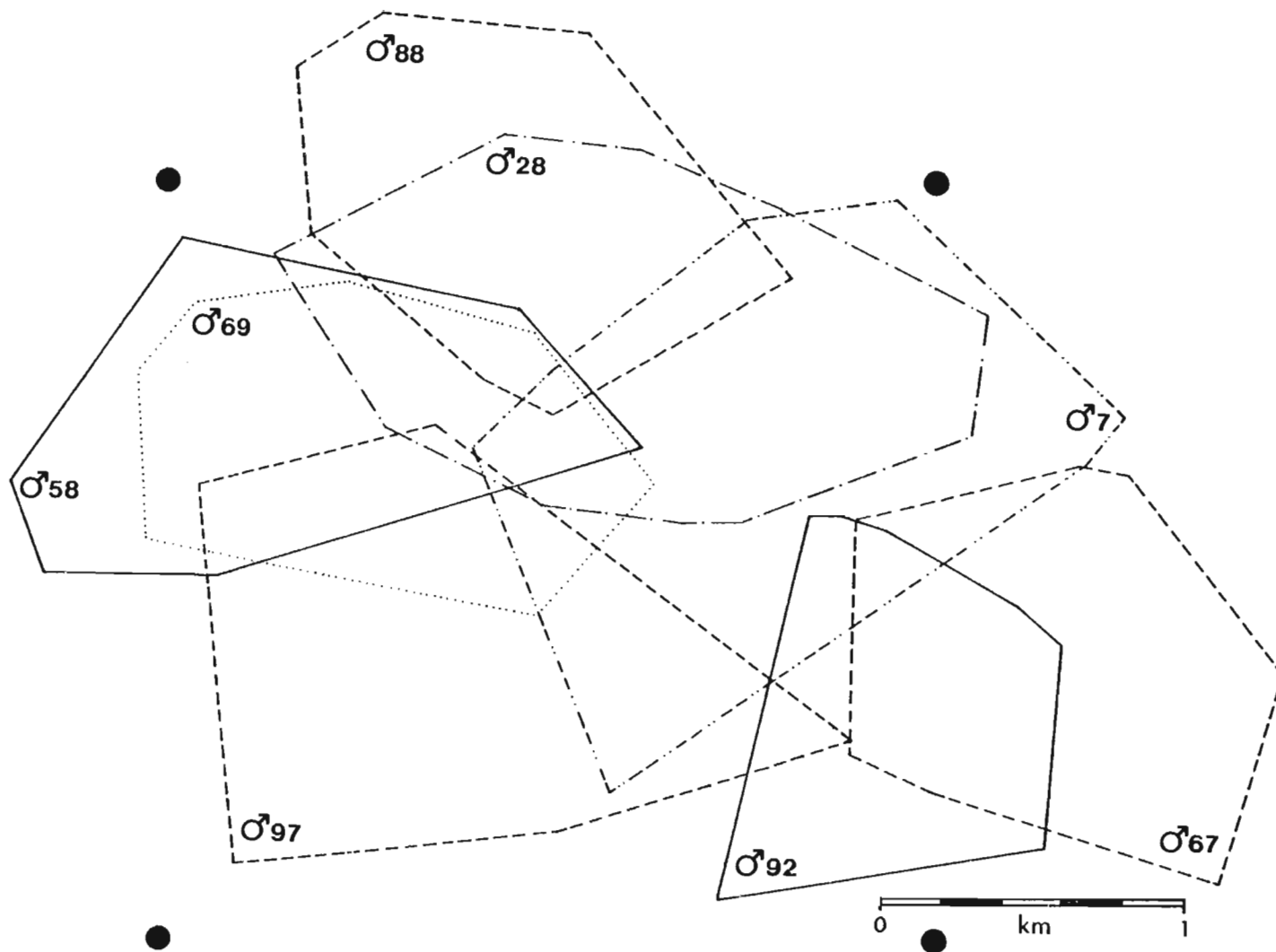


FIGURE 8.4 Home ranges of six adult male and two subadult male (Nos. 67 and 69) bushbuck each located on a minimum of 20 occasions. (Closed circles indicate known reference points for comparisons with Fig. 8.3 and Figs. 8.5 to 8.7; ranges of bushbuck 7 and 28 are duplicated from Fig. 8.3 to facilitate orientation).

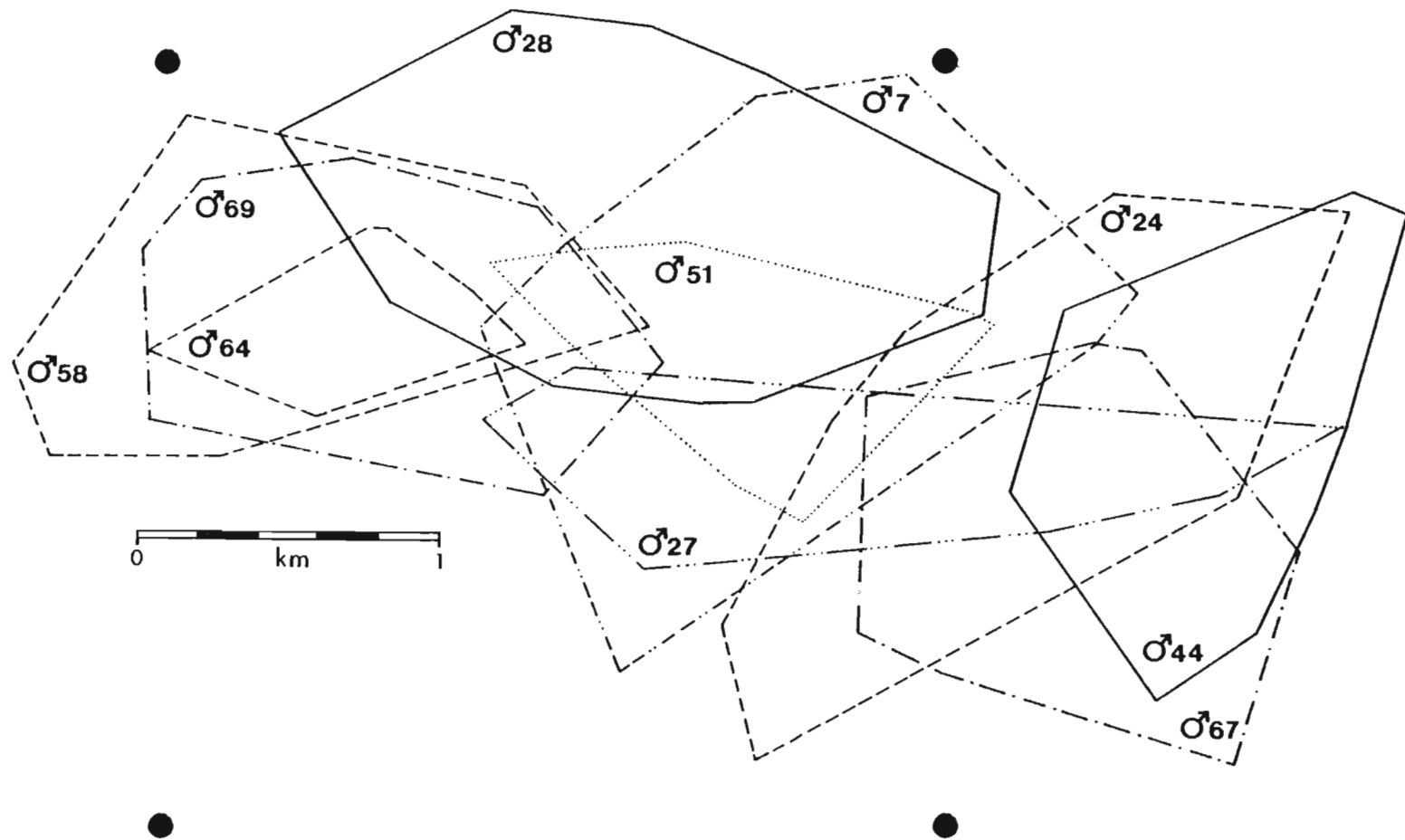


FIGURE 8.5 Home ranges of eight adult male and two subadult male (Nos. 67 and 69) bushbuck each located on a minimum of 20 occasions. (Closed circles indicate known reference points for comparisons with Figs. 8.3, 8.4, 8.6 and 8.7; ranges of bushbuck 7, 28, 58, 67 and 69 are duplicated from Fig. 8.4 to facilitate orientation).

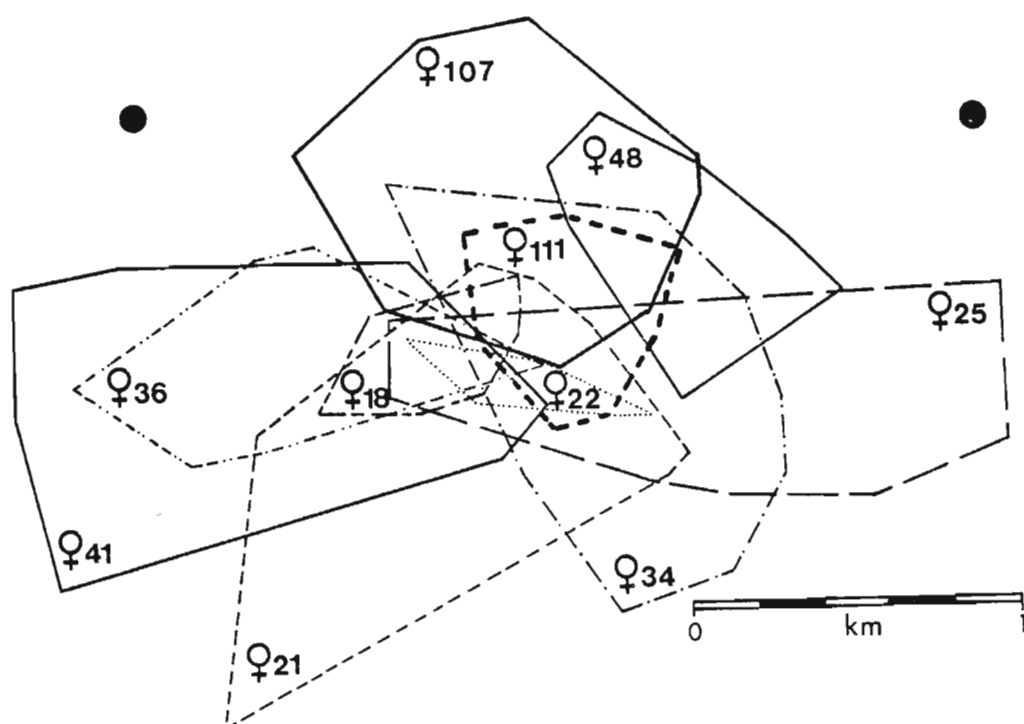


FIGURE 8.6 Home ranges of six adult female and four subadult female (Nos. 21, 25, 41 and 107) bushbuck each located on a minimum of 20 occasions. (Closed circles indicate known reference points for comparisons with Figs. 8.3 to 8.5 and 8.7).

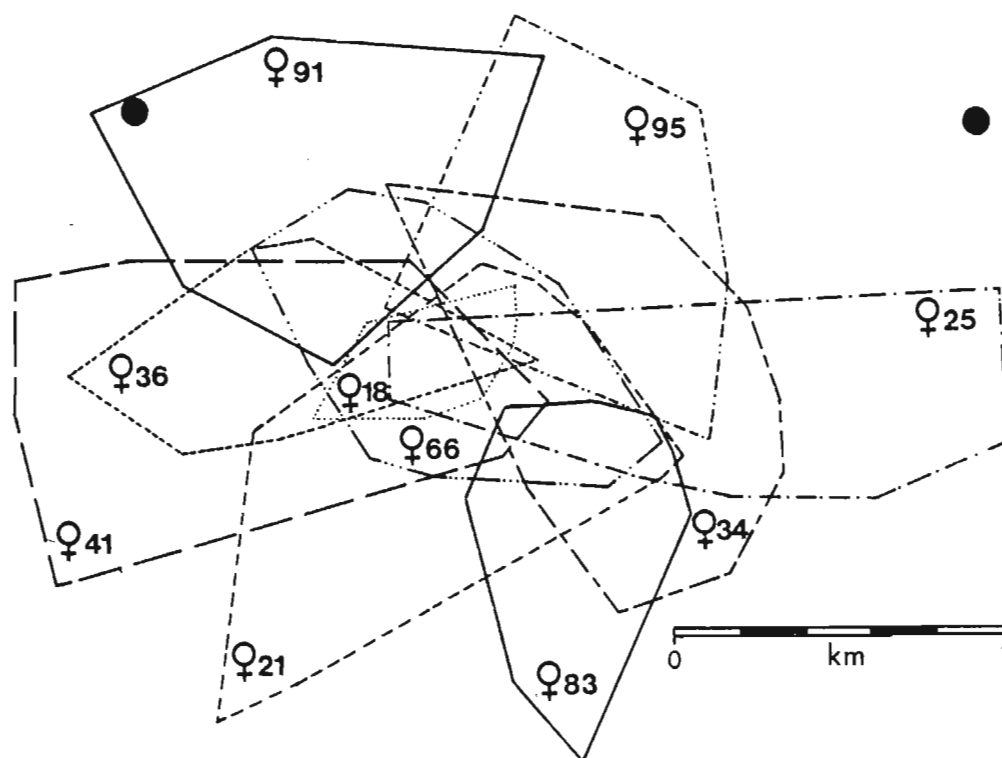


FIGURE 8.7 Home ranges of six adult female and four subadult female (Nos.21, 25, 41 and 66) bushbuck each located on a minimum of 20 occasions. (Closed circles indicate known reference points for comparisons with Figs. 8.3 to 8.6; ranges of bushbuck 18, 25 and 45 are duplicated from Fig. 8.6 to facilitate orientation).

In general, mean home range sizes varied during the course of the year and were largest during the spring and summer months, irrespective of the method of data collection (Table 8.5). Statistical tests of significance were not performed on these data as individual sample sizes varied considerably, while the overall pattern of samplings was greatest in winter and spring (Table 8.6). However, since earlier results indicated that range size increased with sampling intensity under certain conditions, the generally smaller autumn and winter ranges probably reflect a genuine decrease in movements during these periods. Of the 20 most frequently monitored bushbuck in the intensive study area, 75% had larger home ranges in spring or summer compared to autumn and winter when seasonal ranges were determined from sightings, and 85% had larger spring or summer ranges when these were constructed from both radio tracking data and from

TABLE 8.5 Seasonal and overall home range sizes of bushbuck determined from field sightings, radio tracking and both methods.

Method of data collection & Season	Mean home range size (ha) + S.D. (n)			
	MALES		FEMALES	
	ADULTS	SUBADULTS	ADULTS	SUBADULTS
Sightings (n ≥ 10)				
Winter	60,4+42,4 (8)	17,2+16,5 (3)	12,5+5,9 (7)	22,3+24,3 (5)
Spring	57,7+48,0 (7)	21,8 (2)	19,7+17,4 (6)	28,0+20,2 (6)
Summer	51,0+49,5 (4)	10,1 (1)	8,6 (2)	7,9+3,5 (3)
Autumn	25,2+13,8 (6)	12,8 (1)	9,4 + 5,9 (3)	26,6+12,6 (3)
Overall	84,3+53,8 (18)	47,8+42,3 (3)	23,5+18,7 (9)	41,7+31,4 (6)
Radiotracking (n ≥ 10)				
Winter	69,7+37,2 (8)	N/A	50,0 (1)	37,4+22,1 (5)
Spring	100,9+43,7 (6)	67,3 (2)	35,5+20,0 (5)	31,5+14,6 (5)
Summer	93,1+52,5 (7)	95,9 (2)	39,9+27,3 (6)	53,9+41,7 (5)
Autumn	54,7+40,3 (5)	N/A	15,7 (2)	25,9+ 9,2 (4)
Overall	123,5+64,6 (13)	141,2 (2)	60,4+27,5 (7)	74,9+36,5 (6)
Combined (n ≥ 20)				
Winter	72,2+49,1 (12)	29,4+14,0 (3)	36,2+21,3 (6)	49,5+22,8 (5)
Spring	88,7+64,6 (12)	75,5 (2)	39,0+18,0 (6)	43,6+17,4 (5)
Summer	87,9+48,1 (10)	98,2 (2)	48,6+24,2 (6)	55,6+40,2 (5)
Autumn	54,8+40,1 (10)	30,0 (2)	19,9+ 8,7 (4)	33,5+18,2 (5)
Overall	128,6+69,8 (18)	118,3+72,2(3)	56,5+30,9(11)	90,1+29,8 (6)

TABLE 8.6 Seasonal distribution of bushbuck sightings and positions determined from radio tracking; each bushbuck was located on a minimum of 10 occasions.

Method of data collection	Winter	Spring	Summer	Autumn	Total
Sightings	629 36,6%	531 30,1%	228 13,3%	331 19,3%	1 719
Radiotracking	416 24,8%	506 30,1%	477 28,4%	281 16,7%	1 680
Combined	1 958 30,8%	1 048 30,5%	708 20,6%	619 18,0%	3 433

a combination of sightings and telemetry. This trend is similarly reflected in the seasonal variations in individual home range sizes illustrated in Figs. 8.8. and 8.9 (note the exception of female No. 21 in Fig. 6.8; see below). These figures also demonstrate that bushbuck did not make exclusive use of any portion of the total home range during any one season. In the absence of any distinct shifts in seasonal range, animals in spring and summer presumably used the autumn and winter portions of their range less frequently and extended their movements at this time (Figs. 8.8. and 8.9).

Bushbuck also exhibited individual variations in the sizes of their home ranges between years with ranges often larger in 1984 than in 1983, which in turn were usually larger than those of the same animals in 1982. This trend was not consistent however, and home range sizes may clearly have been influenced by differing levels of sampling during the study period. Only one animal, a subadult male, showed a disjunction of ranges used in 1982 and in 1983/1984 (see below). All other animals showed considerable overlap in the ranges occupied during different years, irrespective of whether these ranges increased or decreased in size with time. This pattern is exemplified by bushbuck No. 21 which

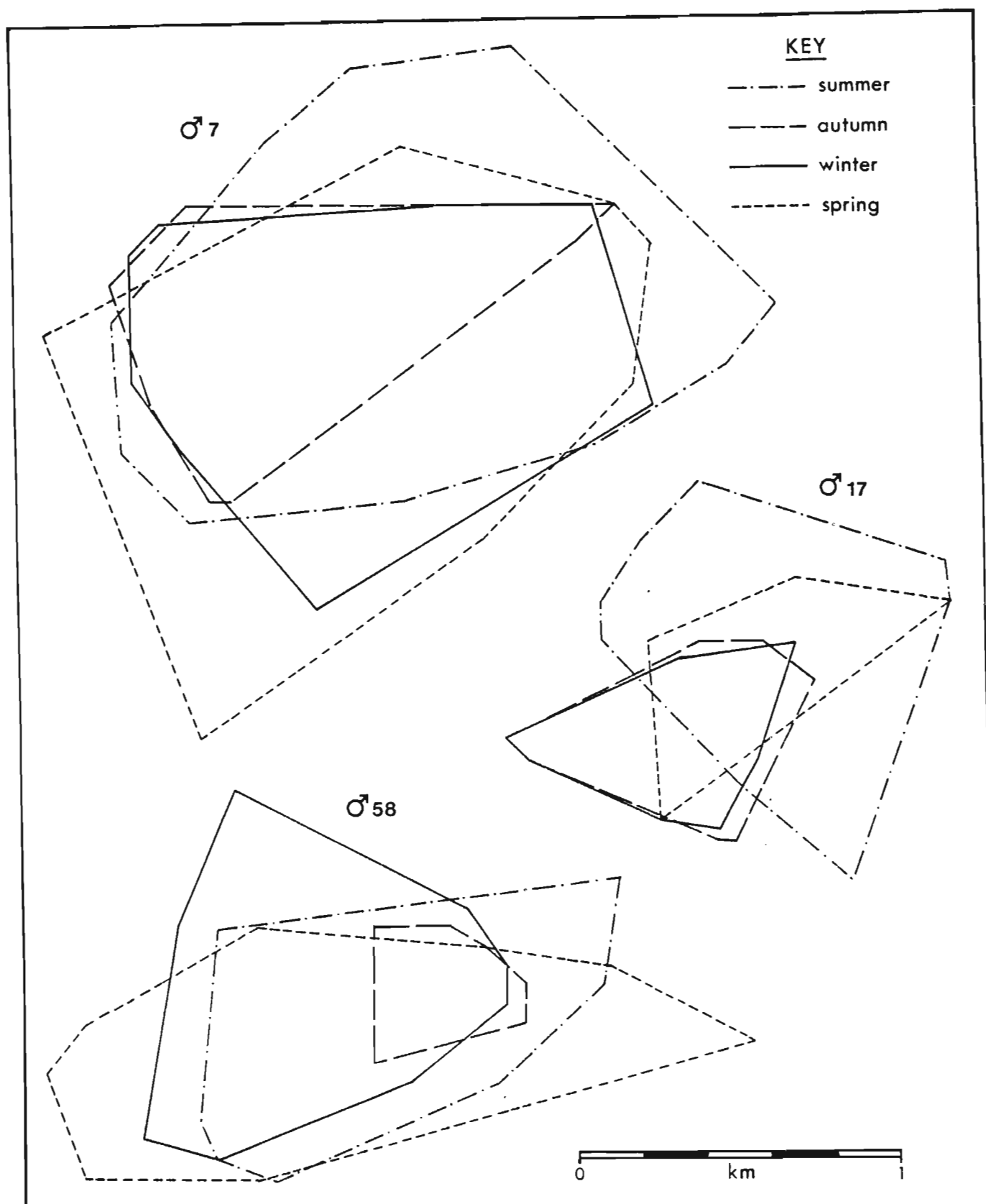


FIGURE 8.8 Seasonal variations in recorded home ranges of male bushbuck at Weza. (Each animal was located on a minimum of 10 occasions each season and on a minimum of 100 occasions overall; male No. 69 (overleaf) was a subadult, all others were adult males).

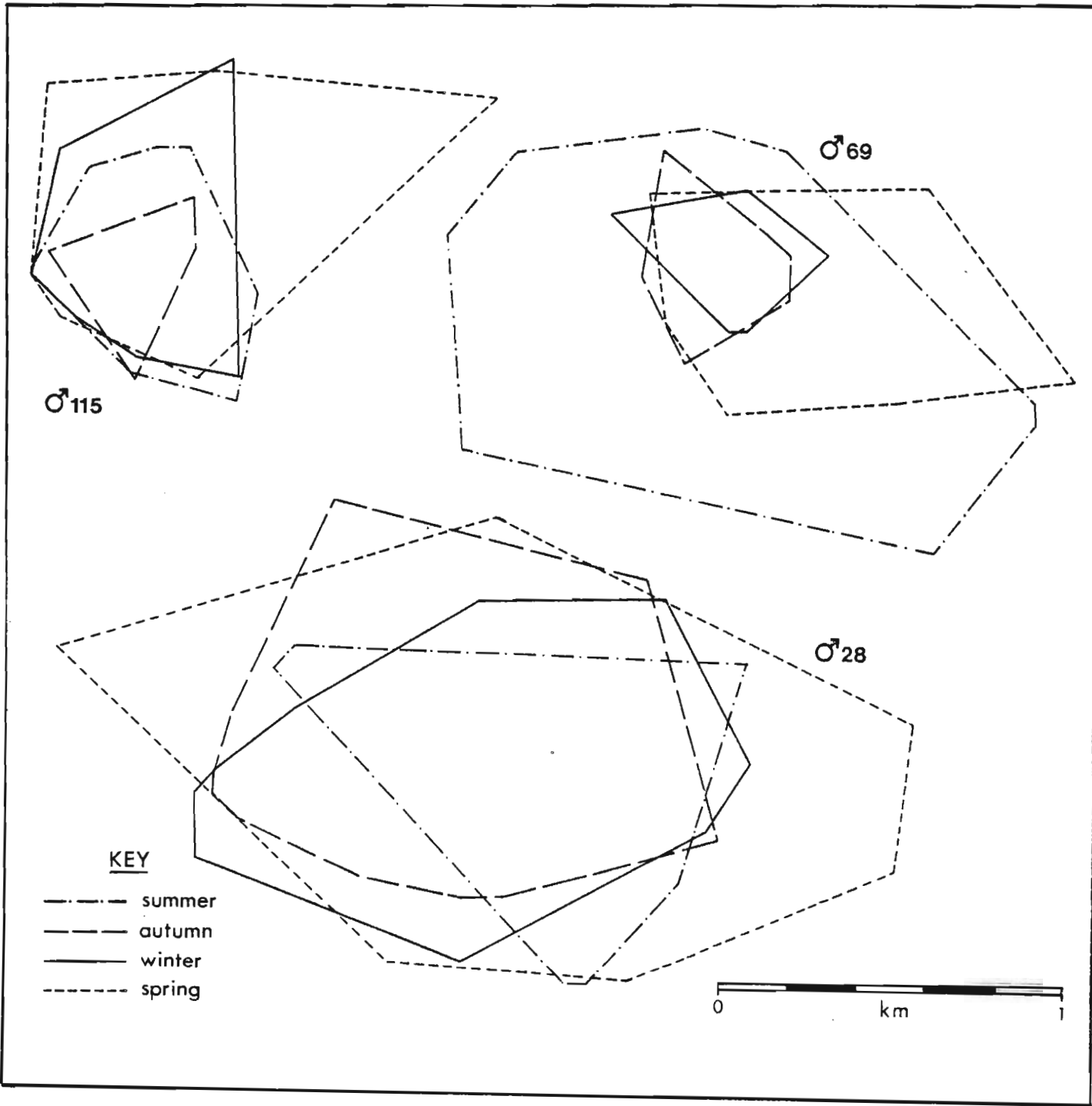


FIGURE 8.8 continued.

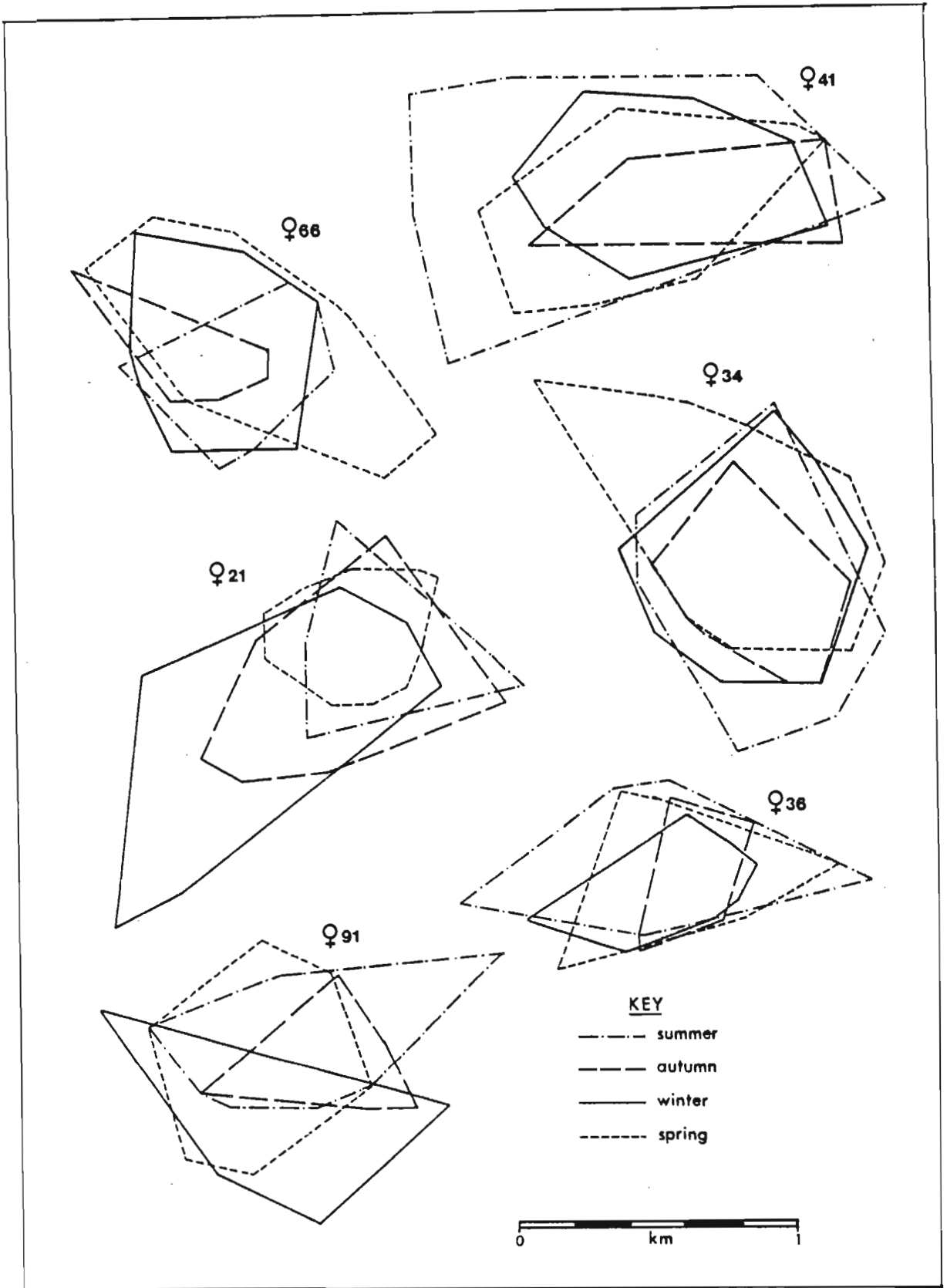


FIGURE 8.9 Seasonal variations in recorded home ranges of female bushbuck at Weza. (Each animal was located on a minimum of 10 occasions each season and on a minimum of 100 occasions overall; female Nos. 21, 41 and 66 were subadults, all others were adult females).

as a subadult, occupied the same range as her marked mother from April 1982 to March 1983 (Fig. 8.10). Although the mother was killed by dogs in December 1982, bushbuck No. 21 continued to occupy the same area the following year (when she was commonly associated with another young female; No. 65, see below) but exhibited more extensive movements at this time. A marked increase in her range was evident between April and July 1984 (Fig. 8.10) although movements were often confined to regions furthest away from the area she occupied as a subadult (this earlier range included dense thickets and oaks, and had a relatively high density of resident male and female bushbuck; see Figs. 8.3 to 8.7). The reason for this range extension became obvious in late April 1984 when bushbuck No. 21 was seen with a neonate at heel. Both mother and infant were seen regularly from June onwards, and from August to October 1984, when field work was terminated, the movements of both animals were confined to the mother's original range, which had therefore been occupied by three

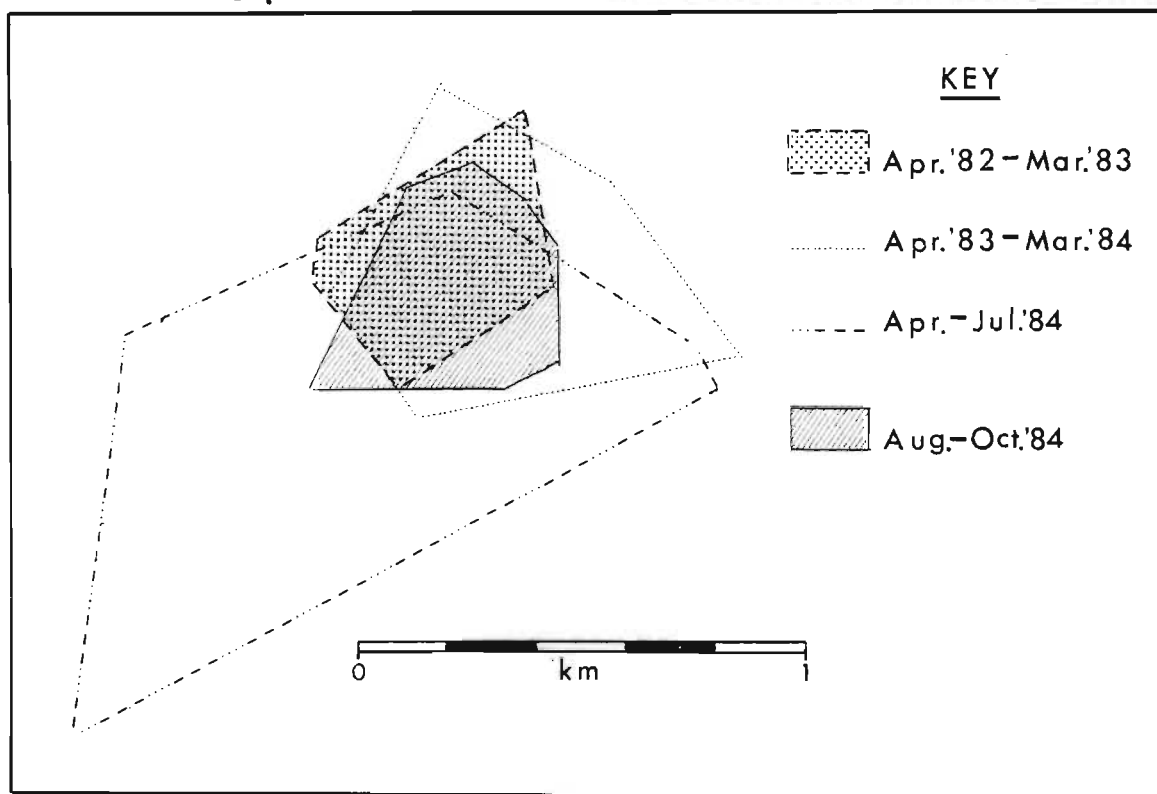


FIGURE 8.10 Annual variations in the home range size and configuration of female bushbuck 21. This animal was a subadult from April 1982 to March 1983 (stippled range) and was first seen with her infant in April 1984; from August onwards her movements were confined to the range shaded by hatching (see text for details).

successive generations. Although several other females also exhibited similar departures from their area just prior to (or after) parturition, such behaviour was not evident in all females when births were imminent, and at least three bushbuck showed no overt signs of range extension while they were nursing and rearing their young in this vicinity.

Although the range occupied by bushbuck No. 21 between April and July 1984 was considerably larger than that occupied prior to parturition as well as her subsequent range on returning to her former area, the daily movements of this animal were no greater when she had a neonate, and were often considerably less (distances of approximately 300 m were recorded at this time). Because home range sizes do not yield information on the frequency or intensity of range use, they should therefore be interpreted with caution. Mapping the intensity with which the most frequently monitored adult male and adult female bushbuck utilized their ranges (these animals were located on 252 and 244 occasions respectively) revealed the presence of frequently used core areas, while the periphery of each individual home range was utilized to a much lesser extent (Fig. 8.11). It was impractical to present similar maps for all of the bushbuck monitored in this study, and instead utilization data have been summarised as centres of activity, which were determined for all marked bushbuck within the intensive study area that were located on at least 10 occasions during any one season. Although males appeared to be more dispersed than females (Figs. 8.12 and 8.13 respectively), more males were monitored in this area. Several males had centres of activity within a few hundred metres of each other (Fig. 8.12) in the area where females activity centres were also most clustered (Fig. 8.13). Although males were generally more dispersed during the day than at night (Figs. 8.14 and 8.15 respectively), this trend was less apparent in females (Figs. 8.16 and 8.17 respectively).

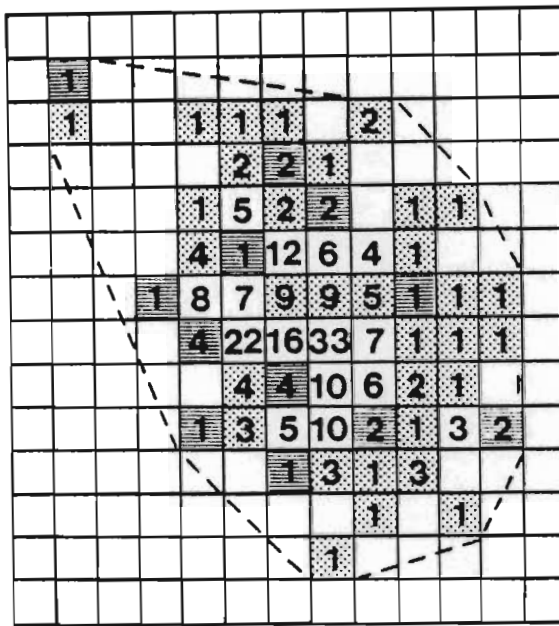
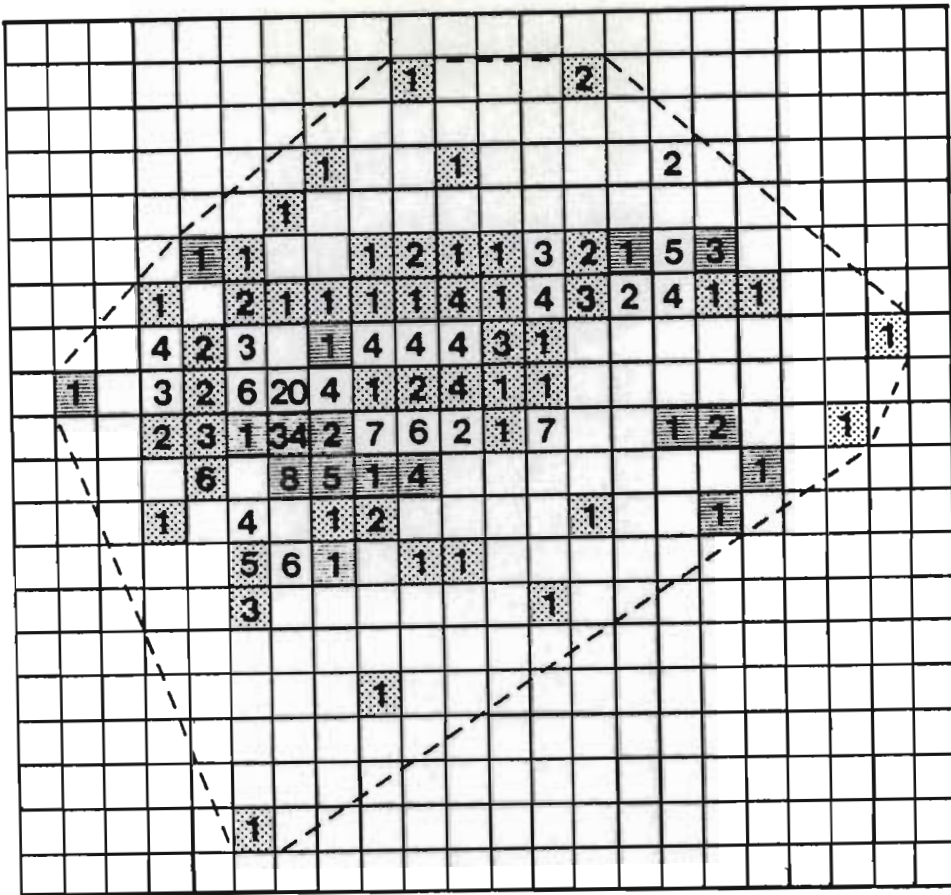


FIGURE 8.11 Frequency distribution of locations recorded for adult male bushbuck 7 (above) and adult female bushbuck 34 (left). Dashed lines delineate home range boundaries; each grid represents 120m ; horizontal lines within any grid denote the locations determined from sightings; grids with stippling denote locations determined from radio tracking and numerical values in grids with no shading indicate that locations were determined from both sightings and radio tracking.

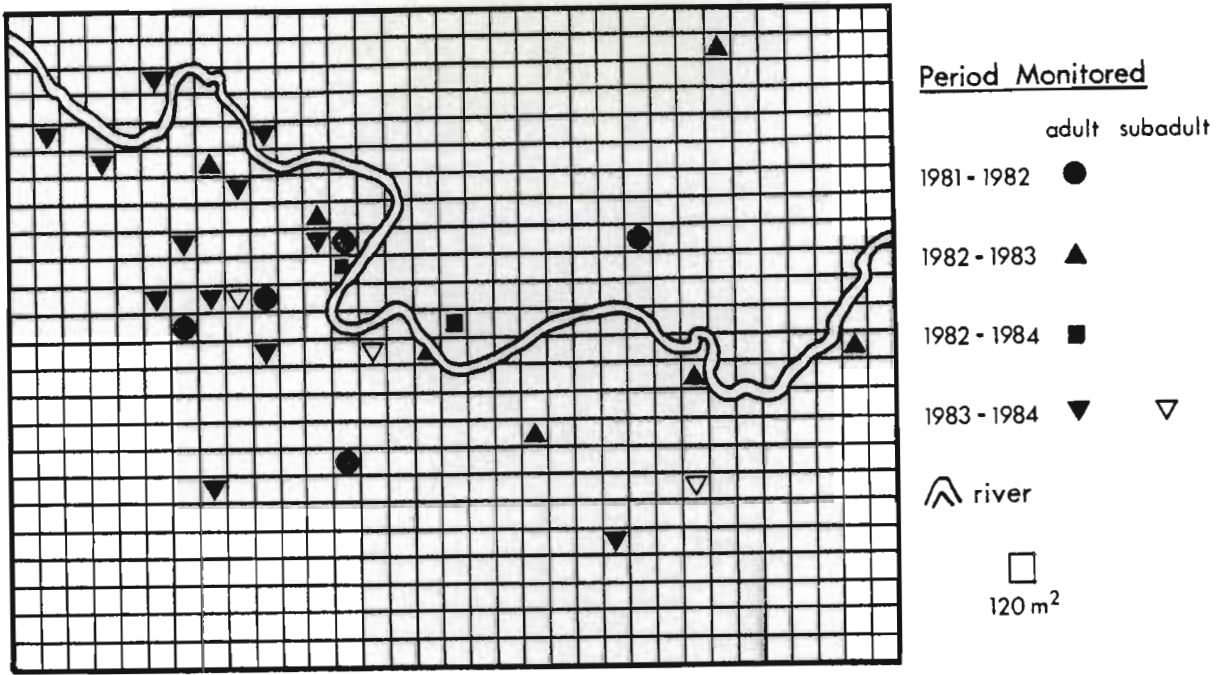


FIGURE 8.12 Distribution of centres of activity of 26 adult and 3 subadult male bushbuck within the intensive study area. (Each animal was located on a minimum of 10 occasions during any one season).

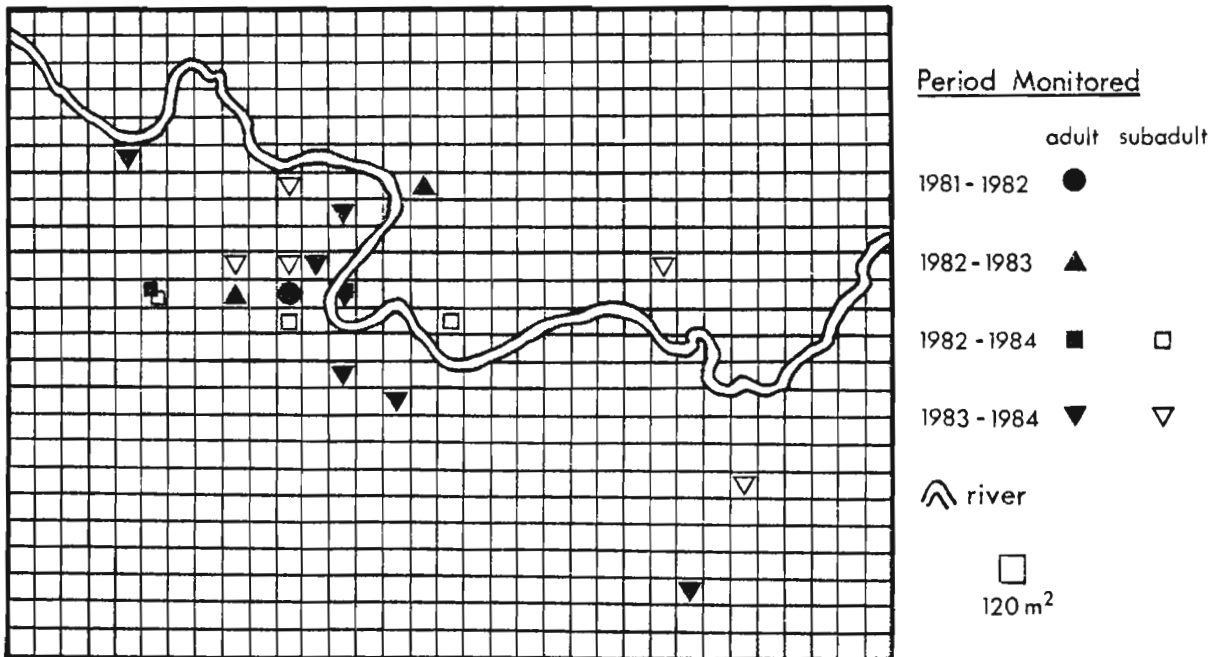


FIGURE 8.13 Distribution of centres of activity of 12 adult and 8 subadult female bushbuck within the intensive study area. (Each animal was located on a minimum of 10 occasions during any one season).

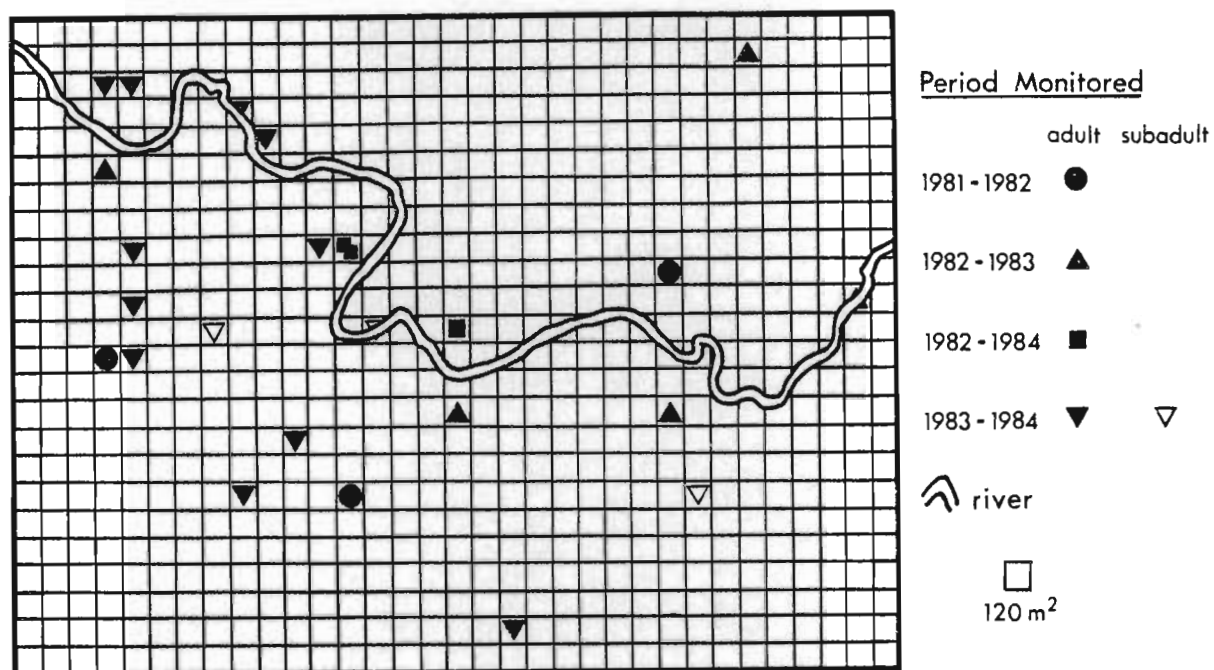


FIGURE 8.14 Distribution of diurnal centres of activity of 22 adult and 3 subadult male bushbuck within the intensive study area. (Each animal was located on a minimum of 10 occasions during any one season).

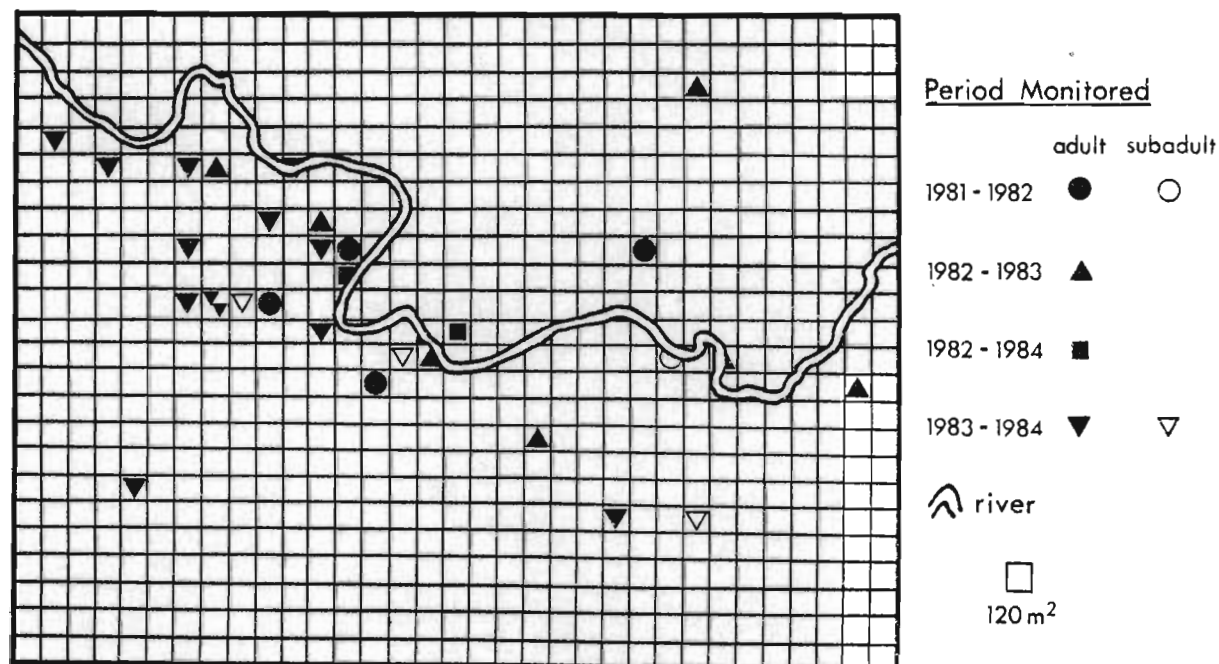


FIGURE 8.15 Distribution of nocturnal centres of activity of 26 adult and 3 subadult male bushbuck within the intensive study area. (Each animal was located on a minimum of 10 occasions during any one season).

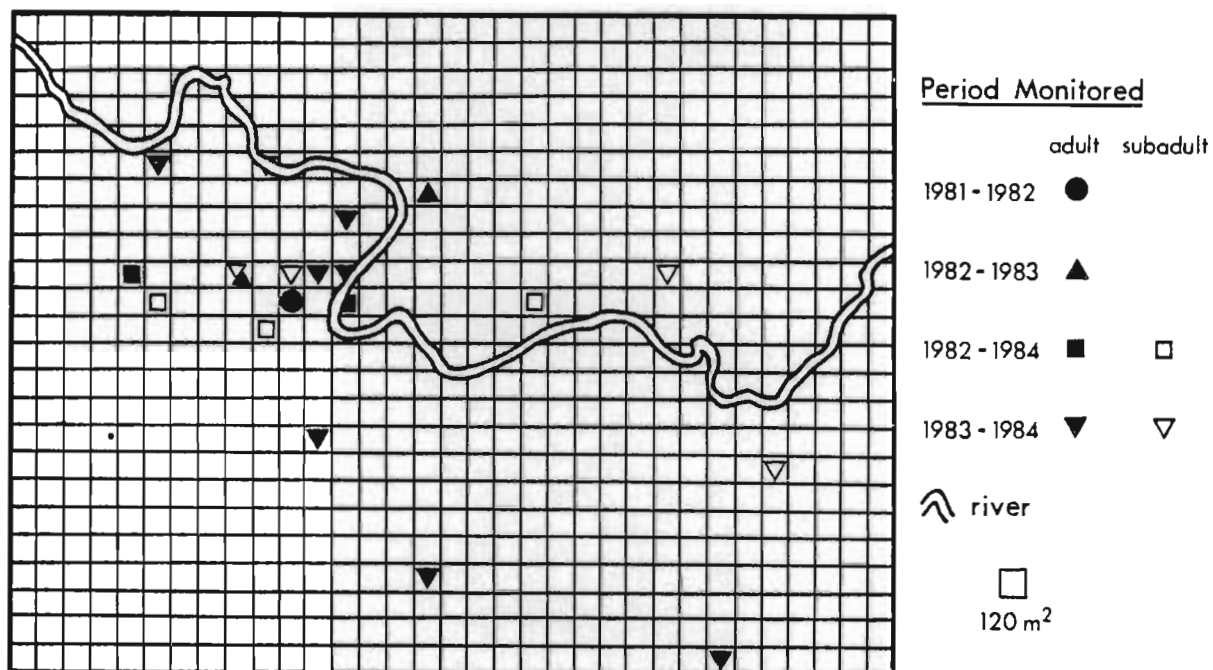


FIGURE 8.16 Distribution of diurnal centres of activity of 12 adult and 8 subadult female bushbuck within the intensive study area. (Each animal was located on a minimum of 10 occasions during any one season).

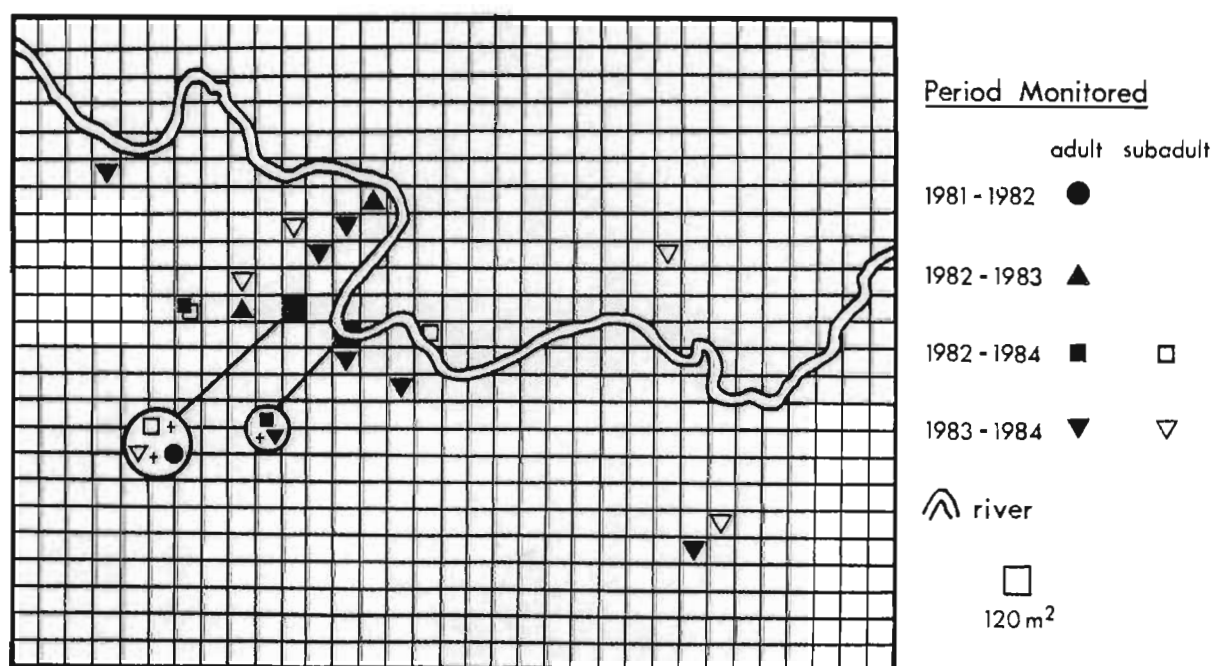


FIGURE 8.17 Distribution of nocturnal centres of activity of 12 adult and 8 subadult female bushbuck within the intensive study area. (Each animal was located on a minimum of 10 occasions during any one season).

Adult males had the greatest differences between individual day and night centres of activity, while these distances were lowest among subadult females (Table 8.7). Due to the extensive variation exhibited by individual bushbuck (Table 8.7), none of the differences between the mean distances separating day and night centres of activity were significant for any sex or age class during any season. but these were generally lowest in spring. Males showed greatest distances separating diurnal and nocturnal activity centres in summer, while females showed the greatest differences during winter (Table 8.7). Individual variation was also pronounced when distances separating seasonal centres of activity were compared on both a diurnal and nocturnal basis (Table 8.8). Nevertheless, these results indicate that distances separating centres of activity during successive seasons were less extensive for females than

TABLE 8.7 Seasonal variations in the mean distances separating the day and night centres of activity of male and female bushbuck.

		Summer	Autumn	Winter	Spring	Overall
Adult males	n	15	11	13	12	20
	$\bar{x}$	337,8	279,8	324,0	257,5	327,3
	S.D.	276,1	183,2	213,2	150,0	171,2
Subadult Males	n	2	2	3	2	3
	$\bar{x}$	375,0	129,0	132,0	210,0	128,0
	S.D.	-	-	43,27	-	33,05
Adult Females	n	8	6	8	9	12
	$\bar{x}$	225,0	233,0	300,8	178,7	239,0
	S.D.	223,4	125,5	242,2	161,1	218,9
Subadult Females	n	5	5	7	5	7
	$\bar{x}$	115,2	230,4	324,9	91,2	202,3
	S.D.	80,8	188,5	196,5	53,2	190,9

males, both at night and during the day (Table 8.8). In addition, these distances were of a similar magnitude to those separating day and night activity centres during any one season (Table 8.7).

TABLE 8.8 Variation in the distances (m) between the seasonal centres of activity determined from individual bushbuck a) at night and b) during the day. Mean values $\pm$ 1 S.E. are shown.

Sex and Age Class	Season	Summer		Autumn		Winter	
		a)	b)	a)	b)	a)	b)
Adult Males	Spring	359 $\pm$ 81	307 $\pm$ 58	333 $\pm$ 93	320 $\pm$ 78	360 $\pm$ 61	335 $\pm$ 76
	Summer	-	-	444 $\pm$ 106	276 $\pm$ 62	415 $\pm$ 60	212 $\pm$ 31
	Autumn	-	-	-	-	289 $\pm$ 67	246 $\pm$ 65
Subadult Males	Spring	543	222	189	354	132 $\pm$ 63	291
	Summer	-	-	612	363	492	330
	Autumn	-	-	-	-	132	108
Adult Females	Spring	137 $\pm$ 38	152 $\pm$ 50	159 $\pm$ 34	173 $\pm$ 61	158 $\pm$ 78	190 $\pm$ 47
	Summer	-	-	106 $\pm$ 14	145 $\pm$ 23	209 $\pm$ 92	268 $\pm$ 92
	Autumn	-	-	-	-	115 $\pm$ 37	334 $\pm$ 98
Subadult Females	Spring	127 $\pm$ 56	122 $\pm$ 27	137 $\pm$ 25	152 $\pm$ 65	201 $\pm$ 55	238 $\pm$ 34
	Summer	-	-	159 $\pm$ 84	233 $\pm$ 28	216 $\pm$ 129	268 $\pm$ 73
	Autumn	-	-	-	-	108 $\pm$ 37	152 $\pm$ 47

8.3.1.1.2 Movements and dispersal

It was not possible to monitor the actual movements of bushbuck at Weza since individual animals could not be followed, and positions of radio tracked individuals were determined by triangulation which was considered too imprecise to detect small scale movements. Instead, movements were measured as the shortest linear distance between two sets of consecutive locations over a standard period of time. Measured in this way, distances travelled

by males over a 24 hour period ($\bar{x} = 528 \text{ m} \pm 47 \text{ m S.E.}$) were significantly greater than those of females ($\bar{x} = 303 \text{ m} \pm 25 \text{ m S.E.}$) during the course of the year ($t = 4,71$; d.f. = 115; $p < 0,001$). Twenty four hour movements of males in winter ($\bar{x} = 450 \text{ m} \pm 93 \text{ m S.E.}$) were also significantly greater ($t = 2,31$; d.f. = 15; $p < 0,05$) than female movements at this time ($\bar{x} = 228 \pm 31 \text{ m S.E.}$) and again in spring ($t = 6,79$; d.f. = 40; $p < 0,001$) when males travelled an average distance of 870 m ($\pm 11 \text{ m S.E.}$) and females 286 m ($\pm 33 \text{ m S.E.}$). Males also ranged over wider distances in summer ($\bar{x} = 440 \text{ m} \pm 45 \text{ m S.E.}$) but these were not significantly greater than female movements during this season ($\bar{x} = 339 \text{ m} \pm 45 \text{ m S.E.}$). Individual movements were not recorded during autumn months. Twenty four hour movements of females therefore increased progressively from winter to summer, but differences between successive seasons were not significant. In contrast, male movements were greatest in spring, and were significantly larger than those recorded in either winter ($t = 2,89$; d.f. = 14; $p < 0,02$) or summer ($t = 3,26$; d.f. = 30; $p < 0,01$). These seasonal trends in daily movements show general agreement with seasonal changes in the sizes of individual home ranges.

Hourly movements were determined in a similar way but due to problems associated with the siting of base and mobile receiving stations, signal reception, weather influences etc. results were somewhat fragmentary and were inadequate for seasonal comparisons. Overall, the average hourly distance travelled by males ($\bar{x} = 348 \text{ m} \pm 43 \text{ m S.E.}$) was significantly greater ($t = 3,21$; d.f. = 117; $p < 0,01$) than that of females ($\bar{x} = 214 \text{ m} \pm 20 \text{ m S.E.}$).

Monitoring movements over a three hour interval proved to be a more practical proposition and such distances were recorded in all season except summer. Female distances travelled showed little seasonal variation ranging from an average of 208 m ($\pm 29 \text{ m S.E.}$) in spring to 217 m ($\pm 27 \text{ m S.E.}$) in autumn. The reverse trend was apparent in males, with shortest distances recorded in autumn ($\bar{x} = 195 \text{ m} \pm 35 \text{ m S.E.}$) and greatest linear distances during spring ($\bar{x} = 312 \text{ m} \pm 42 \text{ m S.E.}$). Although distances travelled by males were

generally greater than those of females, these differences were not significant during any season. Similarly, differences resulting from interseasonal comparisons of either males or females were generally slight, with the exception that male distances travelled in spring were significantly greater than in autumn ($t = 2,07$; $d.f. = 47$; $p < 0,05$). Consequently, data from all seasons were pooled to facilitate comparisons of rates of travel during a 24 hour period. Male movements recorded over three hour intervals were generally greatest during late afternoon and at night (Table 8.9). Female movements were relatively constant for much of the day, but increased during early morning periods when it was still dark. Male movements were generally greater than those of females irrespective of time of day (except between 3.00 a.m. and 6.00 a.m., see Table 8.9), but overall this difference was not significant. Interestingly, the average hourly distance moved by females was the same as that moved over three hours, while in males distances recorded at hourly intervals were greater (but not significantly so) than those recorded at three hour intervals. These results, together with average daily (i.e.

TABLE 8.9 Mean linear distances ($m \pm 1$ S.E.) travelled by bushbuck as determined from individual locations recorded at three-hourly intervals.

Time interval (hrs)	Males	Females
0600 - 0859	223 $\pm$ 44	185 $\pm$ 27
0900 - 1159	212 $\pm$ 37	198 $\pm$ 34
1200 - 1459	201 $\pm$ 45	204 $\pm$ 42
1500 - 1759	341 $\pm$ 42	193 $\pm$ 34
1800 - 2059	347 $\pm$ 53	189 $\pm$ 46
2100 - 2359	408 $\pm$ 131	152 $\pm$ 60
0000 - 0259	396 $\pm$ 102	281 $\pm$ 76
0300 - 0559	309 $\pm$ 159	497 $\pm$ 211
0600 - 0559	277 $\pm$ 21,0	213 $\pm$ 19

24 hour) rates of travel, indicate that both males and females used relatively small areas of their ranges quite intensively (also see Fig. 8.11), and that movements away from such areas were usually gradual rather than rapid. Alternatively, the similar magnitudes of hourly, three hourly and daily travel rates may have been due to inaccurate or insensitive methods of location. However, since natural mortalities could readily be detected from static positions long before decomposition set in, and the accuracy of both equipment and researcher was occasionally tested by an independent observer placing transmitters in the field (see Appendix D), it is unlikely that this latter explanation entirely accounted for such similarities in rates of travel.

Consecutive locations of five adult male and one adult female bushbuck monitored at three hour intervals for a 24 hour period in winter are illustrated in Fig. 8.18. Visual presentation of data in this manner not only permitted measurements of distances moved by individuals with time, but also facilitated assessments of the relationship between movements of individuals that were monitored simultaneously, and this provided a means of examining dynamic interactions (see Macdonald et al. 1980). Such distances between any of six adult males that each had ranges that overlapped with the other five individuals were examined on 125 separate occasions and were based on locations determined from simultaneous bearings obtained largely during the day. Only on four occasions (3%) were males within 120 m of each other, while distances exceeding 500 m most commonly (82%) separated these individuals at any one time. Dynamic interactions determined from visual contacts were not included in this analysis but were treated separately (see below).

Because individual movements varied considerably during any 24 hour period and also varied seasonally, it was extremely difficult to identify movements that may have been attributable to human disturbances. Bushbuck did not exhibit shifts in home range or pronounced movements even where silvicultural or exploitation activities were intense. On the contrary, one marked adult male was repeatedly flushed

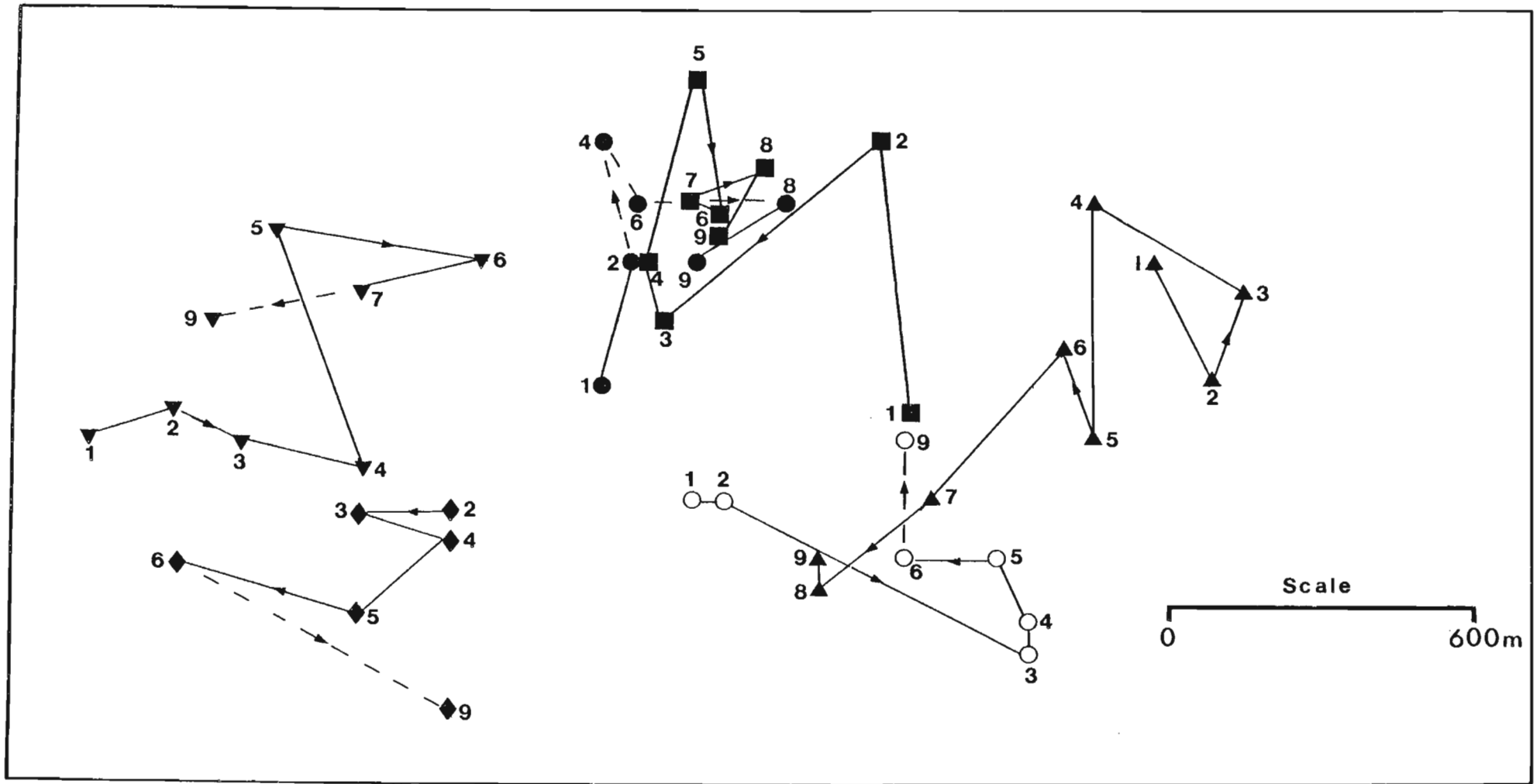


FIGURE 8.18 Twenty-four hour movements of five adult male (closed symbols) and one adult female (open circles) bushbuck recorded at three-hourly intervals in winter. (Solid lines indicate distances travelled over consecutive periods; broken lines indicate distances recorded over periods greater than three hours. Numerical values indicate positions recorded at the following times: 1=06.00hrs; 2=09.00hrs; 3=12.00hrs; 4=15.00hrs; 5=18.00hrs; 6=21.00hrs; 7=00.00hrs; 8=03.00hrs and 9=06.00hrs.

from a dense but small (0,1 ha) patch of bugweed thicket on four consecutive mornings when Forestry staff were in the process of clearfelling a pine compartment less than 100 m away. During this time chain saws were constantly being used to fell mature trees, remove lateral branches and cut the logs into prescribed lengths, while mules and labourers transported the logs to the nearest road which was less than 80 m from this thicket. Bushbuck males and females were also detected in thickets within 150 m of sites where other activities such as thinning and pruning were taking place, while four adult males and three females were frequently located (and observed) both at night and during the day in thickets and overgrown gardens less than 50 m from African staff houses. These observations indicate that bushbuck were largely unperturbed by human activities provided that suitable and adequate cover was available to them.

Three immobilized bushbuck (one subadult male, approximately 14 months old, one adult male and one adult female) were translocated while recumbent to a common release site in the centre of the intensive study area. The linear distances between capture localities and the release site were 1 200 m, 1 900 m, and 2 700 m respectively. The release site was surrounded by habitats heavily utilized by a relatively high density of bushbuck and it was presumed that this area was sufficiently far from all three capture localities to be foreign to each translocated animal. Since none of these animals had been marked previously, the precise location of their home ranges was not known. However, within 12 hours all three animals had left the release site and were travelling back in the general direction where they had been captured. Linear distances travelled from the release site after 12 hours when all three animals were detected by telemetry and observed, were 860 m, 1 520 m and 1 600 m for the subadult male, adult male and adult female respectively. During this interval, both males had moved to areas that were subsequently utilized by them; the younger male was a linear distance of 380 m from his subsequent centre of activity while the linear distance separating the adult male from his activity centre at this time was 600 m (Fig. 8.19). The

adult female died the day after release when she was 1 200 m from her capture site. Although this female had a mid-term foetus, was considered to be in her prime, and had above average fat deposits compared to other 72 month old females collected at this time (September), an extensive post mortem examination provided no indication as to the cause of death. However, this mortality suggest that the practice of moving animals to foreign areas may have very stressful, and consequently translocation experiments, which were to have included marked animals with known spatial distributions, were abandoned.

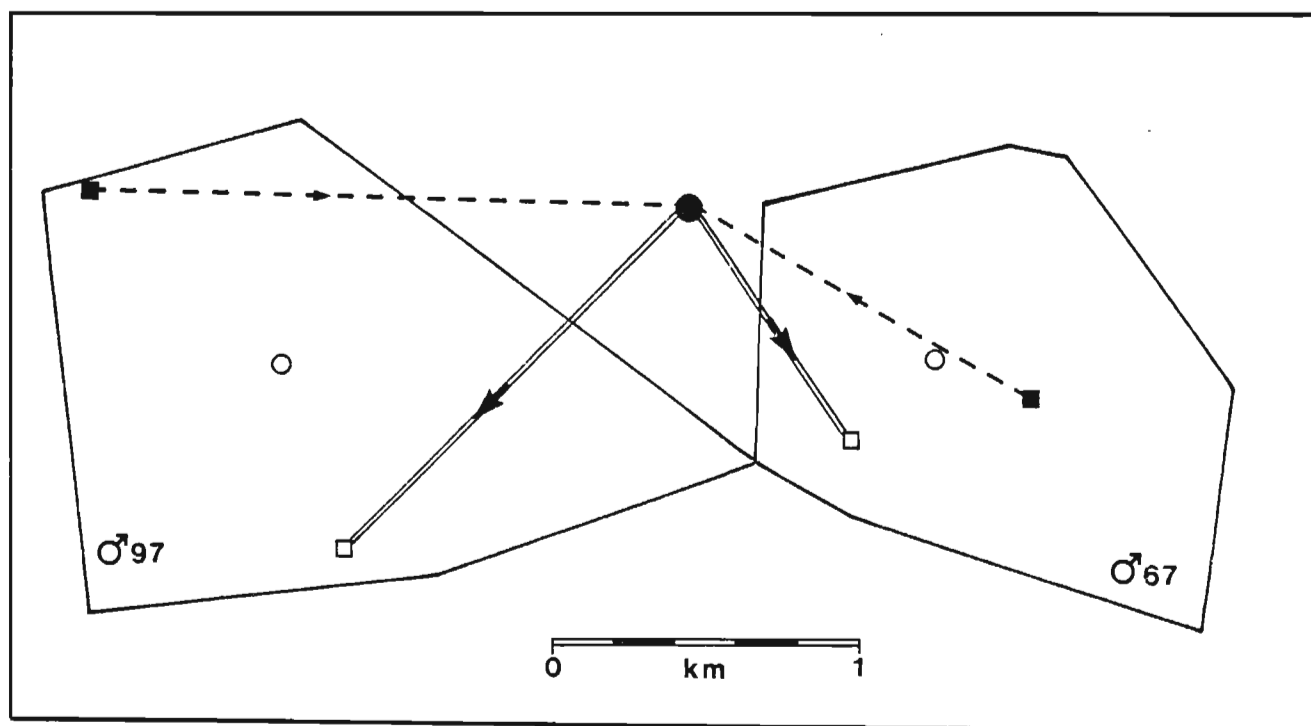


FIGURE 8.19 Movements and subsequent home ranges of two translocated male bushbuck at Weza. Male 67 was a subadult subsequently located on 105 occasions and bushbuck 97 was an adult located on 60 occasions. (Closed squares = capture sites; closed circle = common release site; dashed lines = linear distances between capture and release sites; open squares = position of each male observed within 12hrs of release; double lines = linear distances between release site and positions of observed animals; single lines = subsequent boundaries of home ranges; open circles = centres of activity).

Only one confirmed dispersal, by a subadult male, was witnessed in this study. This animal occupied a range to the east of those illustrated in Figs. 8.3-8.7 during May and June 1983, when approximately 14 months old. Unfortunately, the animal was fitted with a visual rather than a radio collar, and was not seen again until exactly two months later. The linear distance separating the last position in its former range to the first sighting in August 1983 was 3 000 m. This animal was recaptured in its new range and fitted with a radio transmitter in November 1983 when it had been seen on 16 occasions, but the transmitter failed within the first week. Nevertheless, another 24 positions were recorded from sightings between November 1983 and October 1984 when field work was terminated. All of these positions from August 1983 onwards occurred within an area of 23,3 ha, northwest of the former range, and the linear distance separating the centres of activity of these two ranges was 2 900 m. Although the path travelled by this male between June and August 1983 could not be determined, the easiest and most direct route would have been straight through the center of the intensive study area which was inhabited by many other marked bushbuck (Figs. 8.3 - 8.7). Of the seven other 14 month old bushbuck males that were marked, one was never seen again, while all of the others were repeatedly seen or located in the general vicinity of the areas where they were captured. Two of these died from natural causes in the winter of 1983, one was killed in a poacher's snare in April 1984 (see No. 69 in Fig. 8.4) and another was shot on a neighbouring farm less than 800 m from the area where it was captured (on the boundary of Weza State Forest). This last animal was seen on 20 occasions in the general vicinity of its capture site, and was also frequently observed by some of the staff of the farm where it was shot. It was last seen on Forestry land exactly one week before its death, and clearly included both Forestry and private land in its home range of 156 ha monitored over a period of 29 months. The remaining two males were still inhabiting areas close to their capture sites when field work was completed in October 1984. The home range of one of these, bushbuck No. 67 is illustrated in Fig. 8.4. Although none of these six subadult males

dispersed, the sequential order of recorded locations were examined to determine if usage of specific areas differed with age. This was done by comparing the ranges based on the first 20 locations with the last 20 locations for each of three individuals, two of which are illustrated in Fig. 8.20 (other subadult males were located too infrequently for this analysis). Although ranges based on the last 20 locations were consistently larger (possibly because all of these included positions determined from radio tracking) these nevertheless overlapped with the earliest ranges, suggesting that home range occupancy and utilization generally remained fairly constant among subadult and young adult males at Weza. An identical trend was exhibited by all six subadult females adequately monitored in this study, with the exception of one animal which ranged over a wider area when first monitored than at the end of this study. The ranges of this female and two other representative animals are illustrated in Fig. 8.20.

8.3.1.2 Duiker

8.3.1.2.1 Home range size

Because radio tracking studies of duiker met with limited success, and marked animals were seen much less frequently than bushbuck, attempts to capture, mark and radio track this species were abandoned in December 1982 (Appendix D). Consequently, the quantity as well as quality of the data obtained from duiker was notably inferior to that recorded for bushbuck, and conclusions regarding the spatial organisation exhibited by duiker is unavoidably somewhat speculative.

Home range sizes of duiker located between 5 and 10 times were significantly smaller than those obtained from animals located on more than 10 occasions ($t = 2,13$; d.f. = 20; $p < 0,05$), but this latter sample did not differ significantly from duiker located on more than 20 occasions. As a result, both data sets were combined (i.e. all animals

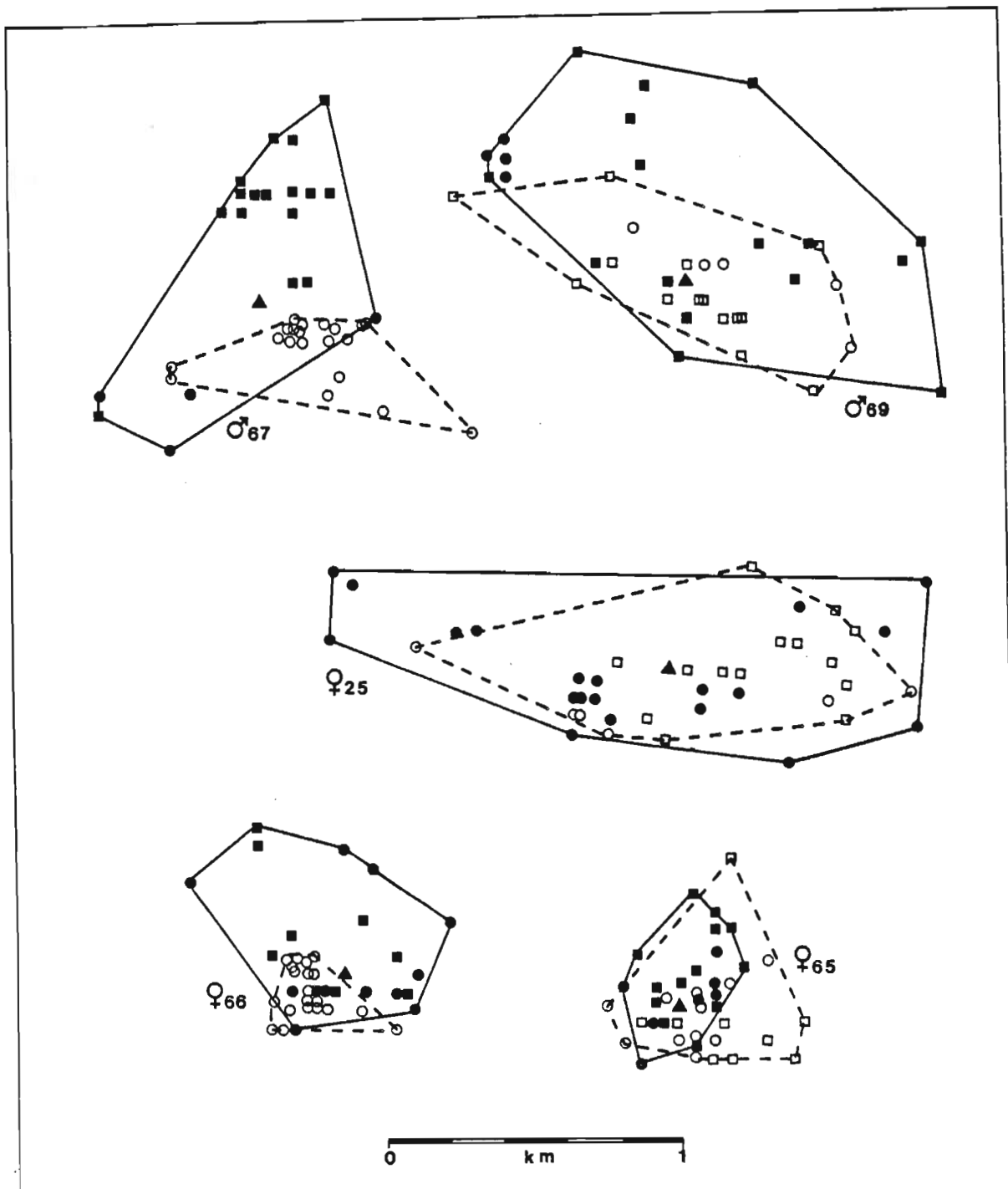


FIGURE 8.20 Home ranges of five subadult bushbuck based on the first 20 locations (open symbols) and last 20 locations (closed symbols) for each animal. (Circles represent observations and squares represent positions determined from radio tracking; closed triangles represent the overall centres of activity determined from all locations recorded for that animal. Periods when the first and last 20 locations were respectively recorded are as follows: No. 67 - May to October 1983 and October 1984; No. 69 - May to July 1983 and January to October 1984; No. 25 - April to May 1982 and August 1983 to October 1984; No. 66 - May to July 1983 and August to October 1984; No. 65 - April to September 1983 and July to September 1984).

seen or located more than 10 times) to increase sample size ($n = 16$, or 42% of the total marked population). Only three animals had sufficient locations obtained from both tracking and sightings to permit comparisons between home range sizes determined from these two methods, and one of these had a larger home range based on sightings (the functional life of the transmitter on this animal was however only 41 days). Of the other two animals which had larger radio tracked ranges, one exhibited exclusive areas determined from radio tracking and sighting data (Fig. 8.21). Since telemetry and sightings were recorded concurrently, this finding suggests that ranges determined from sightings alone may not only underestimate range size but also range utilization. Further information is obviously required to clarify the relationship between range use and method of data collection, but again it must be stressed that the limited results obtained in this study should be interpreted with caution.

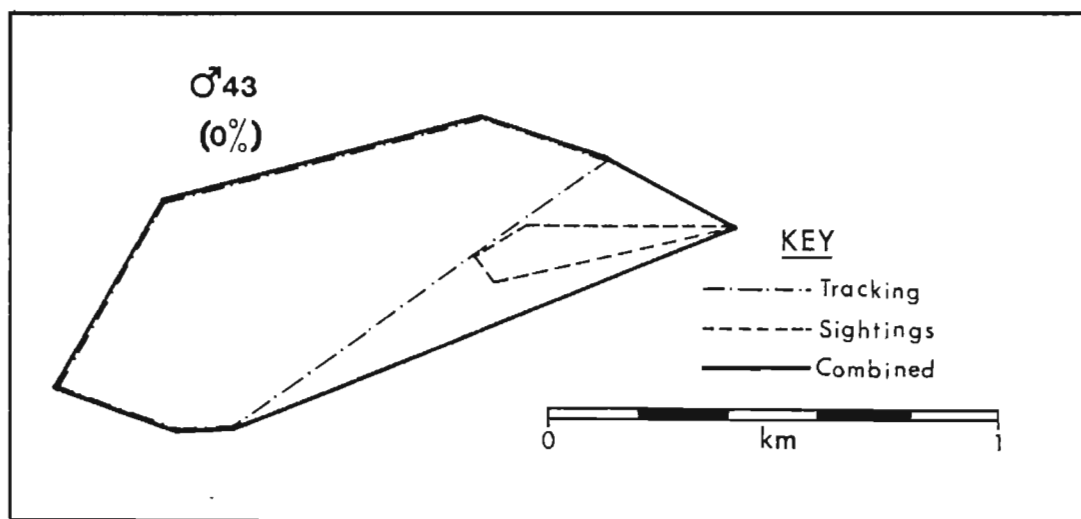


FIGURE 8.21 Home range of adult male duiker 43 as determined from field sightings, radio tracking and from both methods. Note the absence of any overlap between ranges determined from sightings ($n=11$) and from radio tracking ($n=26$).

Male range sizes did not differ significantly from those of females irrespective of area (see below) or whether individuals were located on a minimum of more than 5, 10 or 20 occasions. No distinction was made between subadult and adult animals since comparatively few young animals were marked and regularly monitored, while the rapid growth rates

(Chapter Three) and sexual maturation (Chapter Five) of those that would have rendered such differentiation meaningless.

Spatial overlap of male and female home ranges with those of the same sex was much less pronounced in both intensive study areas. In I.S.A.1 the ranges of two adult males (Nos. 14 and 23) showed fairly extensive overlap (Fig. 8.22), but a closer examination of their respective movements indicated completely distinct and exclusive ranges when considered on a temporal basis. Duiker No. 14 was monitored from November 1981 and was last seen at the end of April 1983. The positions indicating overlap with duiker No. 23's range occurred at a time when No. 23 was confined to a relatively small area, and although the movements of these two animals brought them into close proximity at times, no overlap occurred during concurrent periods (Fig. 8.23). Duiker No. 23's movements into No. 14's range (as outlined in Fig. 8.23) only occurred after duiker No. 14 was no longer observed and had presumably disappeared in September 1983. Thus although the home ranges of these two males overlapped spatially, they did not overlap simultaneously. Similarly, the overlap between the ranges of males No. 42 and 43, and between males No. 22 and 43 (Fig. 8.22) did not occur while animals were being monitored concurrently. Slight overlap between duikers Nos. 22 and 42 did occur at the same time, but only while the former duiker was a subadult male; the majority of the overlap illustrated in Fig. 8.22 occurred after the death of duiker No. 42. As with adult males, the overlap between adult females Nos. 10 and 26 did not constitute a combined temporal and spatial overlap, although adult males shared parts of the same ranges with adult females in both time and space.

Ranges of adult duiker also tended to be avoided by members of the same sex in the second intensive study area (Fig. 8.24), a notable exception being the range overlap between adult females Nos. 7 and 31. However, these two ranges again did not overlap at the same time. Adult female No. 7 was located from August 1981 until June 1982 and was

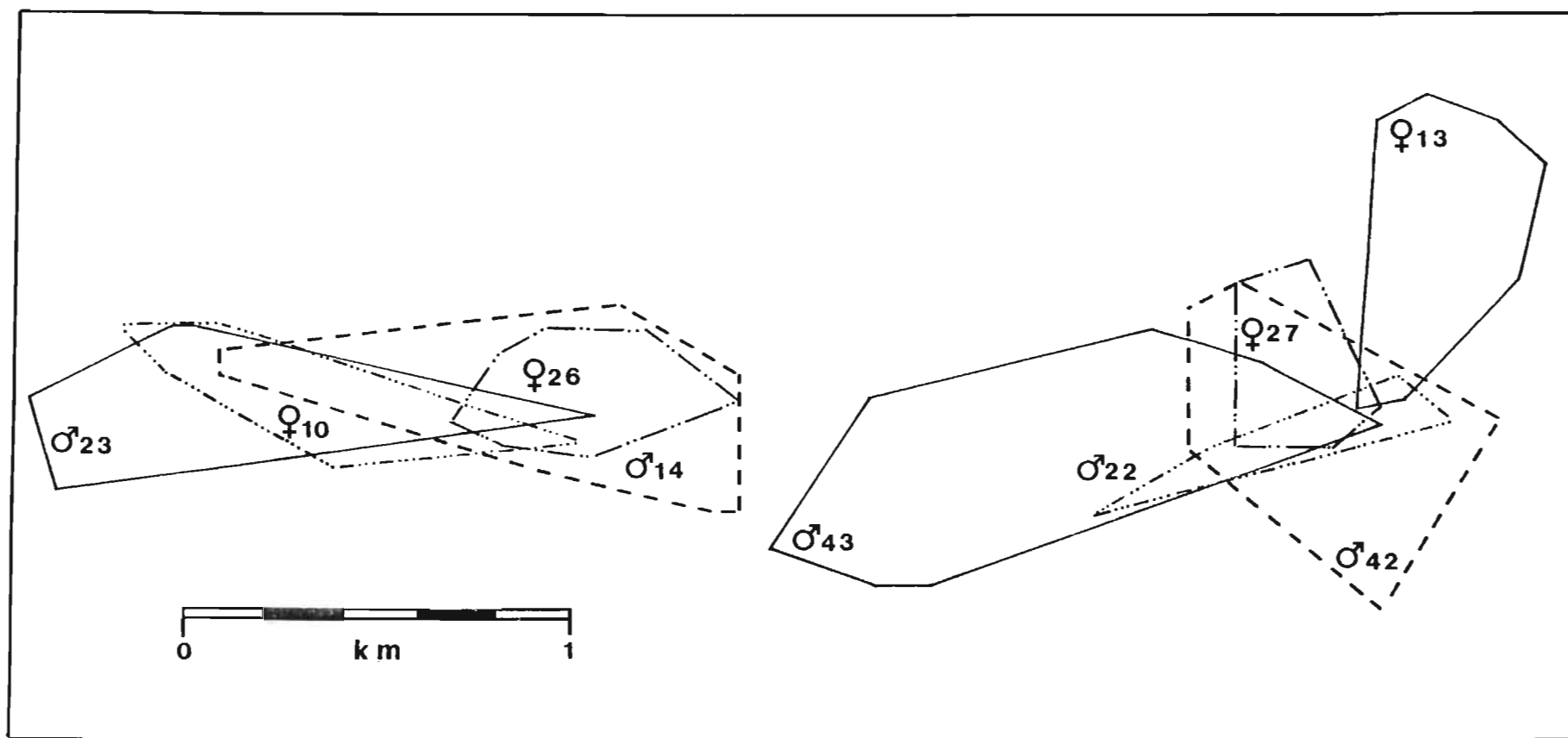


FIGURE 8.22 Home ranges of five male and four female duiker each located on a minimum of 10 occasions in I.S.A.1. (Duiker 22 was a subadult male, all other animals were adult).

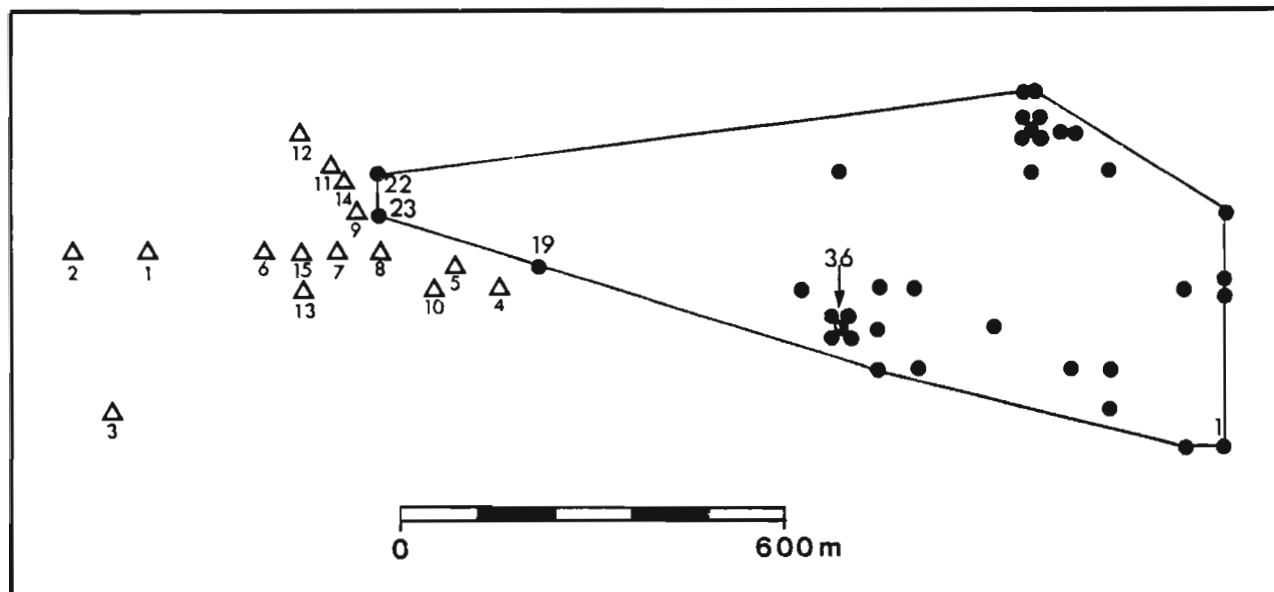


FIGURE 8.23 The locations of adult male duiker Nos. 14 (closed circles) and 23 (open triangles) recorded during the period between November 1981 and May 1983. Dates on which these locations were recorded are:

Duiker 14 - 1 = 25/11/'81; 19 = 12/5/'82; 22 = 5/8/'82; 23 = 11/8/'82; 36 = 29/4/'83 (last observation).

Duiker 23 - 1 = 20/12/'81; 2 = 23/12/81; 3 = 4/2/'82; 4 = 23/4/'82; 5 = 3/5/'82; 6 = 10/6/'82; 7 = 11/6/'82; 8 = 21/6/'82; 9 = 6/7/'82; 10 = 8/7/'82; 11 = 24/9/'82; 12 = 30/9/'82; 13 = 18/10/'82; 14 = 10/2/'83; 15 = 29/5/'83. (this animal was last seen on 28/9/'84 at the same locality as position no.11).

seen on one other occasion (in the same range) in October 1984. Female duiker No. 31 was monitored between April 1982 until June 1983 and was never located within No. 7's range during the period while data were being recorded concurrently. The range of subadult male No. 24 overlapped almost entirely with that of adult male No. 15 for a period of six months. Adult No. 15 was not seen again after Forestry had planted a large area of grassland within this animal's range with pine, while No. 24 was last seen in this vicinity in October 1982, and the skeleton and collar of this animals was recovered approximately 800 m from the centre of his range of 2,5 ha in July 1983. As with duiker ranges in

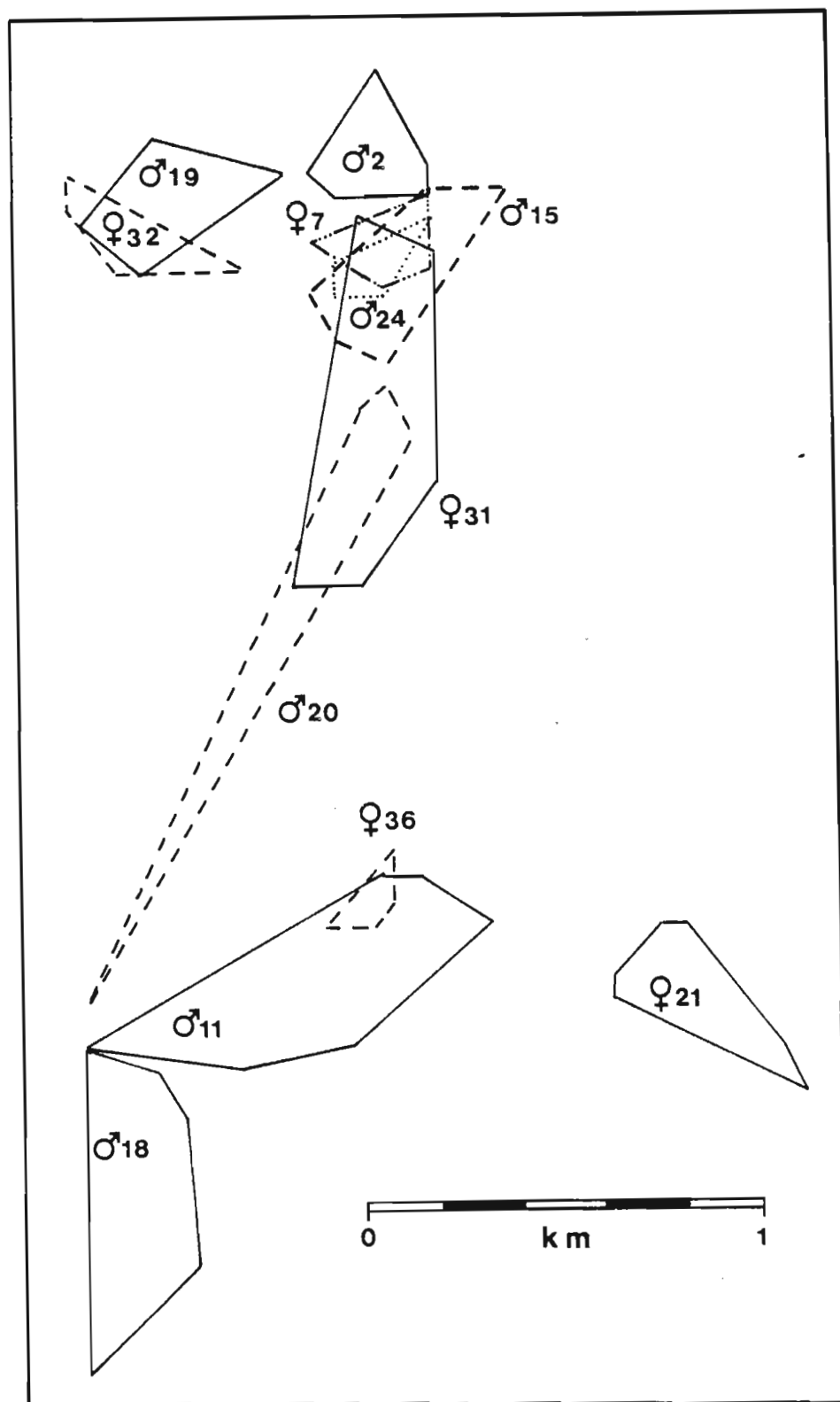


FIGURE 8.24 Home ranges of four adult male (Nos. 2, 11, 15, 18), one subadult male (No. 24) and two adult female (Nos. 7 and 31) duiker each located on a minimum of 10 occasions in I.S.A.2. Ranges of five additional duiker, each located on at least five occasions (but less than 10) occasions are shown for comparative purposes (Nos. 19 and 20 = adult males, Nos. 32 and 36 = adult females, No. 21 = subadult female).

the first intensive study area, those of adult males and adult females overlapped spatially and temporally with those adults of the opposite sex.

Duiker ranges in I.S.A.2 (Fig. 8.24) were significantly smaller than those in I.S.A.1 (Fig. 8.22) whether these were determined from at least 10 locations per range ($t = 2,35$; d.f. = 14; $p < 0,05$) or were based on a minimum of five locations ($t = 3,37$; d.f. = 21; $p < 0,01$). Intensive Study Area 2 contained a much higher proportion of open habitat (grassland, temporary unplanted areas, cultivated areas and clearfelled sites) than I.S.A.1 which was dominated by intermediate aged and mature pines (Chapters Two and Seven). Inadequate sampling (Table 8.10) precluded assessments of seasonal variations in home range size, but duiker generally appeared to occupy smaller areas of their ranges during summer and autumn, although a restricted use of ranges by duiker in I.S.A.2 was noted during winter (Table 8.10) and may have been influenced by localised food resources at this time.

TABLE 8.10 Seasonal variation in the home range sizes of duiker inhabiting the two intensive study areas at Weza.

Study Area		SEASON				
		Winter	Spring	Summer	Autumn	Overall
I.S.A.1	n	6	7	6	7	9
	$\bar{x}$	13,9	14,3	11,4	7,8	27,4
	S.D.	9,8	12,2	11,6	8,6	15,4
I.S.A.2	n	5	3	3	7	7
	$\bar{x}$	3,5	7,9	2,3	5,8	12,1
	S.D.	3,2	9,1	1,4	5,3	8,4
Overall	n	11	10	9	14	16
	$\bar{x}$	9,2	12,4	8,3	6,8	20,7
	S.D.	9,0	11,3	10,3	6,9	14,7
No. of locations		100	140	80	112	432
% of locations		23,1	32,4	18,5	25,9	99,9

8.3.1.2.2 Dispersal

Duiker were monitored too infrequently to provide information on detailed movements and only two animals provided definite evidence of dispersal. One of these was duiker No. 24 detailed above, and the other was also a subadult male (No. 35). This individual was captured and marked in April 1982 and was observed on five subsequent occasions in the same general area (home range size was 4,6 ha) until July 1982. The animal was fortuitously resighted again in October 1983 when the linear distance separating this sighting from the centre of his previous range was 2 500 m. The collar and partially eaten carcass of duiker No. 35 was recovered in September 1984 approximately 300 m from the previous sighting and a linear distance of 2 300 m from his range as a subadult. Two claims of sightings of collared duiker on neighbouring farmland more than 5 km from original capture sites could not be confirmed by the author. However, of the 16 animals that were monitored on more than 10 occasions only 9 (56%) were located during 1984, despite repeated searches. Furthermore, only three (23%) of the remaining 13 marked duiker (monitored in 1983 but seen on less than 10 occasions) were observed during the last year of field work. Except when carcasses or collars were recovered, the fate and linear movements of animals that abruptly "disappeared" could not be ascertained (see Chapter Four). Nevertheless, all of these results indicate that duiker ranges were much more exclusive to members of the same sex than with bushbuck, and that dispersal was probably a more common event in this smaller species.

8.3.2 Activity

Examination of activity patterns on an hourly basis indicated that bushbuck were least active during daylight hours when animals were commonly seen either lying or standing motionless. Bushbuck became more active at dusk, and from 1700h to 0500h the proportion of inactive bushbuck

never exceeded 25% of the observed sample (Table 8.11). The proportion of inactive bushbuck observed between 0600h and 1800h was double the proportion of resting bushbuck observed at night, and overall 25% of all animals rested throughout the 24 hour period. In contrast, duiker exhibited a polyphasic pattern of activity (Table 8.11) but since relatively few animals were observed during the day ($n = 60$) this pattern may have resulted from individual variation and/or inadequate sampling. Nevertheless, duiker were generally less active than bushbuck at night, but showed a similar increase in active behaviour during dawn and dusk periods. Overall, 39% of all duiker observed were either lying or standing motionless (Table 8.11). Bushbuck male activity patterns differed notably from those of females during the day but these differences may have been partially due to inadequate and/or disparate sample sizes during daylight hours particularly since activity patterns of males and females were very similar during the night (Table 8.12). Overall, bushbuck spent over twice the time feeding at night, and were more frequently seen walking than during the day. The proportion of animals seen running at night was almost half that observed during the day and since such behaviour was most frequently caused by the presence of a vehicle or detection of humans, this would indicate that diurnal flight distances were greater than those at night. This trend was evident in both sexes but was more pronounced in female bushbuck. Although other activities such as aggression and courtship were rarely witnessed, these were more common during the day and were largely initiated by males (Table 8.12).

As with bushbuck, inadequate daytime sampling was probably responsible for the differences in diurnal activity between males and female duiker; activity patterns at night showed close agreement (Table 8.13). Both sexes spent a similar or greater proportion of time at night either lying or standing motionless and were less frequently seen walking or running during this period; again the frequency of this latter activity suggests that flight distances were greater during the day for both sexes. Foraging behaviour was the

TABLE 8.11 Hourly variations in the proportions of observed bushbuck and duiker that were a) lying or b) standing.

Time Interval	n	% of Bushbuck			n	% of Duiker		
		(a) Lying	(b) Standing	(a+b) Inactive		(a) Lying	(b) Standing	(a+b) Inactive
0600 - 0659	0		No Data		0		No Data	
0700 - 0759	7	0	29	29	3	0	0	0
0800 - 0859	14	0	36	36	7	29	29	58
0900 - 0959	39	10	31	41	9	11	10	21
1000 - 1059	45	18	31	49	11	45	0	45
1100 - 1159	30	17	27	44	5	0	0	0
1200 - 1259	22	27	14	41	5	20	0	20
1300 - 1359	10	30	60	90	0		No Data	
1400 - 1459	15	0	33	33	1	100	0	100
1500 - 1559	26	27	35	62	5	60	0	60
1600 - 1659	17	28	18	46	6	0	50	50
1700 - 1759	13	0	8	8	8	0	0	0
1800 - 1859	48	17	17	34	6	17	17	34
1900 - 1959	187	7	18	25	89	22	11	33
2000 - 2059	384	8	13	21	193	28	15	43
2100 - 2159	325	9	13	22	220	23	15	38
2200 - 2259	264	8	14	22	149	33	12	45
2300 - 2359	215	13	9	22	93	29	6	35
0000 - 0059	70	9	10	19	62	23	8	31
0100 - 1059	65	14	9	23	44	36	2	38
0200 - 0259	17	12	6	18	14	36	0	36
0300 - 0359	4	0	0	0	5	0	0	0
0400 - 0459	5	0	0	0	0		No Data	
0500 - 0559	2	100	0	100	4	0	0	0
Subtotal 0600 - 1759	238	16	28	44	60	21	11	32
Subtotal 1800 - 0559	1583	9	13	22	879	27	12	39
Total 0600 - 0559	1821	10	15	25	939	27	12	30

TABLE 8.12 Variations in diurnal and nocturnal activity patterns of male and female bushbuck.

Activity	Time	Males	Females	All
Lying (%)	Day	19,5	7,6	15,7
Lying (%)	Night	9,2	10,1	9,4
Standing (%)	Day	23,9	35,4	28,1
Standing (%)	Night	11,1	15,1	12,9
Walking (%)	Day	20,1	12,7	17,9
Walking (%)	Night	26,9	24,6	25,3
Running (%)	Day	12,6	20,3	14,5
Running (%)	Night	7,9	8,2	7,9
Feeding (%)	Day	20,8	22,8	21,3
Feeding (%)	Night	44,6	42,0	44,2
Other (%)	Day	3,1	1,3	2,6
Other (%)	Night	0,4	0,0	0,2
Total (n)	Day	159	79	238
	Night	763	820	1 583
	Combined	922	899	1 821

dominant activity at night, and was almost twice as common as during the day (although animals feeding during the day that were disturbed prior to being observed would have resulted in an underestimate of this activity as the behaviour exhibited after the interruption would have been recorded).

Seasonally, bushbuck evidently spent more time being active (particularly foraging) during the day in summer than at other times of the year, but again these differences may have been an artefact of sampling. Nocturnal activities indicate that bushbuck were more mobile in winter but spent less time actively feeding during this season (Table 8.14). Foraging behaviour at night remained the dominant activity

TABLE 8.13 Variations in diurnal and nocturnal activity patterns of male and female duiker.

Activity	Time	Males	Females	All*
Lying (%)	Day	18,8	25,9	21,7
Lying (%)	Night	28,3	30m7	27,0
Standing (%)	Day	9,4	11,1	10,0
Standing (%)	Night	10,8	11,0	11,6
Walking (%)	Day	18,8	29,6	23,3
Walking (%)	Night	16,4	11,6	14,0
Running (%)	Day	31,3	14,8	23,3
Running (%)	Night	3,6	2,7	4,0
Feeding (%)	Day	21,9	18,5	21,7
Feeding (%)	Night	40,8	44,0	43,3
Other (%)	Day	0,0	0,0	0,0
Other (%)	Night	0,0	0,0	0,1
Total (n)	Day	32	27	60
	Night	360	336	879
	Combined	382	363	939

* - includes duiker that could not be sexed in the field

throughout the year, but increased from 34% in winter, 47% in spring and summer to 59% in autumn. The time bushbuck spent as inactive remained relatively constant throughout the year, while activities such as aggression and courtship were recorded in all seasons except spring (Table 8.14).

Inadequate sampling precluded meaningful comparisons of seasonal activity patterns of duiker during the day. At night, duiker activities varied little during the seasons with the exception that animals were less active in summer

TABLE 8.14 Seasonal variations in the diurnal and nocturnal activity patterns of bushbuck.

Activity	Time	Season			
		Winter	Spring	Summer	Autumn
Lying (%)	Day	20,0	9,5	9,7	33,3
Lying (%)	Night	9,8	8,1	8,7	10,9
Standing (%)	Day	27,7	38,1	12,9	9,1
Standing (%)	Night	15,1	12,1	16,5	7,7
Walking (%)	Day	23,1	18,1	9,7	15,2
Walking (%)	Night	32,2	24,2	20,6	17,0
Running (%)	Day	13,8	13,3	12,9	21,2
Running (%)	Night	8,5	9,0	7,3	5,4
Feeding (%)	Day	10,8	21,0	48,4	18,2
Feeding (%)	Night	33,9	46,6	46,8	59,0
Other (%)	Day	4,6	0,0	6,5	3,0
Other (%)	Night	0,5	0,0	0,0	0,0
Total (n)	Day	65	105	31	33
	Night	611	446	218	312
	Combined	676	551	249	345

when 50% of their time was spent lying or standing motionless (Table 8.15). Animals were less mobile at this time and spent slightly less time feeding during spring and summer compared to autumn and winter. Courtship behaviour was never observed and one incidence of aggressive behaviour, involving the flight of an animal of unknown sex when chased by an adult male for approximately 175 m, was recorded during the course of this study (Table 8.15).

TABLE 8.15 Seasonal variations in the nocturnal activity patterns of duiker.

Activity	Winter	Spring	Summer	Autumn
Lying (%)	23,1	25,4	41,7	26,1
Standing (%)	15,0	13,3	8,3	5,9
Walking (%)	13,4	15,9	6,7	17,0
Running (%)	2,6	4,5	5,0	4,8
Feeding (%)	45,6	40,9	38,3	46,3
Other (%)	0,3	0	0	0
Total (n)	307	264	120	188

8.3.3 Social Organisation

8.3.3.1 Bushbuck

8.3.3.1.1 Monthly variations in the proportion of observed groups and animals

Despite early efforts to observe a standard prescribed number of groups each month, such an approach was impractical due to seasonal variations in animal distribution and ranges of visibility. Conditions for observing bushbuck were optimal during late autumn, winter and early spring, when more than 250 groups (or more than 10% of all groups seen) were observed each month (Table 8.16). At least 340 bushbuck (10% of the total observed) were seen each month between May and October (Table 8.16). Consequently overall assessments of group size and composition are weighted heavily in favour of winter (37,7% and 38,0% of all observed groups and individuals respectively), and spring (29,2% and 29,4% of all observed groups and individuals respectively) sightings and should therefore be interpreted accordingly.

TABLE 8.16 Monthly variation in the proportions of groups of bushbuck observed in Weza State Forest.

Month	% of observed groups containing			% of total no. of observed groups	No. of observed bushbuck	% of observed bushbuck
	Marked Animals	Unmarked animals	Both marked & unmarked animals			
Jan	62	27	89	3,5	115	3,4
Feb	69	27	96	3,8	118	3,5
Mar	48	22	70	2,8	78	2,3
Apr	95	37	132	5,2	171	5,0
May	199	92	291	11,5	407	12,0
Jun	236	142	378	15,0	534	15,7
Jul	198	64	262	10,4	340	10,0
Aug	237	73	310	12,3	420	12,3
Sep	260	67	327	13,0	446	13,1
Oct	209	72	281	11,1	368	10,8
Nov	106	22	128	5,1	186	5,5
Dec	117	41	158	6,3	217	6,4
O/all	1836	686	2 522	100,0	3 400	100,0

8.3.3.1.2 Group size

The difference between the mean group sizes of marked and unmarked animals ($\bar{x} = 1,34 \pm 0,60$ S.D. and $\bar{x} = 1,38 \pm 0,64$ S.D. respectively) was not significant and these data were subsequently combined to increase sample sizes. Solitary animals were the most frequently encountered groups at Weza throughout the year, while the largest groups seen consisted of five individuals (Table 8.17). The only significant deviation from the overall mean group size of 1,35 occurred in February and March when mean group sizes were appreciably smaller (Table 8.17). Typical group sizes never exceeded 2,0 during any month of the year. Overall, groups containing female bushbuck (M.G.S. = $1,54 \pm 0,70$ S.D.) were significantly larger ($d = 7,70$; $p < 0,001$) than groups which included males (M.G.S. = $1,34 \pm 0,66$ S.D.).

TABLE 8.17 Monthly mean and typical group sizes of bushbuck recorded on Weza State Forest between September 1980 and October 1984.

Months	No. of groups of size:					Total no. of groups	Total no. of bushbuck	MGS	S.D.	d*	TGS
	1	2	3	4	5						
Jan	69	14	6	-	-	89	115	1,29	0,59		1,56
Feb	77	16	3	-	-	96	118	1,23	0,49	2,35 p<0,02	1,42
Mar	63	6	1	-	-	70	78	1,11	0,36	5,37 p<0,001	1,23
Apr	98	29	5	-	-	132	171	1,30	0,53		1,51
May	195	79	14	3	-	2912	407	1,40	0,63		1,68
Jun	256	95	21	5	1	378	534	1,41	0,68		1,74
Jul	197	53	11	1	-	262	340	1,30	0,56		1,54
Aug	225	63	19	3	-	310	420	1,35	0,64		1,66
Sep	228	81	17	-	1	327	446	1,36	0,61		1,64
Oct	203	69	9	-	-	281	368	1,31	0,53		1,52
Nov	84	32	11	-	1	128	186	1,45	0,72		1,81
Dec	112	33	13	-	-	158	217	1,37	0,63		1,66
O/all	1807	570	130	12	3	2 522	3 400	1,35	0,61		1,62

* - only d values (Bailey 1959) indicating significant deviations from the overall mean group size are shown.

8.3.3.1.3 Group composition

Using the criteria presented in Chapters Three and Four it was possible to distinguish the same nine group types described by Anderson (1978) and Allen-Rowlandson (1980) for nyala and greater kudu respectively. These were:

- I Solitary adult males (at least 30 months old)
- II Solitary subadult males (approximately 8-30 months old)
- III Solitary adult females (at least 30 months old)
- IV Solitary subadult females (approximately 8-30 months old)

- V Solitary infants (under 8 months of age)
- VI Bachelor groups (containing two or more males of any age)
- VII One-female groups (containing one adult female and at least one subadult of either sex and/or an infant)
- VIII Female groups* (containing two or more adult females or one-female groups)
- IX Mixed groups (containing at least one adult female, with without young, and at least one adult male).

* As pointed out by Walther (1972b) the term "female group" is slightly misleading since subadult males may be present, but the term is preferable to "nursery herd" (Estes 1967; 1974; Underwood 1975) which implies that such groups include unweaned infants.

Several of these group types may be interpreted as temporary or permanent combinations of others (see below). Of the 2 522 groups that were recorded in this study, 2 507 (99,4%) could be classified into one of the above nine categories. Monthly sighting frequencies of each group type (expressed as a percentage of all classified groups seen each month) are presented in Fig. 8.25. Significant variations in these sighting frequencies are detailed below.

8.3.3.1.4 Sighting frequencies of group types

Solitary animals constituted 71,6% of all sighted groups, and 53,2% of all observed bushbuck. Lone adult males and adult females formed 47,3% and 38,1% of all solitary group sightings respectively. This adult sex ratio differed significantly ($X^2 = 48,34$; d.f. = 1; $p < 0,001$) from the population sex ratio of 87 males:100 females obtained from

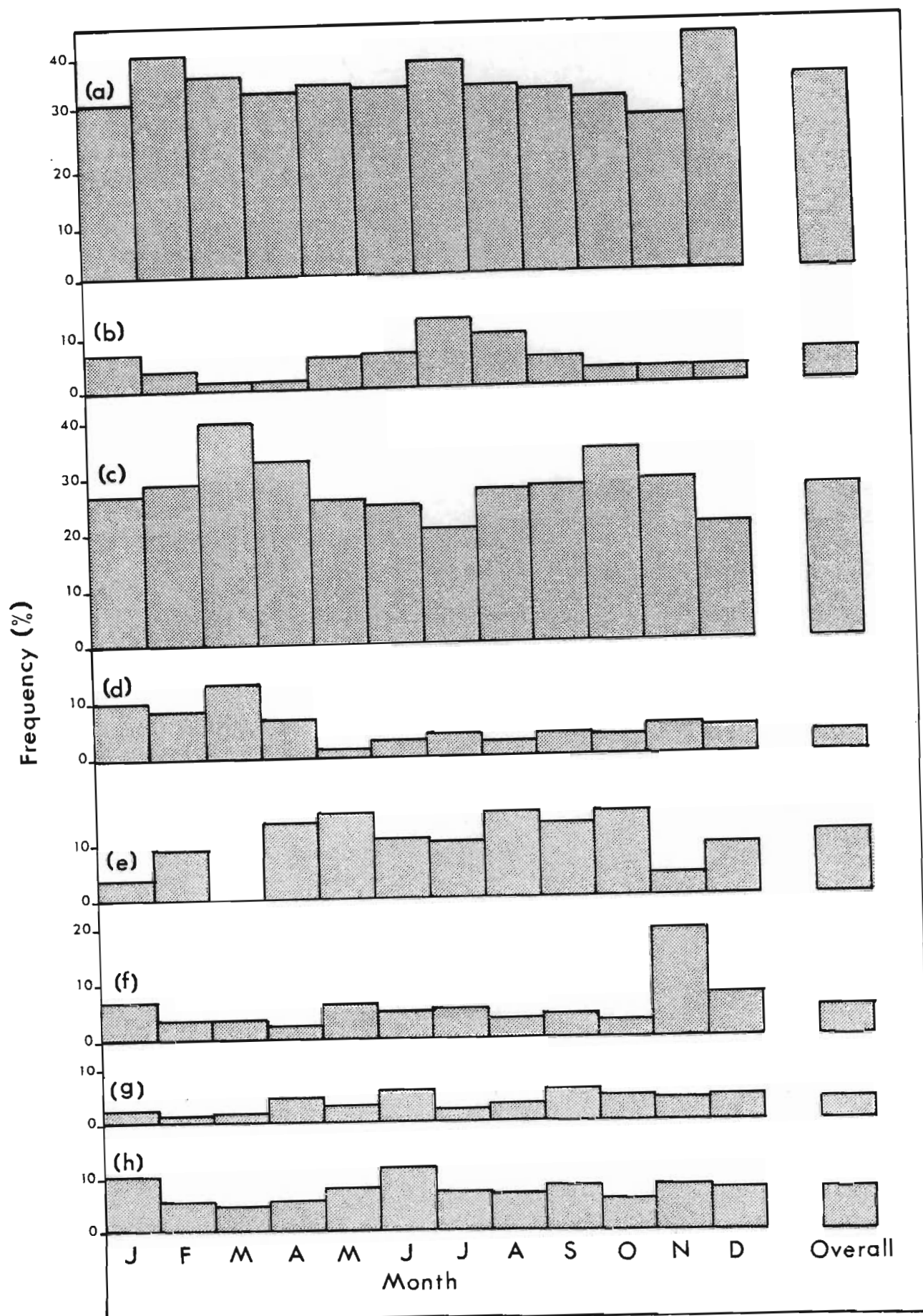


FIGURE 8.25 Monthly variations in the sighting frequencies of bushbuck groups observed at Weza. (a = solitary adult males; b = solitary subadult males; c = solitary adult females; d = solitary subadult females; e = one-female groups; f = female groups; g = bachelor groups; h = mixed groups).

field sightings (see Chapter Nine) but was not significantly different ($X^2 = 1,94$; d.f. = 1) from the population sex ratio of 115,7 males:100 females determined from the culled sample (see Chapter Nine). Variations in the monthly sighting frequencies of solitary adult male groups (Fig. 8.25a) were not significant, but solitary subadult male groups decreased significantly in April ($X^2 = 4,05$; d.f. = 1; $p < 0,05$) and increased markedly during July and August ($X^2 = 16,90$; d.f. = 1; $p < 0,001$ and $X^2 = 5,83$; d.f. = 1; $p < 0,05$ respectively, see Fig. 8.25b). Solitary adult female groups increased notably in March and October ($X^2 = 4,01$; and $X^2 = 5,06$ respectively, both months d.f. = 1; $p < 0,05$) but were less commonly encountered in July ($X^2 = 4,50$; d.f. = 1; $p < 0,05$, see Fig. 8.25c). Solitary subadult female groups were less frequently observed than solitary subadult male groups (4,2% and 5,7% of all observed groups respectively) but were recorded more frequently than expected during January ($X^2 = 7,30$; d.f. = 1; $p < 0,01$) February ($X^2 = 4,34$; d.f. = 1; $p < 0,005$) and March ($X^2 = 13,45$; d.f. = 1; $p < 0,001$). There was a marked decrease ($X^2 = 5,49$; d.f. = 1; $p < 0,05$) in the number of solitary subadult female groups observed in May (Fig. 8.25d). Solitary infants were rarely seen at Weza; only 4 groups were recorded (0,2%) of which three were seen during January.

Excluding solitary animals, one-female groups were encountered more frequently than any of the other group types, and accounted for 11,6% of all groups observed. This proportion decreased significantly during January ($X^2 = 5,17$; d.f. = 1; $p < 0,005$), March ($X^2 = 7,75$; d.f. = 1; $p < 0,01$) and in November ($X^2 = 6,39$; d.f. = 1; $p < 0,05$) but remained relatively constant for the remainder of the year (Fig. 8.25e). The majority of one-female groups consisted of two animals (i.e. an adult female and one offspring) and group size never exceeded four. Overall, mean and typical group sizes were 2,06 ($\pm 0,28$ S.D.) and 2,10 respectively. All one-female groups sighted in July, September and October contained only two bushbuck, and were significantly smaller ($d = 3,66$; $p < 0,001$ for all three months) than other one-female groups seen throughout the rest of the year. The overall proportion of bushbuck seen in one-female groups was

8,6%. Females were more commonly seen with subadults (52,0%) than with either infants (42,8%) or with subadults and infants (5,2%).

Female groups constituted 5,1% of all groups seen at Weza and included 8,6% of all bushbuck encountered. Monthly variations in the proportion of female groups sighted (Fig. 8.25f) were significant only in November when most female groups were observed ($X^2 = 47,37$; d.f. = 1; $p < 0,001$). Female groups ranged in size from two to four, and mean and typical group sizes were 2,29 ($\pm 0,49$ S.D.) and 2,40 respectively. These were significantly smaller in February and March ($d = 6,74$; $p < 0,001$ for both months) and significantly larger in August ($d = 2,49$; $p < 0,02$). The majority of female groups consisted of adult female bushbuck only (78,7%) and groups containing subadults (11,0%) were slightly more common than those containing adults and infants (10,2%). The mean number of adult females in female groups was 2,08 ($\pm 0,30$) although only pairs of adult females were recorded from September to February and again in March. During all these months, the number of adult females was significantly lower ($d = 3,01$; $p < 0,01$) than the rest of the year.

The proportion of bachelor groups seen during the year was 3,9% and included 6,3% of all observed bushbuck. Monthly sighting frequencies of bachelor groups remained relatively constant throughout the year (Fig. 8.25g) and this was the only group type not to exhibit significant monthly variations. Bachelor groups never included more than three individual males, and overall had mean and typical group sizes of 2,17 ($\pm 0,38$ S.D.) and 2,24 respectively. Only pairs of males were encountered during January, February, March and November, and during these months bachelor group size was significantly smaller ($d = 4,47$; $p < 0,001$) than the annual mean. The most frequently encountered bachelor groups (81,6%) consisted of peers, of which 78,6% included groups of adult males and 3,0% were subadult male groups. Groups containing both adult and subadult males therefore accounted for 18,4% of all bachelor groups. The overall mean and typical numbers of adult males in bachelor groups were 1,98

($\pm 0,60$ S.D.) and 2,16 respectively, and these numbers did not fluctuate significantly at any time of the year. Significant differences in bachelor group sizes during spring, summer and early autumn were therefore due to the absence of subadult males in these groups.

The overall proportion of mixed groups observed at Weza was 7,7% and these included 14,2% of all observed bushbuck. With the exception of June, when significantly more groups were observed ($X^2 = 6,73$; d.f. = 1; $p < 0,01$), the proportions of mixed groups seen throughout the year remained relatively constant (Fig. 8.25h). Mixed groups ranged in size from two to five, and the overall mean and typical group sizes recorded were 2,46 ($\pm 0,64$ S.D.) and 2.63 respectively. The only significant deviation from this mean group size occurred in March when sightings were confined to pairs of animals ($d = 10,00$; $p < 0,001$). Groups containing a single adult male and single adult female were most common (60,3%) and groups with at least two adult males and two adult females were rarely encountered (1,5%). The number of mixed groups containing one adult female were almost as common as those containing a single adult male (89,2% and 89,7% respectively). Significantly fewer adult males occurred in mixed groups from January to April ($d = 4,40$; $p < 0,001$ for all months) compared to the overall mean of 1,11 ($\pm 0,35$ S.D.) adult males per mixed group. Similarly, significantly fewer adult females were observed in mixed groups during February to April, and also in July and December (all months $d = 4,04$; $p < 0,001$). The mean number of adult females associated with mixed groups for the entire year was 1,09 ($\pm 0,31$ S.D.) while the overall typical numbers of adult males and females in these groups were 1,22 and 1,18 respectively.

8.3.3.1.5 Sex and age differences in the proportions of bushbuck observed in the various group types

a) Infants (170 animals)

The majority of infants were observed in one-female groups (78,2%) and were more commonly encountered in mixed

groups (12,4%) than in female groups (7,1%) or as solitary individuals (2,4%). These proportions varied between months (Fig. 8.26) and significant differences are presented in Table 8.18).

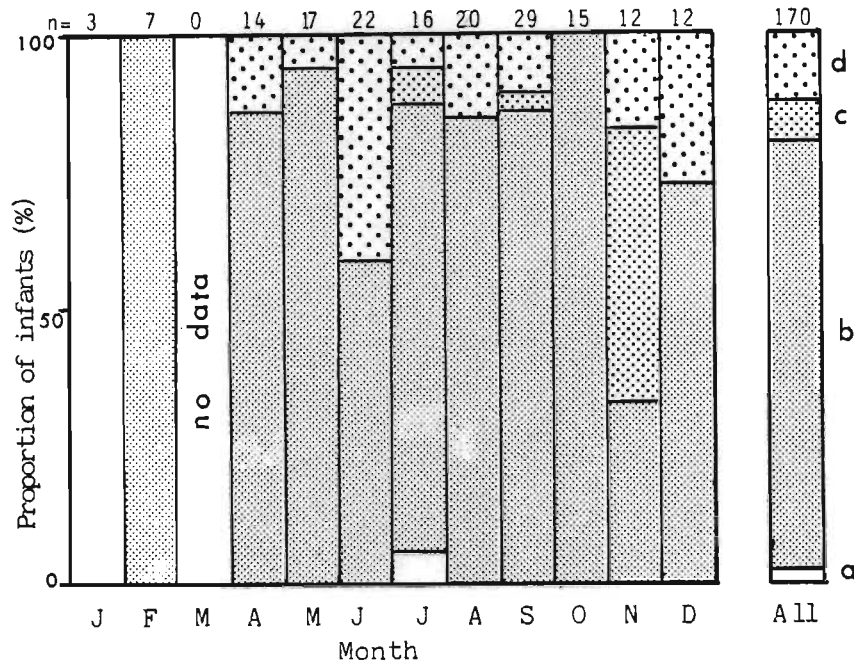


FIGURE 8.26 Monthly and overall proportions of infant bushbuck in (a) solitary, (b) one-female, (c) female and (d) mixed groups.

TABLE 8.18 Significant variations in the number of infant bushbuck observed in solitary, one-female, female and mixed groups. (Months with non-significant variations have been omitted).

Month	Solitary	l-female group	Female group	Mixed group
Jan	Increased $x^2=122,64$ $p<0,001$	n.s.	n.s.	n.s.
Jun	n.s.	n.s.	n.s.	Increased $x^2=14,50$ $p<0,001$
Nov	n.s.	n.s.	Increased $x^2=31,20$ $p<0,001$	n.s.
Dec	n.s.	n.s.	Increased $x^2=8,15$ $p<0,01$	n.s.
Overall	$x^2=127,19$ $p<0,001$	n.s.	$x^2=46,81$ $p<0,001$	$x^2=20,92$ $p<0,001$

b) Subadult females (283 animals)

Overall, subadult females occurred in four group types with the following proportions: in one-female groups (50,9%), as solitary individuals (37,5%), in mixed groups (7,8%) and in female groups (3,9%). Monthly variations in these proportions are illustrated in Fig. 8.27 while significant deviations are listed in Table 8.19.

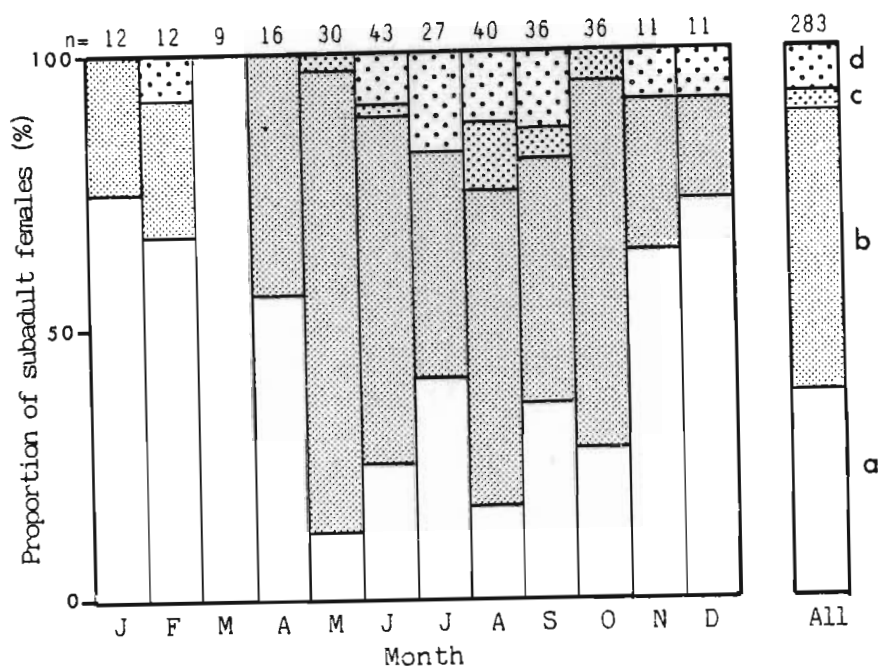


FIGURE 8.27 Monthly and overall proportions of subadult female bushbuck in (a) solitary, (b) one-female, (c) female and (d) mixed groups.

c) Adult females (1445 animals)

Adult females were most frequently seen alone (47,7%) and occurred in one-female, female and mixed groups in fairly similar proportions (19,4%, 18,3% and 14,7% respectively). Monthly fluctuations in the proportions of adult females in each of these groups types were much more pronounced (Fig. 8.28) and showed more significant deviations (Table 8.20) than any other sex or age class during the course of the year.

TABLE 8.19 Significant variations in the number of subadult female bushbuck observed in solitary, one-female, female and mixed groups. (Months with non-significant variations have been omitted).

Month	Solitary	1-female group	Female group	Mixed group
Jan	Increased $\chi^2 = 4,53$ $p < 0,05$	n.s.	n.s.	n.s.
Mar	Increased $\chi^2 = 9,41$ $p < 0,01$	Decreased $\chi^2 = 4,58$ $p < 0,05$	n.s.	n.s.
Jul	n.s.	n.s.	n.s.	Increased $\chi^2 = 4,00$ $p < 0,05$
Aug	Decreased $\chi^2 = 4,25$ $p < 0,05$	n.s.	Increased $\chi^2 = 7,68$ $p < 0,01$	n.s.
Overall	$\chi^2 = 35,38$ $p < 0,001$	$\chi^2 = 21,77$ $p < 0,05$	n.s.	n.s.

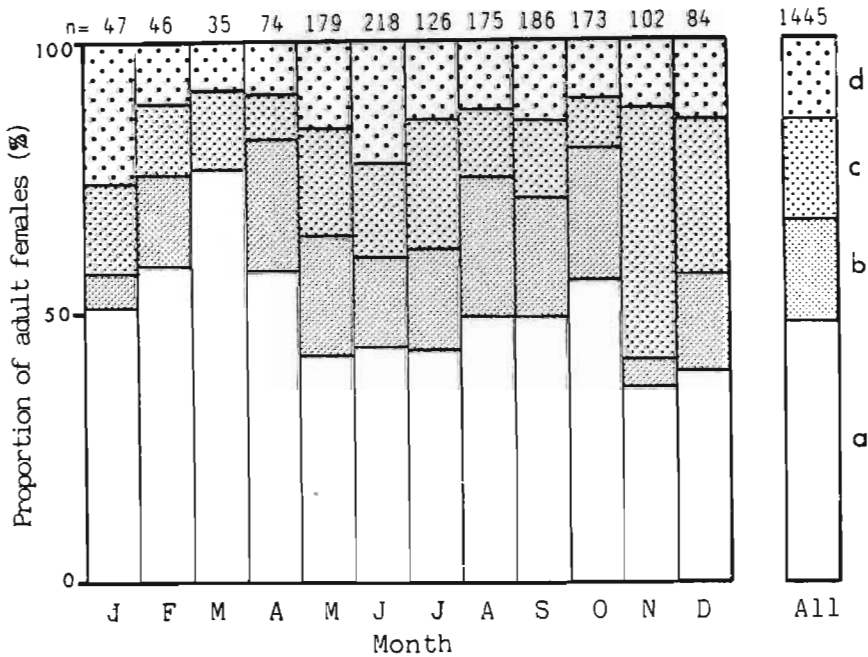


FIGURE 8.28 Monthly and overall proportions of adult female bushbuck in (a) solitary, (b) one-female, (c) female and (d) mixed groups.

TABLE 8.20 Significant variations in the number of adult female bushbuck observed in solitary, one-female, female and mixed groups. (Months with non-significant variations have been omitted).

Month	Solitary	1-female group	Female group	Mixed group
Jan	n.s.	Decreased $\chi^2 = 4,10$ $p < 0,05$	n.s.	n.s.
Mar	Increased $\chi^2 = 6,37$ $p < 0,05$	Decreased $\chi^2 = 6,78$ $p < 0,01$	n.s.	n.s.
Apr	n.s.	n.s.	Decreased $\chi^2 = 4,18$ $p < 0,05$	n.s.
Jun	n.s.	n.s.	n.s.	Increased $\chi^2 = 8,03$ $p < 0,01$
Aug	n.s.	Increased $\chi^2 = 4,31$ $p < 0,05$	n.s.	n.s.
Oct	n.s.	n.s.	Decreased $\chi^2 = 7,71$ $p < 0,01$	n.s.
Nov	n.s.	Decreased $\chi^2 = 11,03$ $p < 0,001$	Increased $\chi^2 = 46,25$ $p < 0,001$	n.s.
Dec	n.s.	n.s.	Increased $\chi^2 = 4,87$ $p < 0,01$	n.s.
Overall	n.s.	$\chi^2 = 31,95$ $p < 0,001$	$\chi^2 = 72,20$ $p < 0,001$	n.s.

d) Subadult males (215 animals)

Although subadult males occurred in five group types, the majority of animals were observed alone (67,0%). The overall proportion of subadult males in one-female groups was 18,1% while 11,6% were seen in bachelor groups. Membership in mixed and female groups was comparatively rare (1,4% and 1,9% respectively). Monthly variations in these proportions are illustrated in Fig. 8.29 and significant deviations from the overall proportions cited above are detailed in Table 8.21.

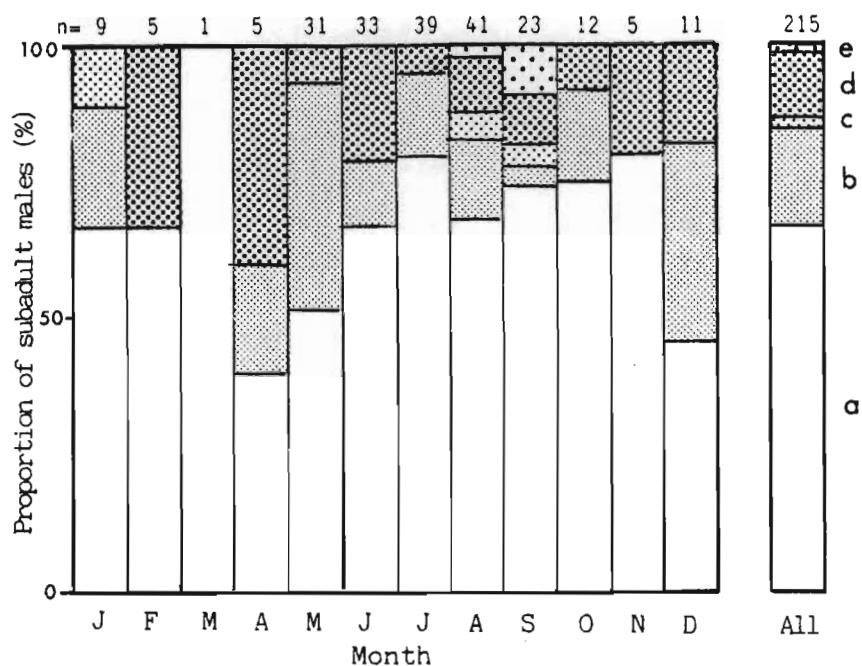


FIGURE 8.29 Monthly and overall proportions of subadult male bushbuck in (a) solitary, (b) one-female, (c) female, (d) bachelor and (e) mixed groups.

TABLE 8.21 Significant variations in the number of subadult male bushbuck observed in solitary, one-female, female, bachelor and mixed groups. (Months with non-significant variations have been omitted).

Month	Solitary	1-female group	Female group	Bachelor	Mixed group
Jan	n.s.	n.s.	Increased $\chi^2=4,05$ $p<0,05$	n.s.	n.s.
May	n.s.	Increased $\chi^2=9,69$ $p<0,01$	n.s.	n.s.	n.s.
Sep	n.s.	n.s.	n.s.	n.s.	Increased $\chi^2=8,82$ $p<0,01$

e) Adult males (1260 animals)

As with subadult males, adult males were most frequently seen as solitary animals (67,9%). Slightly more adult males were recorded in mixed groups (17,1%) than in bachelor groups (14,9%; 13,5% in adult bachelor groups and 1,4% in adult and

subadult bachelor groups). The monthly proportions of adult males in these group types remained fairly constant throughout the year (Fig. 8.30) and significant deviations from overall values occurred only in February, June and September (Table 8.22).

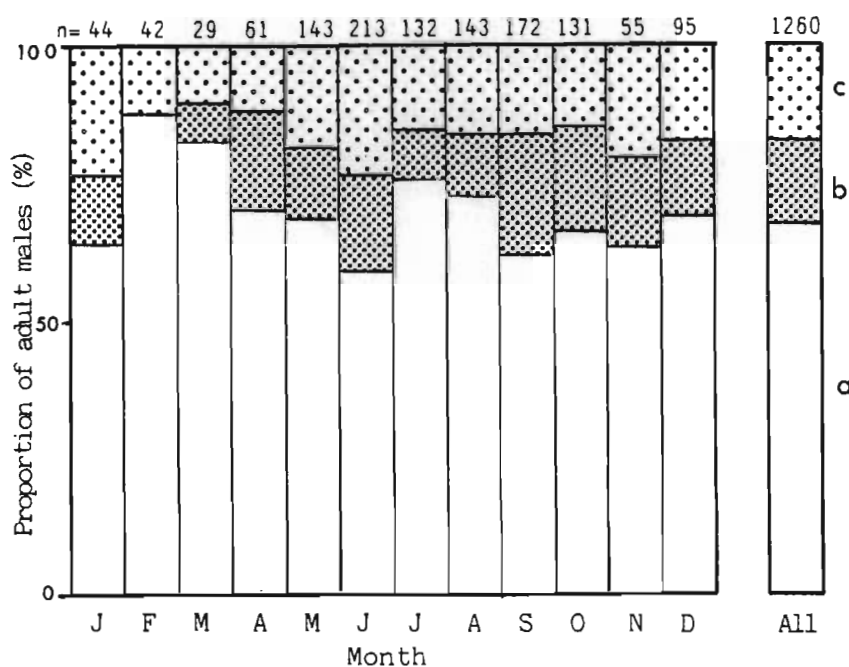


FIGURE 8.30 Monthly and overall proportions of adult male bushbuck in (a) solitary, (b) bachelor and (c) mixed groups.

TABLE 8.22 Significant variations in the number of adult male bushbuck observed in solitary, bachelor and mixed groups. (Months with non-significant variations have been omitted).

Month	Solitary	Bachelor group	Mixed group
Feb	n.s.	Decreased $x^2=6,27$ $p<0,05$	n.s.
Jun	n.s.	n.s.	Increased $x^2=4,27$ $p<0,05$
Sep	n.s.	Increased $x^2=5,93$ $p<0,05$	n.s.
Overall	n.s.	$x^2=21,69$ $p<0,05$	n.s.

8.3.3.1.6 Group stability and inter-individual associations

In the preceding section the term "group" has been considered in a purely operational sense. Overall, indices of association between females (Table 8.23) males and females (Table 8.24) and males (Table 8.25) indicated weak and temporary associations, with only 11 out of 48 (22.9%) known associations having indices exceeding 0,10. Although associations among females were generally the most stable, particularly those involving adult and subadult or subadult and subadult females (Table 8.23), associations were most frequently among individuals of the opposite sex (Table 8.24). The most stable associations among males involved groups of adults (Table 8.25). These results must be interpreted with caution however because only marked animals could be recognised, and even when seen, individual collars were not identified on every occasion. Therefore, certain indices of association may be minimal values. In addition, comparatively few young animals were captured and marked in this study, while sighting frequencies and periods of observation varied considerably between individuals (Table 8.26).

TABLE 8.23 Indices of association between individually known female bushbuck. (Subadult females are marked with an asterisk).

No.	22	25*	34	65*	66*	83	111
18	0,174				0,444		
21*	0,071	0,013	0,021	0,451			
25*				0,019			
34						0,035	
36					0,025		
95							0,032
107							0,030

TABLE 8.24 Indices of association between individually known male and female bushbuck. (Subadults are marked with an asterisk).

m \ f	18	25*	34	36	41*	48	65*	66*	84*	85	91	107*	111	125
7		0,023	0,010				0,013							
28		0,012	0,020											
30*											0,053			
40				0,182		1,00**								
51			0,016							0,043				
58	0,114			0,033	0,051			0,074						
64	0,069													
67*									0,182					0,083
69*	0,067	0,037	0,015					0,072						
92										0,182				
94							0,025							
115												0,030	0,067	
126								0,074						
137*		0,095												

** - Male No. 40 seen on only 5 occasions during two months of observation.

TABLE 8.25 Indices of association between individually known adult and subadult (No.69) male bushbuck.

No.	24	28	42	51	64	69*	94
7		0,009					0,024
27	0,056	0,048		0,087			
37			0,200				
44	0,158						
51		0,017					
58					0,118	0,018	

TABLE 8:26 Numbers of sightings, months of observation and male and female associations of individually known bushbuck (only individuals with known associates are listed).

Male Bushbuck No.	Total No. of obs.	Months under obs.	No. of assoc. with known		Female Bushbuck No.	Total No. of obs.	Months under obs.	No. of assoc. with known	
			Males	Females				Males	Females
7	124	38	2	3	18	60	19	3	2
24	33	16	2	-	21	96	31	-	4
27	11	14	3	-	22	22	8	-	2
28	117	27	3	2	25	62	30	4	2
30	26	22	-	1	34	102	27	4	2
37	35	13	1	-	36	72	27	2	1
40	5	2	-	2	41	71	26	1	-
42	4	1	1	-	48	5	8	1	-
44	24	12	1	-	65	65	18	2	2
51	68	12	2	2	66	107	18	3	2
58	62	22	2	4	83	56	17	-	1
64	21	4	1	1	84	2	1	1	-
67	47	18	-	2	85	11	12	2	-
69	79	10	1	4	91	39	16	1	-
92	25	15	-	1	95	36	15	-	1
94	28	15	1	1	107	23	13	1	1
115	50	12	-	2	111	45	12	1	2
126	5	9	-	1	125	5	10	1	-
137	16	4	-	1					

8.3.3.2 Duiker

8.3.3.2.1 Monthly variations in the proportion of observed groups of animals

As with bushbuck, the majority of duiker groups and individuals were observed during the winter and early spring (June to September) with the proportions of groups and animals both exceeding 10% during these months only (Table 8.27). Overall assessments of groups size and composition were therefore biased in favour of winter and early spring data.

TABLE 8.27 Monthly variation in the proportions of groups and duiker observed in Weza State Forest.

Month	No. of groups containing:			% of total no. of observed groups	No. of observed duiker	% of observed duiker
	Marked animals	Unmarked animals	Both marked & unmarked animals			
Jan	6	45	51	4,4	56	4,2
Feb	26	30	56	4,8	67	5,0
Mar	33	17	50	4,3	67	5,0
Apr	72	37	109	9,4	127	9,5
May	30	49	79	6,8	87	6,5
Jun	31	105	136	11,7	160	12,0
Jul	41	83	124	10,7	142	10,6
Aug	56	83	139	11,9	159	11,9
Sep	83	69	152	13,1	176	13,2
Oct	37	62	99	8,5	110	8,2
Nov	34	35	69	5,9	75	5,6
Dec	47	53	100	8,6	110	8,2
Overall	496	668	1 164	100,1	1 336	99,9

8.3.3.2.2 Group size

Group size of marked and unmarked duiker did not differ significantly ($\bar{x} = 1,17 \pm 0,38$ S.D. and $1,13 \pm 0,36$ respectively) and were subsequently combined to increase sample size. The most frequently encountered group type at Weza throughout the year consisted of solitary animals, while the largest group of 4 animals was observed once, in June (Table 8.28). The only significant deviation from the overall M.G.S. of 1,15 occurred in March when a M.G.S. of 1,34 was recorded (Table 8.28). Typical group sizes never exceeded 1,60 during any month of the year, and groups containing marked males did not differ significantly from those which included marked females ($\bar{x} = 1,20 \pm 0,43$ and $1,15 \pm 0,37$ respectively).

TABLE 8.28 Monthly mean and typical group sizes of duiker recorded on Weza State Forest between September 1980 and October 1984.

Month	No. of groups of size:				Total No. of groups	Total No. of duiker	MGS	S.D.	d*	TGS
	1	2	3	4						
Jan	46	5	-	-	51	56	1,10	0,30		1,18
Feb	48	5	3	-	56	67	1,20	0,52		1,42
Mar	33	17	-	-	50	67	1,34	0,48	2,77 p<0,01	1,51
Apr	93	14	2	-	109	127	1,17	0,42		1,31
May	71	8	-	-	79	87	1,10	0,30		1,18
Jun	114	21	-	1	136	160	1,18	0,44		1,34
Jul	106	18	-	-	124	142	1,15	0,35		1,25
Aug	120	18	1	-	139	159	1,14	0,37		1,26
Sep	128	24	-	-	152	176	1,16	0,37		1,27
Oct	89	9	1	-	99	110	1,11	0,35		1,22
Nov	64	4	1	-	69	75	1,09	0,33		1,19
Dec	90	10	-	-	100	110	1,10	0,30		1,18
O/all	1 002	153	8	1	1 164	1 336	1,15	0,38		1,27

* - only d values (Bailey 1959) indicating significant deviations from the overall mean group size are shown.

8.3.3.2.3 Group composition

A total of 250 groups could not be classified due to uncertainties regarding the sex and/or age of individual animals. All of the remaining 914 groups (78,5% of the total number observed) were placed into one of the nine categories detailed for bushbuck above. Monthly sighting frequencies of each group type are presented in Fig. 8.31 while significant monthly departures from the overall values are detailed below.

8.3.3.2.4 Sighting frequencies of group types

Solitary animals accounted for 85,7% and 75,7% of all classified groups and duiker respectively. The majority of solitary animals consisted of adult males (39,2% of single sightings) and adult females (40,4%). Variations in the monthly sighting frequencies of solitary adult males (Fig. 8.31a) were significant only in December when a higher proportion than expected were observed ($X = 6,74$; d.f. = 1; $p < 0,001$). Solitary subadult male sightings declined significantly during this month ($X = 5,60$; d.f. = 1, $p < 0,05$, see Fig. 8.31b) and these deviations may have been due to inaccurate field classifications. The proportion of solitary adult females (Fig. 8.31c) subadult females (Fig. 8.31d) and infants (only a total of 4 individuals were observed, one each in February, April, August and December) remained relatively constant throughout the year and did not differ significantly from their overall proportions of 34,7%, 6,1% and 0,4% respectively during any month of the year.

Excluding solitary animals, one-female groups were the most frequently encountered group type at Weza, and accounted for 7,0% of all classified groups (Fig. 8.31e). Significantly higher numbers of one-female groups were observed in March and significantly fewer were recorded in October ($X = 18,07$; d.f. = 1; $p < 0,001$ and $X = 5,81$; d.f. = 1; $p < 0,05$ respectively). All one-female groups observed

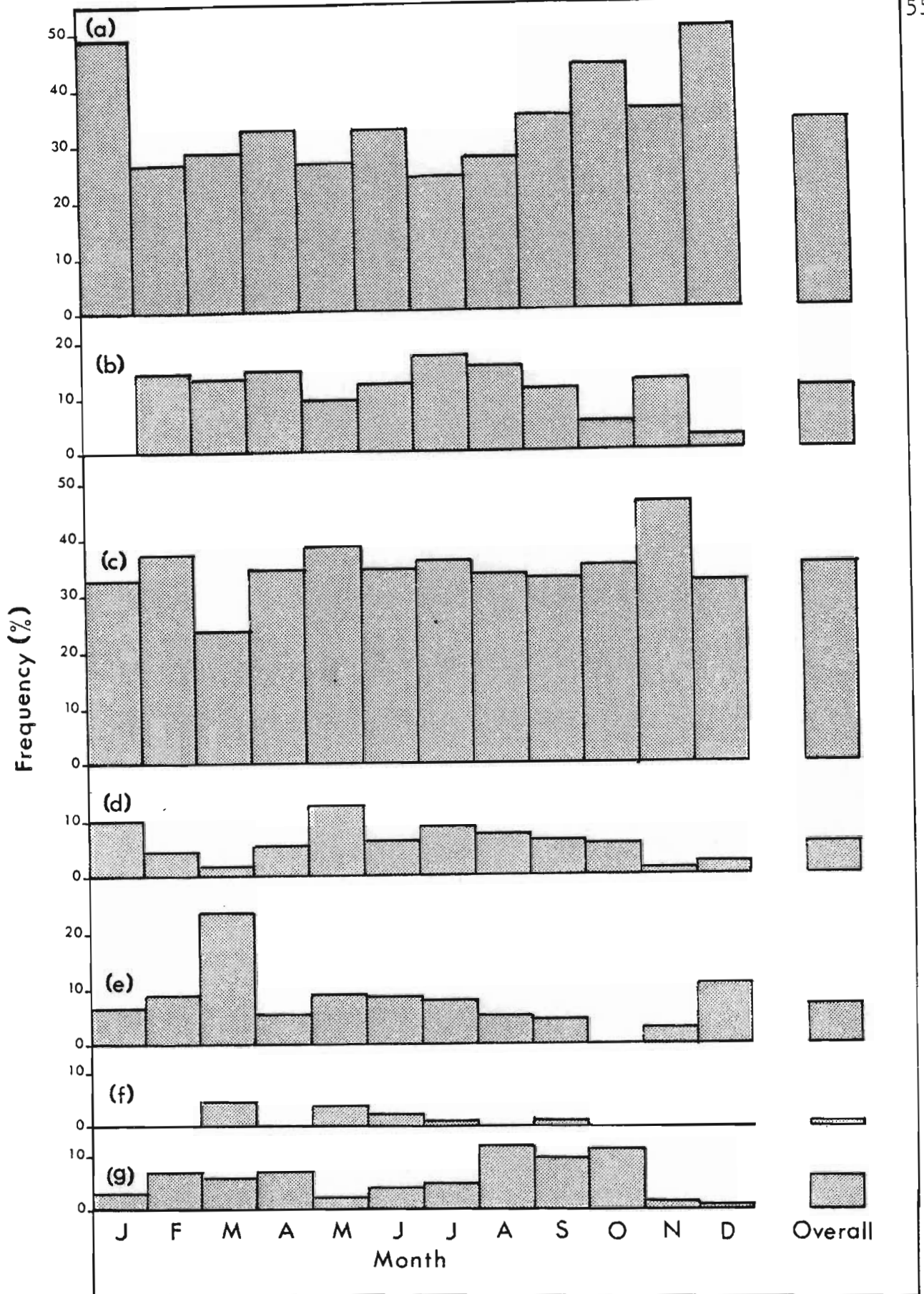


FIGURE 8.31 Monthly variations in the sighting frequencies of duiker groups observed at Weza. (a = solitary adult males; b = solitary subadult males; c = solitary adult females; d = solitary subadult females; e = one-female groups; f = bachelor groups; g = mixed groups).

throughout the year consisted of two animals (i.e. an adult female and offspring).

Duiker apparently formed female groups very rarely, and only one was observed in this study (in July) which consisted of two adult females. Similarly, males rarely formed bachelor groups (Fig. 8.31f) and again these always consisted of pairs of males. Of the eight bachelor groups observed (0,9% of all groups), six consisted of one adult and one subadult male while one group contained a pair of adults and the other a pair of subadult males. Bachelor groups were seen more frequently than expected in March and May ($X^2 = 6,17$ and $4,50$ respectively, both months d.f. = 1 and $p < 0,05$).

Mixed groups were the only group type involving two or more animals that was seen consistently throughout the year (Fig. 8.31g) and contributed 6,2% of all groups seen. The only significant departure from this overall proportion occurred in August when mixed groups accounted for 11,4% of the total groups seen that month ($X^2 = 4,53$; d.f. = 1; $p < 0,05$). Of the 57 mixed groups recorded, 53 (92,9%) consisted of two animals (i.e. an adult male and adult female). The four remaining mixed groups (in which all members could be aged and sexed) all comprised of three animals, and in three of these the third member was an infant or subadult. The fourth mixed group of three animals consisted of one adult male and two adult females. This group (seen in February) and the female groups seen in July were the only records of an association between two adult females (see below).

8.3.3.2.5 Sex and age differences in the proportions of duiker observed in the various group types

a) Infants (22 animals)

The majority of infants observed at Weza occurred in one-female groups (77%), while 18% were solitary and 5% were found in mixed groups. Monthly variations in the proportions

of infants occurring in different groups types were not examined due to the small sample of infants observed in classified groups.

b) Subadult females (65 animals)

Subadult female duiker were most frequently encountered as solitary animals (86,1%) and the only other type of group they formed was one-female groups (13,9%). Monthly variations in the proportions of subadult females occurring in these two group types (Fig. 8.32) did not differ significantly from these overall proportions.

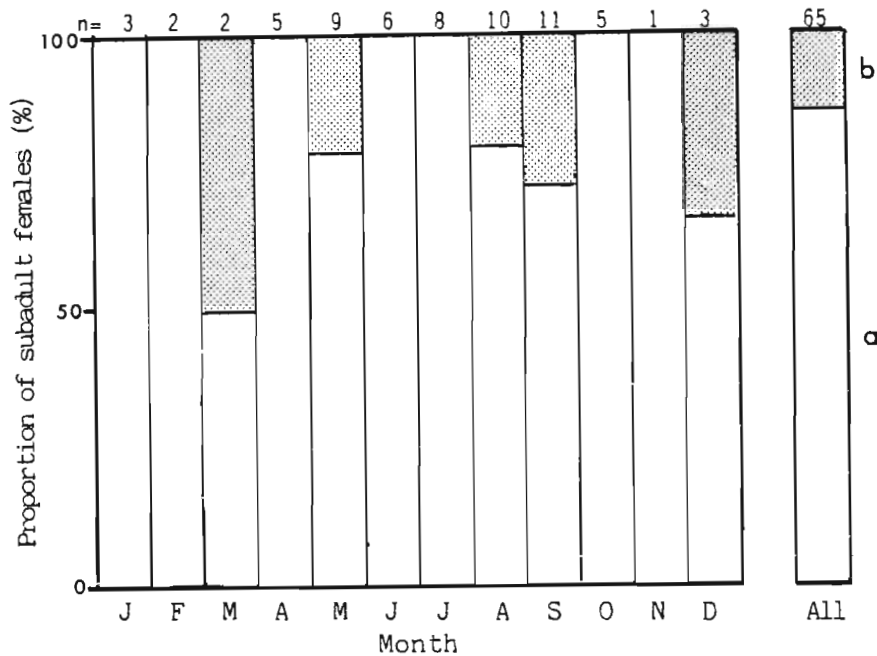


FIGURE 8.32 Monthly and overall proportions of subadult female duiker in (a) solitary and (b) one-female groups.

c) Adult females (439 animals)

Overall, adult females most commonly occurred alone (72,2%) and were more frequently associated with juveniles (14,3%) and with adult males (13,0%) than with other adult females (0,5%). Variations in the monthly proportions of lone adult female duiker (Fig. 8.33) were not significant, but the proportion of females found in other group types varied considerably at different times of the year (Table 8.29).

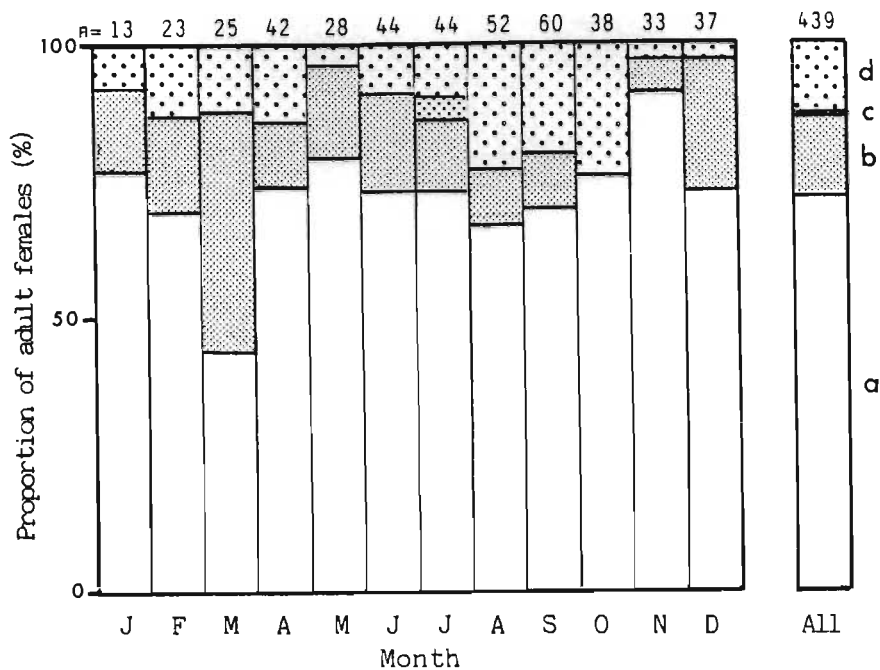


FIGURE 8.33 Monthly and overall proportions of adult female duiker in (a) solitary, (b) one-female, (c) female and (d) mixed groups.

TABLE 8.29 Significant variations in the number of adult female duiker observed in solitary, one-female, female and mixed groups. (Months with non-significant variations have been omitted).

Month	Solitary	1-female group	Female group	Mixed Group
Jan	n.s.	Increased $\chi^2=15,29$ $p<0,001$	n.s.	n.s.
Jul	n.s.	n.s.	Increased $\chi^2=16,20$ $p<0,001$	n.s.
Aug	n.s.	n.s.	n.s.	Increased $\chi^2=4,08$ $p<0,05$
Oct	n.s.	$\chi^2=5,45$ $p<0,05$	n.s.	n.s.
Overall	n.s.	$\chi^2=27,53$ $p<0,01$	n.s.	n.s.

d) Subadult males (138 animals)

Monthly variations in the numbers of subadult males occurring singly did not differ significantly from the overall proportion of 72,5% (Fig. 8.34), but subadult male sightings in one-female groups, bachelor groups and mixed groups all deviated significantly from their overall proportions (21,0%, 5.8% and 0,7% respectively) at different times of the year (Table 8.30).

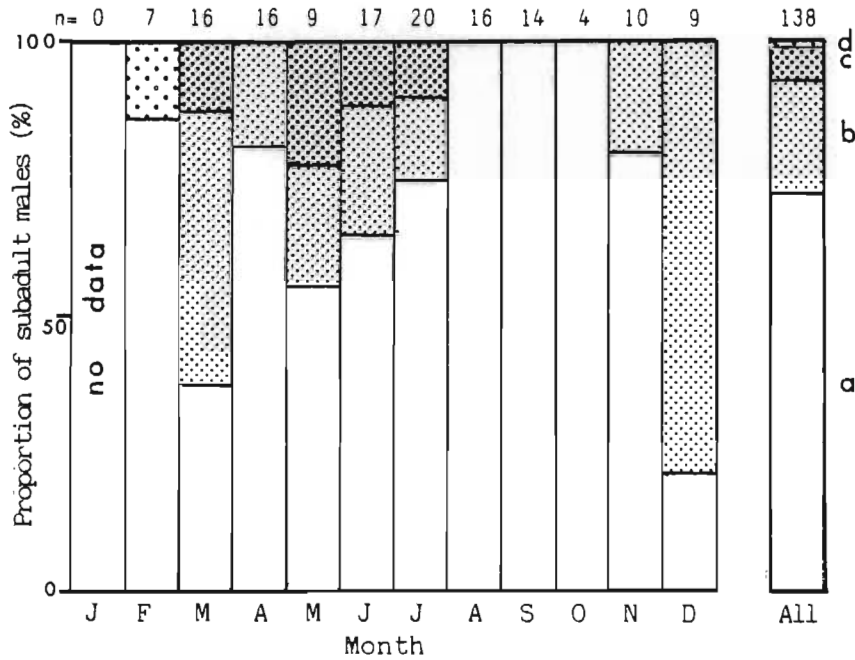


FIGURE 8.34 Monthly and overall proportions of subadult male duiker in (a) solitary, (b) one-female, (c) bachelor and (d) mixed groups.

TABLE 8.30 Significant variations in the number of subadult male duiker observed in solitary, one-female, bachelor and mixed groups. (Months with non-significant variations have been omitted).

Month	Solitary	1-female group	Bachelor	Mixed Group
Feb	n.s.	n.s.	n.s.	Increased $\chi^2=18,05$ $p<0,001$
Mar	n.s.	n.s.	Increased $\chi^2=4,21$ $p<0,05$	n.s.
Dec	n.s.	Increased $\chi^2=13,82$ $p<0,001$	n.s.	n.s.
Overall	n.s.	$\chi^2=29,28$ $p<0,01$	n.s.	n.s.

e) Adult males (372 animals)

As with subadult males, the proportions of adult male duiker occurring as solitary animals did not differ from the overall proportion of 82,5% at any time of the year (Fig. 8.35). Significant variations from the average proportion of males in bachelor groups (2,2%) and mixed groups (15,3%) were however evident during certain months (Table 8.31).

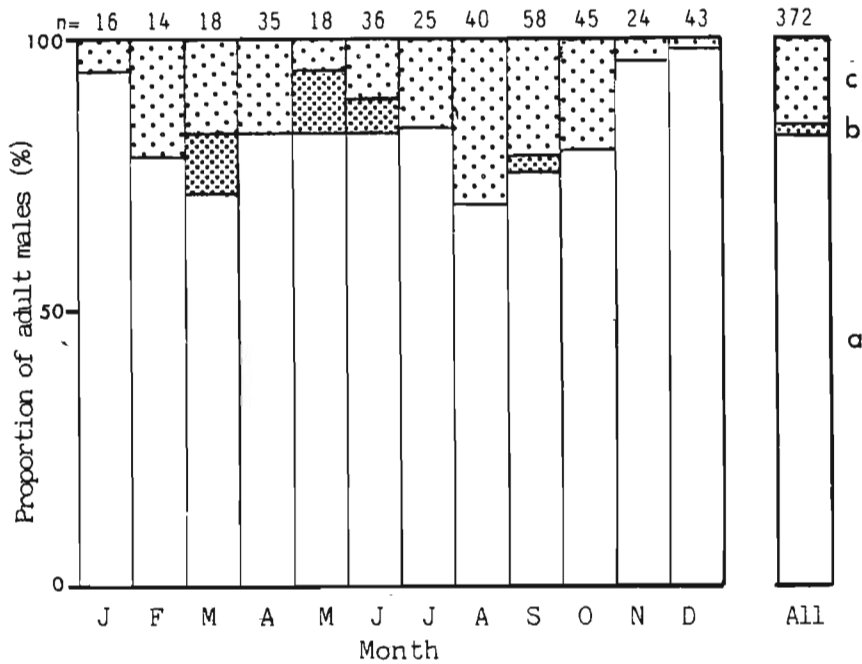


FIGURE 8.35 Monthly and overall proportions of adult male duiker in (a) solitary, (b) bachelor and (c) mixed groups.

TABLE 8.31 Significant variations in the number of adult male duiker observed in solitary, bachelor and mixed groups. (Months with non-significant variations have been omitted).

Month	Solitary	Bachelor	Mixed Group
Mar	n.s.	Increased $x^2=6,65$ $p<0,01$	n.s.
May	n.s.	Increased $x^2=6,65$ $p<0,01$	n.s.
Aug	n.s.	n.s.	Increased $x^2=5,62$ $p<0,05$
Dec	n.s.	n.s.	Decreased $x^2=4,74$ $p<0,05$
Overall	n.s.	$x^2=20,91$ $p<0,05$	n.s.

8.3.3.2.6 Group stability and inter-individual associations

The relatively few meetings between marked individuals together with the low indices of association such encounters produced indicate that duiker groups were open, temporary associations. Male-male encounters were only recorded between three pairs of duiker, and of these two included a subadult male (Table 8.32). The only association indicating any degree of permanence between males and females involved adult female No. 7 and her offspring, subadult male No. 24 (Table 8.33), but dissolution of this bond occurred eight months after the subadult male had been marked. Encounters between two marked females were not recorded in this study, and although adult females must obviously associate with their female young, adult female - adult female associations rarely occurred at Weza (see above). However, these results should be interpreted with caution for the same reasons given above for bushbuck, particularly since comparatively few animals were marked and sighting frequencies and observation periods differed considerably between individual duiker (Table 8.34).

TABLE 8.32 Indices of association between individually known male duiker (subadult males are marked with an asterisk).

No.	D18	D24*	D35*
D11	0,059		
D14			0,182
D15		0,054	

TABLE 8.33 Indices of association between individually known male and female duiker (subadult males are marked with an asterisk).

m \ f	D7	D10	D26	D27	D31
D14			0,136		
D20					0,143
D22*				0,054	
D23		0,067			
D24*	0,457				
D42				0,111	

TABLE 8.34 Numbers of sightings, months of observation and male and female associations of individually known duiker (only individuals with known associates are listed).

Male Duike No.	Total No. of obs.	Months under observation	No. of associat. with known		Female Duike No.	Total No. of obs.	Months under observation	No. of associat. with known	
			Males	Females				Males	Females
11	40	38	1	-	7	24	39	1	-
14	36	18	1	1	10	61	38	1	-
15	22	10	1	-	26	20	11	1	-
18	15	13	1	-	27	21	32	2	-
20	7	35	-	1	31	23	30	1	-
22	22	27	-	1					
23	35	34	-	1					
24	22	11	1	1					
35	4	19	1	-					
42	17	10	-	1					

8.4 DISCUSSION

8.4.1. Home Range Size, Movements and Dispersal

Estimates of home range sizes depend heavily on the methods of determination that are employed (Bowen 1982) while any one method is unlikely to satisfactorily describe the home ranges of all species (Sanderson 1966). The minimum convex polygon method used in this study assumes no a priori utilization distribution or shape (Mohr and Stumpf 1966, Sanderson 1966) but suffers from a dependence on sample size and the assumption that the probability of locating an animal is equal at all points in space (Bowden 1982). The method has been further criticized by Macdonald et al. (1980) since it is very sensitive to movements on the periphery of an animal's range, irrespective of the frequency with which that area is visited, while large areas of land which are never visited can be included within the polygon if an animal's range is an irregular shape.

Attempts to overcome some of these limitations have led to modified versions of the minimum-area method where a predetermined proportion of peripheral locations are excluded in subsequent analyses (e.g. Harvey and Barbour 1965; Odendaal and Bigalke 1979a; Bowden 1982; Murray 1982; Dom and Rennolls 1983). Although such practices may be based on arbitrary decisions regarding the proportion of locations that are excluded, these methods are generally considered acceptable since they still conform to Jewell's (1966) definition of home range as "the area over which an animal normally travels in pursuit of its routine activities". However, Springer (1982) recently argued that every location should be included within an animal's home range because "occasional" movements may in fact link core areas of more intensive use - a similar approach was adopted by Leslie and Douglas (1979).

More sophisticated methods of determining home range size and utilization within that range have been proposed, reviewed and employed in a number of studies (Sanderson 1966;

Adams and Bailey 1967; Jennrich and Turner 1969; Metzgar 1972; Metzgar and Sheldon 1974; van Winkle 1975; Macdonald et al. 1980; Voigt and Tinline 1980; Don and Rennolls 1983). Several of these are less affected by sample size but depend on the assumption of a circular normal (Hayne 1949) or bivariate normal (Jennrich and Turner 1969) distribution of location records. These assumptions may be valid for some species but can lead to serious misinterpretations when the incorrect probability distribution is assumed (Bowden 1982). Furthermore, such methods may also include areas of land which are never visited by the subject and frequently there is a significant lack of fit of the bivariate normal model to observed data (Macdonald et al. 1980).

Because methods of data collection employed in this study may well have biased results, particularly with respect to visual sightings (see Chapter Seven), these limitations did not warrant the inclusion of elaborate analyses of home range size and configuration. The convex polygon method was selected because of its graphic simplicity and statistical stability (Jennrich and Turner 1969; Bowen 1982). Furthermore, since minimum area or convex polygon methods have been used in several tragelaphid studies (e.g. Allsopp 1970; Leuthold 1974, 1979; Waser 1975a; Anderson 1978; Odendaal and Bigalke 1979a; Allen-Rowlandson 1980) as well as in numerous other mammalian studies of home range (e.g. Leuthold and Sale 1973; Smuts 1975b; Leuthold 1977; Berry 1978; Whately and Brooks 1978; Leslie and Douglas 1979; Harris 1980; Hoskinson and Tester 1980; Geduldig 1981; Laundre and Keller 1984), its employment in this study facilitated direct comparisons.

Harestad and Bunnell (1979) have shown that home range size is empirically related to body mass, and that differences in the latter account for a large portion of the differences between male and female (and also adult and subadult) home ranges in mammals. Leuthold (1977) has also noted such a relationship. Since the mass of an adult female bushbuck is approximately 60% of an adult male this difference could account for female ranges being an aver 56%

smaller than those of adult males. Similarly, the approximately equal home range sizes of male and female duiker may be partially due to the slight differences in adult mass exhibited between the sexes of this species. The finding that adult female bushbuck ranges at Weza were approximately half the size of adult male ranges concurs with the results from other bushbuck studies (Allsopp 1970, 1978; Waser 1975a; Odendaal and Bigalke 1979a). However, with the exception of Odendaal and Bigalke's (1979a) study, home range sizes at Weza were appreciably larger than those recorded elsewhere. Verheyen (1955) claimed that bushbuck "territories" (see below) were approximately 2-3 ha in extent. Allsopp's (1970, 1978) work is somewhat confusing; Allsopp (1970) detailed the mean home range size of adult females, adult male and subadult males as 3 000 square yards, 6 800 square yards and 2 400 square yards respectively. Metric conversions indicate approximate ranges of 0,25 ha, 0,56 ha and 2,0 ha respectively - these values have since been cited or used for comparative purposes by numerous authors (Leuthold 1974, 1977, 1979; Estes 1974; Owen-Smith 1977) yet Allsopp's (1978) subsequent publication subscribes a 10 fold increase in these range sizes (2,5 ha, 5,0 ha and 20,0 ha respectively) with no explanation for this conversion. Jacobsen (1974) reported that the average size of an adult male bushbuck territory was 5,7 ha (no range or sample size give but only one male was seen on more than 15 occasions) and Simpson (1974c) reported a similar mean value of 5 ha from six animals (sexes not given) each seen on more than 10 occasions. Waser (1975a) found mean home ranges of adult males and females to be 19,8 ha ($n=3$, range=15-26 ha) and 11,8 ha ($n=5$, range=6-19 ha) respectively while the one subadult male monitored had a home range of 35 ha. In contrast, Odendaal and Bigalke (1979a) recorded home range sizes of 14,6 ha for a lactating female, 113,6 ha for a subadult female, 153,2 ha for a subadult male and 55,0 ha and 174,3 ha for two adult males (mean home range size determined from these five animals was 102,1 ha, $\pm 66,8$ ha S.D.). The mean home range size of 38 male and female bushbuck each located on a minimum of 20 occasions at Weza (100,8 ha $\pm 62,5$ ha S.D.) is therefore somewhat smaller than the mean range

size determined for bushbuck in the southern Cape (Odendaal and Bigalke (1979a) employed the modified minimum home range method of estimation), although the difference may be partly attributable to the small number (five) of animals monitored in the earlier study.

Various factors may be responsible for these pronounced differences in home range size between bushbuck inhabiting timbered areas and those occupying more natural habitats in Botswana, Zimbabwe, Kenya and Uganda. Odendaal and Bigalke (1979a) found a significant negative relationship between home range size and bushbuck densities (also see Jewell 1966 and Sanderson 1966), although smaller home range sizes may also result from reduced competition (Leuthold 1977). However, the most probable reason for these differences concerns the productivity of the different habitats (Jewell 1966); Odendaal and Bigalke (1979a) found a significant relationship between bushbuck density (and therefore by inference, home range size) and rainfall during the growing season (the latter being considered as a function of productivity; see Coe et al. 1976). Similar findings of an inverse relationship between home range size and habitat quality have been noted in a number of other studies (e.g. Leuthold and Sale 1973; Smuts 1975b; Amstrup and Beecham 1976; Leuthold 1977; Lindzey and Meslow 1977; Loft et al. 1984;). These results therefore suggest that bushbuck inhabiting timbered areas at Weza (and in the southern Cape, Odendaal and Bigalke (1979a)) occupy ranges that are much more inferior than those occupied in more natural vegetation types. Differences in habitat quality would also explain the comparable home ranges sizes of bushbuck at Weza and the much larger congeneric kudu inhabiting bushveld in the Eastern Cape (Allen-Rowlandson 1980). At the local level, duiker ranges in I.S.A.2 were significantly smaller than those inhabited in the first intensive study area. Since the latter region consisted largely of intermediate aged and mature pines which were non-preferred duiker habitats (Chapter Seven), the quality of such stands may have contributed to the larger duiker ranges observed in this area. Finally, results from this study have demonstrated

that home ranges determined from telemetry were generally larger than those determined for the same individuals from sighting data. Since all bushbuck home range sizes reported from natural habitats were based on sightings, but those obtained in this study and by Odendaal and Bigalke (1979a) were based partly and entirely on radio tracking data respectively, then the magnitude of the actual differences in home range sizes may be considerably less than that indicated above (also see Amstrup and Beecham 1976).

The subadult male bushbuck studied by Waser (1975a) and Allsopp (1970, 1978) had larger home ranges than adult males. A similar trend was apparent in this study when male ranges were determined by telemetry, but subadult male ranges were not significantly larger than those of adult males when sighting and radio tracking data were combined, and were considerably smaller when based solely on observations. Similarly, the size (153 ha) of the subadult bushbuck home range studied by Odendaal and Bigalke (1979a) fell within the two values of 55,0 ha and 174,3 ha recorded for adults. These differences in subadult male home range sizes relative to adult males may have been due to the small numbers of animals monitored in each of these studies, and also because the shift in home range as a result of dispersal witnessed in this study was not included in home range size analyses. The significantly larger home range sizes of subadult females compared to adult females observed at Weza may have been due in part to the frequency with which each age class was monitored and also to movements of primiparous females seeking more isolated areas (particularly as they subsequently returned to their former ranges - these extended movements never resulted in dispersal).

Seasonal variations in the sizes of bushbuck home ranges recorded at Weza initially appear somewhat surprising. In view of the above discussion, smaller ranges would be expected during spring and summer, since habitats were most productive at these times and food was considered to be superabundant. Contrary to these expectations, bushbuck ranges were generally larger in spring and summer. The most

plausible explanation for this apparent anomaly is that autumn and winter ranges included habitats containing localised food resources; an obvious example being the oak stands in I.S.A.1 which were highly selected at these times (Chapter Seven). It is therefore suggested that bushbuck were socially more tolerant at times when food resources were limited and exhibited a greater degree of mutual intolerance as forage quality and availability improved. Although somewhat speculative, the larger daily and three hourly movements of both males and females during spring and summer and the general, but not significant, increase in group size during late autumn and winter (which is considered to have resulted from aggregations rather than any change in group stability or cohesion), when animals spent less time foraging than at other times of the year, support this conclusion. Aggregations in response to localised food resources have been noted in several other herbivore species (Hanks et al. 1969; Hawkins and Klimstra 1970; Geist 1974; Leuthold 1978a, 1978b; Leuthold and Leuthold 1975b; Hardin et al. 1976; B. Leuthold 1979; Leuthold and Leuthold 1978; Dzieciolowski 1979; Russell 1979; Bresinski 1982; Green et al. 1984). Alternatively, bushbuck may simply have spent less time feeding during winter, when food reserves were poor relative to individual requirements, and utilized fat reserves in an attempt to minimize energy expenditure; Dunbar (1979) suggested that such a strategy is adopted by Klipspringer in Ethiopia (also see Chapter Four). However, the increase in active behaviour exhibited by bushbuck during winter nights, even though actual distances travelled and the proportion of time spent feeding were less than other times of the year, does not support the suggestion of a voluntary reduction in winter foraging.

Since bushbuck never used any portion of their home ranges exclusively during any one season, the population at Weza (or at least in the intensive study area) must be regarded as a largely sedentary one. Since shifts in home range were not apparent, seasonal changes in the intensity of range use could be detected by changes in the centres of activity. Although geometric centres of activity have been

determined in numerous ungulate studies (e.g. Hawkins and Klimstra 1970; Downing and McGuinness 1975; Inglis et al. 1979; Leslie and Douglas 1979; Murray 1982; Gavin et al. 1984), it is appreciated that if individuals have several biological centres of activity, none of these may necessarily coincide with the arithmetic mean of locations (Don and Rennolls 1983). Nevertheless the mean linear distances separating day and night centres of activity both seasonally and throughout the year (Table 8.7) never exceeded 350 m and again illustrate the sedentary nature of all marked bushbuck monitored at Weza. (Interseasonal distances between both day and night centres of activity were generally larger but never exceeded 550 m; see Table 8.8.) Few previous bushbuck studies have considered seasonal patterns in home range use. Jacobsen (1974) recorded a seasonal shift in the home range of one adult male (the only adult male observed on at least 15 occasions) and noted local movements resulting in concentrations of bushbuck during the dry season and dispersal in the months receiving high rainfall. Similar movements were recorded by Simpson (1974a, 1974c) which he claimed were in response to the availability of surface water; the validity of such an assumption has been seriously questioned (see Chapter Seven) and furthermore was not supported by Jacobsen's (1974) emphatic statements regarding movements of the population studied in Zimbabwe.

While their ranges were considerably smaller, and inadequate sampling prevented any evaluation of seasonal variations in range use, the determination of centres of activity, or individual movements, duiker generally exhibited a similar trend in that animals ranged over the largest areas in spring (Table 8.10). This species differed from bushbuck however in that winter ranges were generally larger than those occupied in summer and autumn, although most duiker ranges in winter did not include obvious localised food resources such as oaks etc.

Caution should be exercised in the interpretation of movements and distances travelled by bushbuck in this study. Although the practice of measuring linear distances between

two consecutive locations is common in the literature (Alexander 1968; Goddard 1970c; Samuel and Glazener 1970; Woolf et al. 1970; Hawkins et al. 1971; Kurz and Marchington 1972; Verme 1973; Augee et al. 1975; Amstrup and Beecham 1976; Inglis 1976; Miller et al. 1977; Sempere 1980; Springer 1982) the resultant distance must be regarded as a minimal value. Bushbuck movements recorded over differing time intervals clearly illustrate this underestimation. Daily (24 hour) movements of males averaged 525 m while those recorded at three hourly and one hourly intervals were 227 m and 348 m respectively. Earlier it was stated that the similar magnitudes of daily, three hourly and one hourly travel rates may have been due to inaccurate and/or insensitive methods of location. Such a situation is considered unlikely for the following reasons. Firstly, travel rates of male bushbuck were invariably greater than those of females irrespective of season or time interval, and in most instances these differences were significant. If locations were inaccurately recorded, then errors would presumably have been common to both sexes, and these would not have yielded significant differences. Secondly, individual movements measured over daily or three hourly intervals on a seasonal basis showed close agreement with the sizes of home ranges occupied during that period (e.g. increased movements by males during spring). Again if movements were based on erroneous locations, these would have occurred throughout the year and should not have provided significant differences in seasonal movements. Finally, movements determined over three hourly intervals generally corresponded with the dominant activities of bushbuck during the corresponding period (Tables 8.9 and 8.11). Consequently, these results are considered to be a true reflection of bushbuck movement patterns. Since the difference between daily and hourly or three hourly distances travelled were slight, this suggests that bushbuck movements were either confined to a fairly intensive area throughout the day or that on leaving one site, they ranged over a wider region before returning to the general vicinity of that original site. Individual distances monitored over a 24 hour period suggest that both patterns of movement may be exhibited by different animals at the same time (Fig. 8.18).

Summation of the average (minimal) distances travelled by bushbuck every 3 hours during a 24 hour period (Table 8.9) indicate that males and females travelled 2 437 m and 1 899 m respectively yet were located on average 525 m and 303 m respectively from their original positions 24 hours earlier. Movements of a similar magnitude have been reported from other populations. Waser (1975b) recorded mean distances of 1 265 m and 780 m travelled by male and female bushbuck respectively during daylight hours, yet these animals had appreciably smaller mean home range sizes of 19,8 ha and 11,8 ha respectively, of which only approximately half of these areas were used during the day (Waser 1975a). Okiria (1980) studied the same population of bushbuck and found that actual distances (by following individuals) averaged 505 m during the day and more than doubled to 1 163 m at night for both sexes. In addition to greater movements at night, Waser (1975a) found that bushbuck ranged over a comparatively wide area after dark which was not utilized during daylight hours.

Bushbuck are generally considered to be nocturnal (Dorst and Dandelot 1970; Wynne-Jones 1980; Smithers 1983) and since little direct information on their nocturnal activity is available, these conclusions are presumably based on the degree of daytime inactivity shown by this species. Comparisons of three-hourly distances travelled by bushbuck throughout a 24 hour period and the greater proportion of time spent both feeding and walking at night, support these conclusions. In contrast, Waser (1975a) could not detect any nocturnal peaks in the population he studied, and in the absence of any 24 hour cycles of behaviour, he concluded that bushbuck distributed their activities in a pattern of short-term cycles. Furthermore, nocturnal-diurnal comparisons revealed that bushbuck spent less time feeding at night (25% compared to 38% during the day) and a similar trend was evident for lying behaviour, while both sexes displayed pronounced crepuscular peaks of movement. Differences in the activity patterns of bushbuck at Weza and those studied by Waser (1975a) may partly be attributable to the effects of disturbance caused by the more intensive management practices at Weza; a change in activity patterns

(often with a shift towards more nocturnal activities) in areas where animals are subjected to disturbances (including hunting) has been noted for bushbuck (Smithers 1971; Kingdon 1982) and duiker (Wilson and Roth 1967; Rautenbach 1982; Smithers 1983) and numerous other ungulates species (Batcheler 1968 cited in Geist 1971b; Behrend and Lubeck 1968; Geist 1971c cited in Schultz and Bailey 1978; Roseberry and Klimstra 1974; Leuthold 1977; Mitchell et al. 1977). However, Waser's (1975a) findings were not supported by Okiria (1980) even though the same population was studied. Okiria (1980) concluded that bushbuck were less active during the day than at night and that a greater proportion of time was spent feeding after dark. Possible reasons for these different findings obtained from the same population were not considered in the more recent study by Okiria (1980).

Although limited by sample size, the results of this study indicated that duiker had shorter cycles of activity that were more uniformly distributed throughout the 24 hour period (Table 8.11), but feeding remained the dominant activity at night (Table 8.13). Since an animal's activity budget is determined by its energy requirements (Dunbar 1979), these findings closely correspond with those expected of a small ruminant with relatively high energetic demands (i.e. with a small rumen volume, short turnover time, high fermentation rate and a highly selective diet; see Chapter Six).

The three translocation experiments performed at Weza clearly demonstrate the strong attachment bushbuck have to a home range. Homing experiments with the territorial Uganda Kob (Adenota kob thomasi) revealed a similar fidelity to specific areas, even though animals were released in new surroundings that appeared perfectly suitable to the researcher (Leuthold 1966, 1970b). Strong attachment to a home area is not confined to territorial species however (e.g. Hanks 1968 cited in Leuthold 1977); natural examples of this phenomenon have been witnessed in all social categories of an impala population (Jarman 1970) and also among cervids (Adderson 1958 cited in Leuthold 1970b;

Marshall and Whittington 1968 cited in Mitchell et al. 1977; Verme 1973; Staines 1974). As Jarman (1970) points out, one can only speculate on the functions of this behaviour, although familiarity with the resources and topography of an area have obvious advantages in predator avoidance and efficient utilization of the habitat. That bushbuck were seemingly unaffected by human disturbances associated with forest management practices provides further evidence of their attachment to specific areas, and it is suggested that it is the outcome of such activities rather than the actions alone that are likely to influence bushbuck movements and range utilization. Even when disturbances are much more pronounced (e.g. hunting, harassment by dogs or intensive ranching) deer have been shown to maintain fidelity to their home ranges (Progulske and Baskett 1958; Sweeney et al. 1971; Hood and Inglis 1974; Downing and McGinnes 1975) and this behaviour led Leuthold (1977) to redefine home range as "the area that an animal is familiar with and does not leave voluntarily". Finally, McCullough (1969) cited in Mitchell et al. (1977) makes the obvious but valid point that disturbance will only cause animals to move permanently away if there is another suitable area nearby. Thus the response to any disturbance is probably influenced by the strength of the stimulus, the alternatives facing the animal and learning from previous encounters (Mitchell et al. 1977)

Since several of the marked subadult males occupied their natal home ranges throughout the duration of field work, and these overlapped extensively with those of adult bushbuck, this would indicate that the one incidence of bushbuck dispersal witnessed in this study was a voluntary movement. Similarly, extended movements of young kudu bulls could not be attributable to expulsion by or harassment from older males or females, although mothers appeared to be intolerant of their offspring during the highly seasonal calving period of this more social species (Allen-Rowlandson 1980). Due to the age of this male at the time of dispersal, it is unlikely that the animal left in search of a mate and none of the other possible reasons proposed by Hough (1980) as to why an animal may leave its home range (e.g.

unsuitable habitat, better food resources elsewhere and climatic or weather influences) provide a satisfactory explanation (also see Hawkins et al. 1971). Disturbance as a cause of this dispersal also seems unlikely in view of the above discussion (also see Downing and McGinnes 1975). While the dispersal by one sex may be in response to selection against inbreeding whenever individuals are closely related and costs of such movements are low (Packer 1979 cited in Murray 1982), dispersal would have to be much more common than that observed at Weza to have any adaptive value. Clearly, the data obtained in this study fall far short of the information required for a detailed study of dispersal (Caughley 1977) but this tendency towards greater movements by subadult bushbuck and duiker, (especially males) is consistent with general patterns of dispersal in ungulates and other mammals (e.g. Hawkins and Klimstra 1970; Hawkins et al. 1971; Hitchins and Vincent 1972; Jarman and Jarman 1973; Verme 1973; Downing and McGinnes 1975; Hardin et al. 1976; Greenwood 1980).

Although duiker dispersal was only witnessed on one occasion, the high incidence of marked animals that were rarely seen after capture or that "disappeared" during field work suggests that dispersal occurred more frequently in this species. Since duiker ranges tended to exclude other adult members of the same sex, dispersal was most probably due to expulsion of those animals approaching sexual maturity, although the precise ages of animals exhibiting extended movements could not be ascertained in this study. Duiker occupied much smaller ranges than bushbuck and local disturbances and modifications to habitats may have had a much more serious consequence to duiker; this aspect is considered in more detail in Chapter Ten.

8.4.1.1 Exclusiveness of home ranges

Bushbuck at Weza do not appear to have exclusive home ranges because there was substantial overlap within and between all sex and age classes (Fig. 8.3 to Fig. 8.7). Not

all of the animals in the intensive study area were marked, and overlap was probably much greater than that determined in this study. As a result of this overlap, which was 100% in certain instances (e.g. Fig. 8.3), any exclusive use of even a small portion of a home range must have involved temporal rather than spatial separation. While such temporal separation was evident among males (e.g. the relatively low incidence of bachelor groups, the low proportion of males occurring in such groups and the low indices of association between marked males) it was also evident among females as well. Indeed, grouping patterns of both males and females tended to exhibit mutual avoidance of other individuals of the same sex, but this avoidance need not necessarily imply any functional significance with regards to exclusiveness of range use, as such avoidance was also evident among members of the opposite sex for much of the time. It is therefore suggested that mutual avoidance serves as an antipredator strategy since this species largely relies on crypsis and stealth to avoid detection. Such a strategy would presumably be less effective as group size increased because of increased auditory signals and a greater difficulty in remaining inconspicuous (Geist 1974; Waser 1975b). Clearly, avoidance of conspecifics need not be solely due to antipredator behaviour; this behaviour would also be advantageous if bushbuck selected discrete food items that had a patchy or localised distribution (Jarman 1974; Barrette 1977). However, the extent of home range overlap manifested by the Weza population renders such an explanation improbable (also see Waser 1975b).

Most other detailed bushbuck studies have also demonstrated a high degree of range overlap among and between all sex and age classes (Jacobsen 1974; Waser 1975b; Odendaal and Bigalke 1979a, although these last authors did not monitor all of their five animals simultaneously). In contrast, Verheyen (1955) concluded that males and females defended individual territories (even though they shared common feeding grounds) while Walther (1964) reached the same conclusion regarding territoriality on the basis of captive animals showing a general avoidance of conspecifics. Allsopp

(1970, 1978) did not consider home range overlap in any detail and his figures of three exclusive male ranges (Allsopp 1970, 1978; Kingdon 1982) are considered to be misleading as he was studying a population of 31 identifiable males in an area of 2,59 km² which also included other animals not easily recognizable from their natural markings. Allsopp (1970) also delineated boundaries around possible "discrete groups", several of which included two or more adult males; these were later referred to as "family groups" (Allsopp 1978), which I consider to be misleading (see below).

Thus there have been no published accounts unequivocally demonstrating exclusive home range use in bushbuck. It is contested that these earlier accounts of bushbuck spatial organisation have been misleading; these together with highly ambiguous interpretations of territoriality have provided little to but rather hampered our understanding of the social organisation of this species and the Tragelaphines in general. This aspect is considered in further detail below.

In contrast to bushbuck, all the available evidence gathered in this study demonstrates that individual duiker exclude adult members of the same sex from their home ranges. Even in the few instances where ranges overlapped, duiker were separated on a temporal basis, while the incidence of same sex associations between adults (1% of all observed groups) demonstrates a much greater mutual avoidance than that exhibited by bushbuck.

A similar pattern of duiker spatial organisation with male ranges overlapping with those of females but not with those of the same sex (ages not specified) was recorded by Dunbar and Dunbar (1979). Males apparently defended the boundaries of their ranges, while female ranges "may have overlapped to some extent" (duration of field work was 4,5 months). In addition, these authors found that male and female ranges were of approximately equal size (dimensions not given); this trend was also evident at Weza. Sommerlatte (quoted in Owen-Smith 1977) described a slightly different

pattern of duiker spatial organisation where two or three females occupied fairly discrete home ranges within each male's slightly larger territory. However, it is not known how intensively individual female movements were studied in relation to their neighbours, and if these were not considered in any detail there is every indication to suggest that females from all three populations exhibited identical patterns of spatial organisation.

8.4.2 Group Size, Structure and Stability.

8.4.2.1 Bushbuck

Most general accounts of the bushbuck describe it as a solitary antelope (e.g. Dorst and Dandelot 1970; Wynne-Jones 1980; Smithers 1983). All of the detailed bushbuck studies (including this one) have confirmed this description in that single animals invariably constituted more than 50% of the total number of observed groups (Table 8.35). Nevertheless,

TABLE 8.35 Variations in the frequency distribution of solitary bushbuck expressed as a percentage of the total number of observed groups.

No. of groups	% Solitary	Source
44	81,8	Boulière & Verschuren (1960) *
30	86,7	Walther (1964)
74	71,6	Wilson & Child (1964)
310	57,4	Jacobsen (1974)
N/A	58,0	Simpson (1974c)
109	70,6	Waser (1975b)
188	67,0	Sheppe & Haas (1976)
399	53,9	Allsopp (1978)
31	80,7	Mason (pers. comm.)
2507	71,7	This study
* - cited in Elder & Elder (1970).		

reservations regarding the solitary nature of bushbuck have been stressed by both Elder and Elder (1970) and Waser (1975b) because many other types of groupings have been observed in this species. Furthermore, the term "solitary" has not always received consistent use among biologists, and although bushbuck can certainly be regarded as solitary in a spatial sense, this should not connote any knowledge of social behaviour or be regarded as a synonym for "asocial" (Waser 1975b; Barette 1977). As Waser (1975b) points out, the social criteria defining an animal as solitary have rarely been explicit but the term has usually been applied to situations where animals either actively avoid each other or are antagonistic to conspecifics when these are encountered. Mean and typical group sizes determined from this and other studies (Table 8.36) do not support a strategy of constant mutual avoidance while the low incidence of overt aggression observed at Weza and elsewhere (Jacobsen 1974; Simpson 1974c; Waser 1975b; Allsopp 1978) implies that mutual tolerance rather than antagonism is the predominant behaviour shown towards other individuals of the same or differing status.

TABLE 8.36 Mean and typical group sizes of bushbuck.

Total Groups	Total Bushbuck	M.G.S. $\pm$ S.D	T.G.S.	Range	Source
44	52	1,8 $\pm$ 0,39	1,31	1-2	Boulière & Verschuren (1969)*
30	35	1,17 $\pm$ 0,46	1,34	1-3	Walther (1964)
74	97	1,31 $\pm$ 0,52	1,52	1-3	Wilson & Child (1964)
167	232	1,39 $\pm$ 0,77	1,82	1-6	Elder & Elder (1970)
399	642	1,61 $\pm$ 0,76	1,97	1-5	Allsopp (1978)
36	N/A	1,33 $\pm$ 0,53	N/A	1-3	Evans (1979)
31	37	1,19 $\pm$ 0,40	1,32	1-2	Mason (pers.comm.)
2522	3400	1,35 $\pm$ 0,61	1,62	1-5	This study
*- cited in Elder & Elder (1970)					

Variations in a) the proportion of bushbuck groups consisting of solitary animals (Table 8.35) and b) mean groups size (Table 8.36) may be partly due to the disparate numbers of groups and bushbuck observed in these studies. Research conducted on other ungulate species has indicated that a positive correlation may exist between group size and population density (e.g. Spinage 1969c; Jungius 1971b; Laws 1974; Estes 1974; Joubert and Bronkhorst 1977; Leuthold 1977). However, bushbuck densities ranging from 3-5 animals per km² where 61% of all animals were solitary (Odendaal 1977) to 26 animals per km² where 71% of all animals were solitary (Waser 1975b) or 66,7 animals per km² where 57% of all groups consisted of single animals (Jacobsen 1974) suggest that bushbuck grouping patterns are largely unaffected by population size. Waser (1975b) reached a similar conclusion by comparing bushbuck densities with those of more social species in his study area.

The most probable factor influencing group size in this species concerns antipredator behaviour (Waser 1975b) although other aspects such as food availability, difficulties in maintaining group cohesion in densely structured habitats etc. cannot be entirely discounted (Jarman 1974; Allen-Rowlandson 1980; also see above). Numerous intraspecific studies have revealed a tendency towards larger group formation in those populations inhabiting more open habitats (Leuthold 1970a, 1976; Leuthold and Leuthold 1975b; Jungius 1971b; Walther 1972b; Hirth 1977; Mitchell et al. 1977; Evans 1979; Allen-Rowlandson 1980). It is interesting to note that such a relationship generally exists between members of the Tragelaphus genus, with group size increasing from bushbuck and sitatunga (Owen 1970) through lesser kudu and nyala (Leuthold 1974, 1979; Tello and van Gelder 1975; Anderson 1978) to mountain nyala (Brown 1969) and greater kudu (Wilson 1975; Owen-Smith 1977; Underwood 1978; Allen-Rowlandson 1980). However, it is unlikely that such a trend is solely due to differences in the habitats that these congeneric antelope occupy and other factors such as body size and feeding strategies are also undoubtedly important (Jarman 1974).

Reasons for the significant decrease in the mean group size of bushbuck during February and March when compared to the overall value of 1,35 animals per group at Weza are not immediately obvious. Considerable attention was given to the examination of monthly variations in group composition and the proportions of animals forming these various group types in the hope that this might provide additional data on seasonal trends in social organisation that were too subtle to detect from general observations on group size. Factors affecting grouping patterns may include environmental conditions (e.g. see Leuthold 1970a; Anderson 1972; Jarman and Jarman 1973, 1974 for comparative studies of impala, Estes 1966 and 1969 for wildebeest and Spingie 1969c and Hanks *et al.* 1969 for waterbuck) or the influences of reproductive behaviour, particularly in seasonal breeders (Rodgers 1977; Allen-Rowlandson 1980). The similar trends emerging from this and previous studies of bushbuck social organisation conducted in a wide variety of natural and unnatural habitats suggest that the basic grouping pattern exhibited by this species is largely unaffected by environmental conditions (although few previous studies have examined monthly variations in group size or variations in the levels of associations within these groups). The smaller sizes of groups in February and March were associated with an increase in the number of lone adult and subadult females at this time, as well as a decrease in the number of observed one-female groups. In addition to the greater proportion of females occupying a solitary existence, there was a concomitant decrease in the proportions of adult and subadult females occurring in one-female groups and a similar reduction in the numbers of adult males associating in bachelor groups. Since the majority of these significant changes involved subadult and adult females, the most plausible explanation for these monthly differences would involve reproductive influences. As with many other ungulates (Fraser 1968; Spencer-Booth 1970; Jungius 1970) female bushbuck probably isolate themselves prior to parturition. The duration of this pre-partum isolation is not known, since sighting frequencies of solitary females

show no distinct trends. Records from other ungulates range from 3-4 weeks in reedbuck (Jungius 1970) to a few minutes in impala (M. Jarman 1976) but most studies indicate a period of a day or so (e.g. Spinage 1969a; Clutton-Brock and Guinness 1975). After birth, the mother remains with her calf for the post-partum period (Lent 1974) which lasts for approximately 24 hours in this genus (Walther 1964). The infant then leaves its mother and selects a hiding place usually against "something vertical" and often under a canopy of vegetation (Walther 1964).

Could such differences in group size during February and March be due to an increase in the isolation behaviour of parturient females at this time, as has been suggested by Allen-Rowlandson (1980) for kudu? Since bushbuck infant hiding or lying out behaviour (Gosling 1969) lasts for four to five months (Allsopp 1970; Kingdon 1982) any increase in births during February and March should also result in an increase in the frequency of observed one-female or female groups during the period from June to August. Furthermore, assuming a gestation period of six months (Chapter Five), any increase in births during February and March should have resulted in an increase in the number of male-female associations (mixed groups) during August and September of the previous year. Neither of these expected trends were evident, and while the proportions of adult females occurring in one female groups increased significantly in May, and the proportions of both adult males and adult females in mixed groups substantially increased in June, such fluctuations were also noted at other times of the year without revealing any consistent trends. Lastly, the possibility of increased births during February and March is not supported by data from culled animals, and it is therefore considered highly unlikely that these changes in group size and composition were directly related to seasonal peaks in reproduction. These findings differ from those of Odendaal and Bigalke (1979a) but corroborate the earlier conclusion (Chapter Five) that bushbuck at Weza breed throughout the year.

Fluctuations in group size may also have been influenced by other variables at Weza. Since animals were most frequently seen alone in late summer and early autumn, when foraging conditions were probably optimal and female, bachelor and mixed groups were significantly smaller at this time, this dispersion may have been directly linked to habitat quality (also note the formation of aggregations during winter). Similarly, conditions for sighting bushbuck were generally least favourable at these times because the dense structure of the vegetation and understory impeded sighting distances; consequently group size estimation may have been underestimated by biases in visibility ranges. Finally, the lack of any trend in the proportions of animals observed in the different group types suggest that at least some of these variations may have been no more than sampling artefacts, particularly since overall values were heavily biased by the predominance of winter sightings.

Since groups containing adult female bushbuck were significantly larger than those that included adult males, this implies that females were more gregarious than males. A similar trend has been found in other Tragelaphines (Leuthold 1974, 1979; Allen-Rowlandson 1980) as well as in numerous other ungulates (Leuthold 1977). However, female group size may be biased by the presence of juveniles. Results from this study infer that it is the dependence of young animals which is largely responsible for this increased sociability among females; 68% of all adult males were observed alone but only 48% of adult females were solitary - this proportion increased to 67% if females occurring in one-female groups were included. Similarly, 67% of all subadult males observed were solitary but this proportion increased to 87% if associations (presumably non-sexual) with females were included, while subadult females seen alone accounted for 37,5% of all subadult female observations and this increased to 92% if associations with adult females were added. Since one-female groups were the most frequently observed type of group involving at least two animals and contained higher proportions of adult females, subadult females, subadult males and infants than any other level of association, this

implies that an adult female and her immediate offspring (with or without previous young) is the basic social unit in bushbuck. Further support for this conclusion comes from the fact that indices of association between females and immatures had the only values indicative of any degree of stability or permanence. These findings show general agreement with those of Waser (1975b), Allsopp (1978) and Odendaal and Bigalke (1979a). Jacobsen (1974) tended to dismiss the importance of the matriarchal group, stating that "being an obligatory association, it is not representative of true social grouping". However, since one-female groups did not consist entirely of single females and their immediate young, but may have included other older offspring as well, such units, although consisting of related individuals, were certainly social rather than obligatory groups. Similar cohesive and stable matriarchal groups, albeit with larger numbers of related females as members, have been reported for lesser and greater kudu (Leuthold 1979; Allen-Rowlandson 1980; Owen-Smith 1984), while the social units of bushbuck also resemble but are often smaller than the matriarchal or "family" groups of several deer and sheep species (de Vos et al. 1967; Hawkins and Klimstra 1970; Franklin et al. 1975; Harding et al. 1976; Leslie and Douglas 1979; Lagory et al. 1981). Indeed Allsopp (1978) used the term "family group" to demonstrate the persistence of a strong mother/young bond and a suppression of aggressive interactions between adult and maturing males. However, Allsopp (1978) included adult males in this grouping pattern, and since the term implies a degree of relatedness as well as cohesion and stability (albeit not necessarily throughout life) the inclusion of adult males in such units is not warranted (see below) and simply adds an element of confusion.

The fact that mixed groups were seen less frequently than one-female groups, and that a lower proportion of adult females occurred in such groups compared to one-female and female groups, this indicates that male-female associations were less stable. Indices of association confirm this and demonstrate the transitory nature of such relations. Similarly, both Waser 1975(b) and Allsopp (1978) remarked on

the temporary nature of male-female associations which rarely lasted longer than a few days (Waser 1975b). Since mixed groups were simply temporary associations generally between one-female social units and one or more adult males, and were evident throughout the year in relatively constant proportions, this again demonstrates the aseasonal breeding pattern exhibited by this species.

Comparisons between the other types of associations observed at Weza and elsewhere are limited by the inconsistent use of group and age classifications (e.g. Simpson 1974c) and the different interpretations regarding associations within groups of varying composition (see for example Elder and Elder 1970; Allsopp 1978; Odendaal and Bigalke 1979a). Interpretation of Allsopp's (1978) study is further hampered by the fact that the sum of his percentage frequencies of association amount to 106,4%. However, the other association that has been commonly described in bushbuck concerns relations between males. Bachelor groups at Weza were seen less frequently than any other group type involving two or more animals (irrespective of the numbers of adults within such groups) which corroborates the earlier conclusion that males are less gregarious than females. Similar findings regarding the frequency of male associations, or the relatively low proportions of males in bachelor groups, have been noted by Allsopp (1975) and Odendaal and Bigalke (1979a). As with mixed groups, indices of association indicate that associations between males were transient. Aggressive encounters were rarely witnessed at Weza, and only involved dominance or threat displays as described and/or illustrated in Walther (1964), Jacobsen (1974), Waser (1975b), Allsopp 1978 and Kingdon (1982); overt fighting was never observed. In addition, although fewer subadult males remained in one-female groups than subadult females, these results may have been biased by inaccurate classifications, while there was no evidence to suggest that young males were harassed or evicted by adult males. Allsopp (1978) reached a similar conclusion and a lack of intimidatory or aggressive behaviour by adult males towards subadults was also noted in the kudu by Allen-Rowlandson

(1980). Simpson (1974c) also commented on the low incidence of aggressive encounters among male bushbuck and Waser (1975b) concluded that "aggression does not seem to be a characteristic of bushbuck social organisation". In contrast, Allsopp (1978) went to some lengths to describe conflict situations among males, but the incidence of these was not quantified. Jackson's (1955) account of the intensity of bushbuck fighting is considered misleading as it infers this to be a common event. Similarly, Stevenson-Hamilton (1947) cited in Smithers (1983) stated that males competing for females will fight to the death and thought that more males were killed in this way than any other African antelope; such unsubstantiated claims are undoubtedly responsible for the persistent accounts of aggression, pugnacity and "courage" that have pervaded general accounts on this species (see Shaw 1947; Duckworth 1948; Dorst and Dandelot 1970; Bainbridge 1973; Zaloumis and Cross 1974; Wynne-Jones 1980; Rautenbach 1982). Additional aspects of male associations are considered below.

8.4.2.2 Duiker

Duiker are also commonly considered as solitary antelope, and are rarely seen in groups larger than two (Smithers 1966, 1971, 1983; Dorst and Dandelot 1970; Bigalke 1974; Zaloumis and Cross 1974; Hendrichs 1975a; Wynne-Jones 1980; Kingdon 1982; Rautenbach 1982; Wilson *et al.* 1984). Results from this study are in general agreement with this description, and duiker were considerably more solitary than bushbuck at Weza in both spatial and social terms. With the exception of the records of Wilson and Clarke (1962), the proportion of duiker observed as solitary animals at Weza showed close agreement with those studied elsewhere (Table 8.37) while mean and typical groups sizes were also similar (Table 8.38). Reasons why Wilson and Clarke's (1962) data differ from all other studies are not known, but their observations were made during intensive culling operations. Inadequate data prevented an examination of group size in relation to density.

TABLE 8.37 Variations in the frequency distribution of solitary duiker expressed as a percentage of the total number of observed groups.

No. of Groups	% Solitary	Source
185	68,1	Wilson & Clarke (1962)
232	85,8	Dunbar & Dunbar (1979)
41	82,9	Mason (pers. comm.)
1164	86,1	This study.

TABLE 8.38 Mean and typical group sizes of duiker.

Total Groups	Total Duiker	M.G.S. $\pm$ S.D.	T.G.S.	Range	Source
185	249	1,35 $\pm$ 0,53	1,55	1-3	Wilson & Clarke (1962)
232	266	1,15 $\pm$ 0,37	1,26	1-3	Dunbar & Dunbar (1979)
95	N/A	1,05 $\pm$ 0,22	N/A	1-2	Evans (1979)
41	49	1,20 $\pm$ 0,46	1,37	1-3	Mason (pers. comm.)
1164	1336	1,15 $\pm$ 0,38	1,27	1-4	This study.

As with bushbuck reasons for the significant deviation in M.G.S. during March when compared to overall group size are not immediately obvious, particularly since the deviation involved an increase in M.G.S. (bushbuck groups were significantly smaller at this time). Both one-female groups and bachelor groups were seen more frequently than expected during this month, and there were also significant increases in the proportions of adult females and subadult males in one-female groups and also a concomitant increase in the proportion of adult male associations.

The increase in one-female groups corresponded with an increase in the frequency of male-female associations (and the proportions of adult males and females in mixed groups) during August (adding a gestation period of 6,5 months on from August would indicate a birth peak in February-March).

However, these sightings do not account for lying-out behaviour (see Wilson and Clarke 1962; Dorst and Dandelot 1970; Rautenbach 1982; Smithers 1983; Kingdon 1982) while a birth peak in autumn is not supported by culled material. Furthermore, reproductive influences are unlikely to account for an increase in male-male associations at a time when one-female groups were most common, and in view of the fact that fewer groups were seen in March than at any other time of the year, these deviations are considered to be artefacts of sampling, as also proposed for bushbuck.

Females were slightly more gregarious than males, and this difference was undoubtedly due to the influence of offspring since 82,5% and 71,5% of all adult males and females respectively were solitary, but this latter proportion increased to 81% if females in one-female groups were added. In addition, one-female groups never exceeded a size greater than two. As only one classified female group was observed in this study, and none of the marked females associated with each other, this suggests that females either actively avoided one another or were antagonistic to members of the same sex. A similar trend was evident among males, and of the eight bachelor groups observed (0,9% of all recorded groups) six of these included single adult male-single subadult male associations, one involved two subadult males and only one involved an association between two adults. The most common association between two adults involved both sexes, but mixed groups were seen less frequently than one-female groups, indicating that these were temporary encounters. Indices of association between marked adult males and adult females confirm this conclusion. Since male and female ranges were of similar size and each excluded other members of the same sex but overlapped with those of the opposite sex, such an arrangement would suggest that the potential to associate with specific individuals of the opposite sex was relatively high. In the absence of any evidence of stable or cohesive mixed group formation, it must be concluded that males and females were socially intolerant of adults of the opposite sex except for breeding purposes. The most stable social unit was therefore probably the

one-female group, which was apparently less cohesive and of shorter duration than in bushbuck, since exclusive ranges and low indices of association suggest that animals approaching sexual maturity were evicted from their natal areas. Pubertal females were probably harassed by their mothers, while subadult males may have been expelled either by maternal aggression or more probably by one or more of the adult males with ranges overlapping different areas of the mother's range. A summary of duiker spatial and social organisation is presented below.

8.4.3 Dominance, Territoriality and Mating Strategies

8.4.3.1 Bushbuck

Conclusions regarding the level of social organisation exhibited by the bushbuck are at variance, with the result that several tantalising questions regarding social relations within the Tragelaphines in general have been posed (Estes 1974; Jarman 1974; Leuthold 1974, 1977, 1979; Owen-Smith 1975a, 1977). The primary factor responsible for this uncertainty concerns the concept of territoriality and whether or not this is displayed by bushbuck.

It is contested that the varying opinions regarding the existence or absence of territoriality in bushbuck are largely due to inconsistent (but unstated) definitions of this term. (In this regard it is interesting to note that the term territoriality has generally been avoided in the literature on North American cervids (Gavin *et al.* 1984)). This problem is not confined to studies of the Tragelaphines; there is a general lack of agreement among zoologists as to the basic characteristics or functions of territoriality, as evident from the numerous definitions that have been proposed (these have been reviewed, among others, by Jewell (1966), Leuthold (1977) and Owen-Smith (1977)). Similarly, the term "dominance" has been used inconsistently and it is obvious that both these terms require definition before embarking on

any meaningful discussion of social organisation. Dominance can be characterized as "an attribute that provides its holder with access to certain resources in precedence over other individuals, without actual contest" (Leuthold 1977). Dominance may be manifest in one of two ways; if the highest social rank achieved by an individual remains the same irrespective of external circumstances, such dominance is referred to as absolute dominance, but if the position is dependent upon some environmental parameter, such as space, then the possessor is said to have relative dominance (Leyhausen 1971 cited in Leuthold 1977). Since most definitions of a territory involve the concept of a fixed area (see Owen-Smith 1977; Brown 1975 cited in Gavin et al. 1984), Leuthold's (1977) definition that "A territory is a spatially fixed area within which a given animal consistently prevents certain other individuals from engaging in certain activities" is considered adequate for the purposes of this discussion. Hence, territoriality can be regarded as a variety (probably the most important example) of relative (space-related) dominance.

Earlier studies of bushbuck social organisation that have advocated the existence of territoriality in this species include those of Veheyen (1955), Walther (1964), Allsopp (1970) and Jacobsen (1974). These opinions influenced Owen-Smith's (1977) inclusion of bushbuck in his listing of territorial species, which did not include any other members of the Tragelaphus genus. Since all the direct and indirect evidence obtained in this and certain other studies (Waser 1975b, Kingdon 1982) do not support this opinion, re-examination of those studies claiming territoriality is deemed necessary on the grounds that previous comparisons have never considered the influence of inconsistent terminology. Simpson (quoted in Owen-Smith 1975a) also apparently concluded that bushbuck were territorial and although his findings and conclusions have yet to be published, Owen-Smith (1977) considered Simpson's evidence (pers. comm.) to be equivocal.

The earliest reference to territorial behaviour in bushbuck was made by Verheyen (1955) and was based on observations that both males and females were extremely sedentary (pear-shaped territories less than 3 ha in size), each individual inhabited small thickets and that the same paths were used when animals entered more open, common or "neutral" areas for foraging, fighting and mating. The functional significance of such territorial behaviour apparently exhibited by both males and females was not given, nor did he suggest that these "territories" were defended or exclusive. Consequently, it is contested that this interpretation is highly questionable, and such behaviour may simply have been a strategy of predator avoidance within individual home ranges (see above). Walther's (1964) implication of territoriality in this species was based on the sizes and composition of 30 groups of bushbuck observed in the wild, and the fact that captive animals tended to avoid one another, except when courting or playing; the latter activity often resulted in minor fights. Walther (1964) suggested that these findings were in accordance with Verheyen's (1955) descriptions.

In his consideration of territoriality Allsopp (1970, 1978) suggested that males do not defend an area but rather an association with an oestrous female. However, competition for females is likely to be severe in any population with aseasonal reproduction, and the potential for male-male conflict over any female in oestrus is likely to be high whether the species exhibits territoriality or not. In other words, attempts to secure the temporary mating rights with a female are no indication of territoriality as detailed above. Furthermore, it is unfortunate that Allsopp (1970, 1978) inadvertently portrayed an impression of exclusive home ranges among males (see Leuthold 1974, 1977, 1979) even though he stated that "Territorial defence was not observed", and that "the presence of several males in peaceful co-existence within any one home range would seem to contraindicate territoriality" (Allsopp 1978).

Possibly the most confusing yet emphatic statements

concerning territoriality in this species are those of Jacobsen (1974), who stated "Owing to the large number of bushbuck in the study area it appears at first that they did not possess a territory. However, several later observations indicated the contrary". I contend that Jacobsen's (1974) conclusions regarding territoriality are highly spurious, in much the same way that his initial assessments were based solely on a consideration of population size or density which has no direct relevance to social organisation. Furthermore, Jacobsen's (1974) findings of extensive home range overlap among adult males, and a conspicuous lack of serious and overt aggression between adult males were not adequately considered in his assessments of the social organisation of bushbuck. What then were the reasons why Jacobsen (1974) considered adult males to be territorial? Firstly, he established that males exhibited a dominance hierarchy which was probably based on size and/or age, as older males threatened younger individuals, irrespective of activity, when the latter approached too closely. This alone is no criteria for territoriality. A dominance hierarchy has also been noted in bushbuck elsewhere (Allsopp 1978), but in the latter study no evidence of a linear hierarchy was apparent. Although Jacobsen (1974) avoided the terms and concepts of "absolute" and "relative" dominance, he stated that a resident territorial male threatened any other dominant or subdominant male in his territory, but fighting was avoided if the intruder either returned to his own territory or acted submissively. These findings now have spatial connotations and could be interpreted as territorial behaviour (relative, space-related dominance) in much the same way as that exhibited by the solitary white rhinoceros, Ceratotherium simum (see Owen-Smith 1972, 1975b). However, Jacobsen's (1974) evidence for such behaviour is exceedingly scant. He states "on several occasions male 1 threatened male 2 when the latter was trespassing, causing him to move to his area. The reverse procedure was likewise observed. Accordingly male 1 frequented the south bank of the Lutope River and male 2 the north bank" (Jacobsen 1974). Unfortunately the samples of observations and home ranges of these two animals given in Jacobsen's (1974) Fig. 7 (page 82) do not support these

statements; neither animal's range overlaps with the other, while "male 2" was only observed on a total of five occasions, yet Jacobsen (1974) supposedly witnessed interactions between these males "on several occasions" in both ranges or "territories". Jacobsen's (1974) conclusions regarding territoriality based on these observations are therefore considered to be as highly conjectural as the irregular home range configuration he illustrated in Fig. 7 for a subadult male observed a mere three times.

Jacobsen's (1974) final indication of territoriality involves scent marking. He claimed that males rubbed their heads on branches and reeds leaving a sticky secretion with a distinct odour. Although this behaviour has also been noted by others (e.g. Walther 1964; Waser 1975b) and in this study, all of these authors have failed to detect the substances and odours described by Jacobsen (1974) and indeed Schaffer (1940) cited in Waser (1975b) found no histological evidence of glandular tissue in the forehead region. Jacobsen (1974) also proposed that urine was used to mark a home range or territory but observations from this and earlier studies (Waser 1975b; Allsopp 1978) indicate that neither urine or faeces are spatially confined in any obvious way (unlike duiker, see below). Finally, Jacobsen (1974) made no mention of the obvious inguinal glands on this species but since these are active in both subadult and adult males and females (Allsopp 1978; personal observations) it is highly improbable that such glands are used for territorial marking.

In summary, Verheyen's (1955) and Walther's (1964) conclusions are regarded as equivocal, and Allsopp (1970, 1978) considered that bushbuck were not territorial in the sense of defending an area (his comments regarding "defence" of an oestrous female are equally applicable to any ungulate species exhibiting dominance, and are therefore somewhat misleading, see below). Jacobsen's (1974) comments regarding territoriality in bushbuck are considered to be irrational and are not supported by his raw data and figures. Consequently, in my opinion, there has not been one single

study that has unequivocally demonstrated territorial behaviour in this species. Nevertheless, the social organisation of bushbuck continues to be questioned, and as a result general conclusions regarding the genus Tragelaphus have been tentative. For example, Odendaal and Bigalke (1979a) suggested that spatial territoriality was absent in bushbuck, then added that some evidence of temporal spacing was observed, and concluded that spatial territoriality, if present, was restricted to a relatively small segment of the adult male population. These opinions were based on results obtained from two adult males monitored over a period of 85 and 12 days respectively. Based on this sample size, it is not surprising that their closing remarks included "uncertainty exists whether adult males possess territories which are defended" (Odendaal and Bigalke 1979a). Since the results of both Waser's (1975b) study and this one have not provided any evidence whatsoever indicating that bushbuck are excluded from any fixed areas, and undisputable evidence to the contrary has yet to be obtained, I see no reason why bushbuck should not be considered to be truly non-territorial. If this proposal is accepted, then the similarities in group structure exhibited by the Tragelaphines also extend into their social organisation as a whole (as intimated by Leuthold 1974) since none of the larger members of the genus Tragelaphus exhibit territoriality in a well-defined form (Leuthold 1977, 1979; Owen-Smith 1977, 1984; Anderson 1978; Allen-Rowlandson 1980). Such a proposal is also in accord with the views of Leuthold (pers. comm. to Jarman 1974) who also considered that the Tragelaphines are non-territorial.

Both Leuthold (1974, 1979) and Owen-Smith (1975a) have commented that the social organisation of the Tragelaphines, and more particularly their mating system, appears to be intermediate between the territorial bovids and those with an absolute dominance hierarchy, suggesting that their social behaviour has more affinities with that exhibited by some members of the Cervidae (e.g. de Vos et al. 1967). The main factor indicative of an intermediate position between that of territorial species and that of species exhibiting an obvious

dominance hierarchy is the absence of several fully adult males in the simultaneous presence of adult females (Leuthold 1974). The infrequency with which adult bushbuck males are found associated also prompted Jarman (1974) to remark on their similarity with other territorial species, yet the defence of a 'geographically fixed and defined area is lacking. This study (and others; see Waser 1975b; Odendaal and Bigalke 1979a) has however demonstrated that Jarman's (1974) concept of "mutual antagonism" is not confined to males but is present between females, and between males and females as well. No author other than Verheyen (1955) suggested that females are territorial, yet they generally display the same patterns of behaviour towards conspecifics other than their offspring. It is therefore suggested that the intermediate level of social organisation exhibited by the Tragelaphines is strongly and directly influenced by their antipredator behaviour, which is most pronounced in bushbuck and by virtue of increasing group size, less apparent as body size increases (e.g. see Allen-Rowlandson 1980).

Accepting the considerable influence that antipredator behaviour may play in the social organisation of this species (also see Waser 1975a, 1975b) the following brief and necessarily speculative discussion demonstrates that the mating strategy of bushbuck differs little in principle with that employed by many other species with a dominance hierarchy.

Competition for mate acquisition is usually more pronounced in males than in females, because in competing a male can increase his reproductive output more than a female can (Trivers 1972). Such competition results in a dominance hierarchy with the top males often achieving exclusive breeding rights. It also leads to enhanced sexual dimorphism, such as increased body and/or horn size in males (Geist 1974; Bertram 1978; Clutton-Brock and Harvey 1983). Dominance may therefore be assessed by age-related attributes (Geist 1966b, 1971a; Bubenik 1968; Lincoln et al. 1970; Lincoln 1972; Estes 1974; Topinski 1974; Jarman 1974). In

such instances, contests between same-aged individuals must be decided by other means including varying forms of display and fighting (Geist 1966b; Clutton-Brock et al. 1979). As well as indicating social rank, the frequencies and/or durations of displays are often related to fighting ability, which may change markedly even over a short period of time (Clutton-Brock and Albon 1979).

The dominance hierarchy usually develops within bachelor groups, which commonly consist of peers (e.g. De Vos and Dowsett 1966; Estes 1967, 1969; Hanks et al. 1969; Leuthold 1970a, 1978a; Jewell 1972; Gosling 1974; Hirth 1977; M. Jarman 1979). Although relatively few bachelor groups were recorded at Weza, and these contained low proportions of the total number of males observed, it is suggested that these frequencies were influenced in part by antipredator behaviour (but see below). Sparring etc. has been noted in other populations (Jacobsen 1974; Waser 1975b; Allsopp 1978) and it is interesting to note that 82% of all bachelor groups at Weza consisted of peers. Thus, while the tendency to form bachelor groups may be less than in other species, there is a considerable amount of evidence to suggest that when formed, dominance is established during these associations.

All the data obtained from this study (e.g. overlapping home ranges, the low incidence of aggressive encounters etc.) indicate that adult bushbuck maintain an absolute social hierarchy throughout life. Similar conclusions can be drawn from the results of other bushbuck studies (e.g. Jacobsen 1974; Waser 1975b; Allsopp 1978) and since territorial behaviour is most pronounced in areas of high population density (Estes 1974; Leuthold 1977), its absence from these earlier studies (see above) is particularly significant. The same conclusion can be drawn from the absence of marking behaviour and specific urination/defaecation sites, since marking would probably be virtually indispensable to territorial species inhabiting densely structured habitats (Leuthold 1974). In addition, the extreme sexual dimorphism (which is most pronounced in the Tragelaphines, see Jarman 1974; Estes 1974; Geist 1974) and prolonged growth (see

Chapter Three] corroborate the conclusion that bushbuck have an absolute dominance hierarchy (Estes 1974; Geist 1974).

Now, assuming that bushbuck are aseasonal breeders, male competition for females is likely to be high, since comparatively few will be in oestrus at any one time. At such times, dominance is likely to be fiercely contested if more than one prime male is attracted to the oestrous female (see Allsopp 1978; Anderson 1978). Initially, this is likely to take the form of highly ritualized and elaborate threat and intimidation displays (described by Walther 1964; Jacobsen 1974; Waser 1975b; Allsopp 1978; Kingdon 1982). These displays may result in one of the males departing from the contest, since the possible costs incurred in fighting may be sufficiently great (see Geist 1971a; Wilkinson and Shank 1976; Clutton-Brock *et al.* 1979) that they outweigh the benefits of mating. If neither male retreats, then overt fighting, as witnessed by Allsopp (1970, 1978), Jacobsen (1974), Waser (1975b) and Kingdon (1982), is likely to occur, but all of these authors imply that such encounters are rare. Thus the benefits are likely to exceed the costs when a prime male approaches a male of lower status (usually younger and therefore smaller) associating with an oestrous female. In this situation the approacher should avoid possible injury by departing and searching for another opportunity. If he elects to stay, evidence suggests that he may be tolerated provided that no interest in mating is shown (also see Allen-Rowlandson 1980; Owen-Smith 1984). Since the ritualized courtship of bushbuck and other Tragelaphines is fairly elaborate (Walther 1964) any attempt to mate by the subordinate male would quickly attract the attention of the dominant animal, and presumably result in the former's eviction. Such a strategy assumes that males should avoid all others of an identical or higher status (which is predetermined during previous encounters). Thus the low frequencies with which males associate with one another may not be due solely to antipredator behaviour, but may also be influenced by strategies favouring mate acquisition. Such strategies would also partially account for the different levels of gregariousness and group cohesion exhibited between

males and females (although an additional factor influencing female group stability is undoubtedly the mother-offspring bond.)

Owen-Smith (1977) has suggested that two forms of mating system may exist in ungulates possessing an absolute hierarchy. The first involves a stable ranking dominance as found in buffalo (Sinclair 1974, 1977) and eland (Underwood 1975), while the second is based on a more temporary, roving dominance, which is established in the presence of oestrous females (e.g. Geist 1971a; Grubb 1974b). Anderson's (1978) reasoning for suggesting that nyala have a roving dominance (e.g. unstable male groups and association, widely overlapping home ranges etc.) are equally applicable to bushbuck both at Weza and elsewhere (Jacobsen 1974; Waser 1975b), except that there was no evidence from this study suggesting that dominance is determined in the presence of an oestrous female (but see Allsopp 1970, 1978 and Kingdon 1982). However, as in this study, Anderson (1978) rarely witnessed courtship and mating and never observed males fighting. The fact that dominance contests in the presence of an oestrous female were never seen at Weza need not imply that they did not occur; mating was also never observed but the high rates of productivity recorded during this study indicate that this was hardly a rare event. Consequently the possibility that bushbuck have a temporary roving dominance cannot be dismissed.

Nevertheless, it is probably that bushbuck and other Tragelaphines (see Leuthold 1974, 1977; Allen-Rowlandson 1980; Owen-Smith 1984) contest for social rank throughout the year, since dominance displays and interactions were observed in the absence of females, often when males were feeding, and frequently when one animal was prompted to move by the presence (disturbance) of the author. The establishment of such a social hierarchy would be facilitated by the small-scale movements and sedentary nature of this species, which presumably result in a high potential for repeated contact; also see Waser (1975b) and Owen-Smith (1984). Once social positions have been established, methods of assessing

the rank of potential competitors in future encounters may be based on individual recognition or on traits so subtle that they have yet to be recognised by biologists. Such assessments would explain the mutual avoidance of males and low incidences of conflict exhibited in this and other aseasonally breeding Tragelaphine species (Anderson 1978; Leuthold 1979). Protracted overt fighting is then only likely between two equally matched strangers or between two mutually known animals with little difference in their social status, when both consider the benefits of mating to justify the risks of fighting. In all other instances the social status of any individual male will largely depend on the ranks of the other males in his company; this will clearly fluctuate according to his temporary associations while searching for females. The mating system of bushbuck and other Tragelaphines (see Allen-Rowlandson 1980; Owen-Smith 1984) may therefore be intermediate between a stable ranking dominance and a temporary roving dominance, particularly since these are not mutually exclusive systems (Owen-Smith 1977).

In conclusion, data resulting from this study clearly illustrate that the social organisation of the bushbuck is very similar to that of other Tragelaphines, with the exception that antipredator behaviour is most pronounced in this species and results in a more solitary disposition than that observed in other members of the genus. In this regard, bushbuck do not conform precisely to the characteristics of Jarman's (1974) Class B level of social organisation, but there are sufficient other similarities to warrant their inclusion in this category. Jarman (1974) also acknowledges the difficulties of subdividing a continuum. The only other social category bushbuck might conform to is Jarman's (1974) Class A, but comparisons between the level of social organisation of bushbuck and a representative of this latter class, the common duiker, reveal such pronounced differences (see below) that any uncertainties regarding the inclusion of bushbuck with other Class B ungulates (see Jarman (1974) and Leuthold (1977)) can immediately be dispelled. Although Jarman (1974) placed nyala and kudu in a different category

(Class C), further research (Anderson 1978 and Allen-Rowlandson 1980 respectively) has indicated that his division of the Tragelaphus species into two levels of social organisation was not justified (Allen-Rowlandson 1980); results from this study and the above review of earlier work on bushbuck corroborate this conclusion.

8.4.3.2 Duiker

There is much less controversy surrounding the level of social organisation exhibited by duiker, and in contrast to bushbuck, all available evidence obtained in this study corroborates earlier findings suggesting that this species is territorial (Verheyen 1951 cited in Kingdon 1982; Bigalke 1974; Estes 1974; Jarman 1974; Hendrichs 1975a; Leuthold 1977; Owen-Smith 1977; Dunbar and Dunbar 1979; Kingdon 1982). Although the solitary nature of this antelope (particularly when compared to bushbuck) need not imply territoriality (see above and Barrette 1977) the most convincing evidence indicative of territorial behaviour concerns the lack of spatial and/or temporal overlap of home ranges among members of the same sex. Other indications of territorial behaviour include scent marking with pre-orbital glands and the formation of dung piles, both of which were observed in captive animals during this study. One 24 month old male kept in semi-captivity marked fence poles, shrubs and tree stumps with his pre-orbital gland; this action left a visible, dark deposit on the marked surface. Marking intensity greatly increased when secretions from other (culled) adult male glands, smeared onto stakes, were introduced into his enclosure. Although other objects were also marked, stakes containing secretions from conspecifics were marked six times more frequently than untreated stakes placed less than 2 m away. Pre-orbital gland scent marking has also been observed in wild as well as captive common duiker elsewhere (Bigalke 1974; Zaloumis and Cross 1974; Dunbar and Dunbar 1979; Kingdon 1982). Pre-orbital glands in female duiker are much less pronounced, and the captive female at Weza was never seen marking; a similar lack of

marking by females was noted by Dunbar and Dunbar (1979) but apparently was witnessed by Bigalke (1974). Similarly, the mutual scent marking by individual Maxwell's duiker recorded by Ralls (1971, 1974) was not observed by Dunbar and Dunbar (1979) or during the course of this study, but Sikes (1958) observed a male marking a female during courtship. Although duiker also possess interdigital and inguinal glands (Muller-Schwarz 1983), neither sex exhibited any form of behaviour to suggest that these are actively used in scent marking (similarly, bushbuck were never seen to mark with their inguinal glands) and the functions of these glands remains rather obscure (Leuthold 1974; Walther 1978; Mainoya 1980). Both captive animals at Weza tended to defaecate in localised areas, particularly along the perimeter of their enclosure and this presumably elicited a response from other, free-ranging individuals as eleven piles of dung were counted on the outer boundary of the fenced enclosure within three months of construction. Localised duiker defaecation sites have also been observed by Hopkins (1966), Bigalke (1974) and Kingdon (1982). While neither scent marking nor dung piles unequivocally demonstrate territoriality but may be associated with other functions (see Mykytowyz 1970; Ralls 1971; Johnson 1973; Muller-Schwarze 1983) marking in this manner undoubtedly is used in a social context and may be related to social status (Ralls 1971; Leuthold 1977). Nevertheless, most authors consider scent marking and localized dung piles to be indicative of territorial behaviour in this species (Bigalke 1974; Estes 1974; Jarman 1974; Zaloumis and Cross 1974; Kingdon 1982). Interestingly, Sikes (1958) noticed a strong odour emanating from the pre-orbital glands of two male duiker during periods of conflict.

Another behavioural aspect indicative of territoriality concerns the frequency and intensity of aggressive encounters between individuals of the same sex. Only one such encounter was observed in this study, but since courtship behaviour was never seen (yet must be a fairly common event in view of the conception rates of this species and bushbuck), this need not infer that aggression is rarely exhibited by this antelope

(see above). The aggressive interaction witnessed involved the rapid pursuit of one unsexed animal (presumably a male) by an adult male duiker over a distance of more than 150 m; the activity ended when the protagonist ceased the chase but the pursued animals continued to flee from the area. Similar extremely fast chases involving males, when the chaser often attempts to jab at his fleeing opponent's rump, have been noted by Dunbar and Dunbar (1979) and Kingdon (1982). Dunbar and Dunbar (1979) considered it probable that some of these chases involved subadult males that had strayed into adult male territories and under such circumstances constituted genuine cases of territorial defence against neighbours, but unlike Wilson and Clarke (1962) and Kingdon (1982) these authors never observed aggressive chases and butts involving two females. Wilson and Clarke (1962) considered such behaviour to be "strongly suggestive of an animal with a territorial system" while Bigalke (1974) remarked that the housing of two adult males in one pen usually resulted in the death of one individual. Although Shortridge (1934) cited in Bigalke (1974) noted that males in the field appear to fight much among themselves, the frequency of several of the encounters described above may have been a consequence of captivity in confined, artificial areas. For example, Bramley (1970) remarked that fights between roe deer bucks inhabiting adjacent territories were rare, and that most aggression was directed at non-territorial bucks. Thus aggressive encounters in territorial species, including duiker, may be fairly infrequent (Owen-Smith 1977; Dunbar 1979; Dunbar and Dunbar 1979) and this level of organisation yields both low costs and low benefits when compared to rank or roving dominance systems (Owen-Smith 1977).

The functional significance of territorial behaviour in duiker could not be determined in this study and remains largely unknown. Owen-Smith (1977) points out that "in most ungulates territoriality is exclusively a male mating strategy" and that "almost without exception, territoriality is exhibited only by adult males". It is considered unlikely that territorial behaviour has evolved primarily or exclusively as a male mating strategy in this species since

all available evidence strongly suggests that females are also territorial (e.g. exclusive ranges of similar sizes to those of males, low indices of association with other adult females, emigration (through harassment?) of subadult females from their natal ranges, mother-young bonds of comparatively short duration, and reported aggressive encounters). As mentioned above, this study was more detailed than that of Dunbar and Dunbar (1979) who concluded that "Females' ranges may have overlapped to some extent" and Sommerlatte (quoted in Owen-Smith 1977) where "two or three females occupy discrete home ranges within each male territory". These earlier findings have led several authors to suggest that duiker have a level of social organisation similar to muntjacs (Muntiacus spp.); see Leuthold (1977); Owen-Smith (1977); Dunbar and Dunbar (1979, 1980) and Dunbar (1984). However even male muntjac may not be territorial (Barrette 1977) and such comparisons may therefore be misleading. If, as indicated from the results of this study, territoriality in female duiker can be confirmed, this would be the first account of a species exhibiting exclusive home ranges in both sexes. Such a system (where females may be accompanied by immature offspring but generally associated with males only for mating, even though ranges overlap with those of the opposite sex) is generally inferred to apply to a number of small artiodactyls (Jarman 1974; Leuthold 1977; Cohen pers. comm. with Owen-Smith 1977). However, none of these species have been studied in sufficient detail to permit firm conclusions regarding females holding territories independently of males (Leuthold 1977; Owen-Smith 1977). The closest level of social organisation to the system proposed above has been recorded among dik-dik, klipspringer, and reedbuck, where females restrict their movements to individual male territories but do not necessarily manifest other behavioural characteristics of territoriality (Hendrichs and Hendrichs 1971 cited in Leuthold 1977; Jungius 1971 cited in Owen-Smith 1977; Hendrichs 1975a, 1975b; Dunbar and Dunbar 1980; Oliver et al. 1978; Dunbar 1984). Evidently, cohabitation occurs mainly where suitable habitat is only locally available, and disappears where more extensively favourable habitats are occupied (Owen-Smith

1977)). Such a level of social organisation usually involves exclusive and relatively long term pair bonds, where the females may also mark the territory and mutual marking of partners occurs (Leuthold 1977). Dunbar and Dunbar (1980) examined the functional aspects of the pair bond in klipspringer and although the significance of the territory in this monogamous species remains unclear, Dunbar (1984) suggested that predator detection is greatly enhanced by such an arrangement (also see Bertram's (1980) discussion of groups size in ostriches). Kleiman (1977) proposed that duiker are monogamous and based this decision on the findings of Wilson and Clarke (1962) in that "the members of a pair occur in close proximity" and that "unisexual aggression is common". The type of pair bond Kleinman (1977) suggested duiker exhibit is facultative monogamy, which may result when a species exists at very low densities and only a single member of the opposite sex is available for mating. However, male and female duiker at Weza were observed together in mixed groups on less than 7% of occasions, whereas in the monogamous klipspringer the members of a pair were seen together approximately 85% of the time (Dunbar and Dunbar 1980). Dunbar and Dunbar (1979) also noted that duiker mixed groups constituted less than 10% of all groups seen. In addition, indices of association between marked individuals indicate that male-female encounters are relatively rare rather than stable and permanent (also see Kingdon 1982).

Nevertheless, although there is no evidence from this study to indicate that duiker are monogamous, males may contribute to an individual female's reproductive success by preventing any other males from using the resources within his territory and thus within part of that occupied by the female (also see Dunbar and Dunbar 1980). In addition, females are probably quite capable of defending their resources from other females. The combined effects of intrasexual aggression would presumably lead to spacing behaviour and could ultimately have a regulatory influence on population density (see Wynne-Edwards 1962; Ewer 1968). In their review of the role of dominance, spacing behaviour and aggression Watson and Moss (1970) list four conditions which

are necessary and adequate to demonstrate that social behaviour is an important limiting factor. Two of these conditions, namely a) a substantial portion of the population does not breed and that b) certain members of the population are capable of breeding if the dominant or territorial animals are removed, are met by the level of social organisation exhibited by duiker (see above and Dunbar and Dunbar 1979). Further research may demonstrate that duiker populations also meet the other conditions listed by Watson and Moss (1970).

While female duiker may clearly benefit from this type of organisation, in that territories tend to apportion the available habitat and this ensures that any breeding female and her young have almost exclusive access to the resources they require, it is difficult to envisage the functional significance of male territorial behaviour. Due to the largely solitary nature of this species, exclusive home ranges in both sexes are unlikely to confer any advantages in predator detection. Furthermore, if the primary effects of territoriality are to provide a framework within which individual males compete to win exclusive mating rights in a given area and once established can exert these rights with a minimum of interference by other males (Jarman 1974; Leuthold 1977; Owen-Smith 1977) adult male duiker are unlikely to benefit from such an arrangement. This is because female ranges do not overlap entirely with those of males, but rather partially overlap with two or more individuals. Neither male therefor has automatic nor exclusive breeding rights with any individual female. If territory size is largely a function of resource requirements and habitat quality, (as suggested in this study) then female territories are unlikely to be much smaller than those of males (see above). One way males may then secure mating rights is to extend their territories to encompass those of one or more females; however, it may not be physically or practically possible to defend such extended areas effectively (see Barrette 1977; Dunbar 1984), particularly in timbered areas where "essential" territories may in any case be much larger than those in more productive areas for the same reasons give

above. Unfortunately there have been no published accounts qualifying territory size in this species; Wilson (1966a) and Wilson and Roth (1967) simply refer to duiker occupying "a very small or restricted home range". Varying densities of duiker recorded in different habitats (see Chapter Nine) suggest that density and therefore presumably territory size is related to habitat quality. Could duiker male territories increase in size compared to areas occupied by females in more productive areas, and totally include the territories of one or more females, as in the arrangements suggested by Sommerlatte (quoted in Owen-Smith 1977)? Results from this study suggest that such a situation is unlikely; territory sizes in I.S.A.2 were significantly smaller than in I.S.A.1 yet showed the same spatial arrangement as in the latter area, while territory sizes did not differ between the sexes. Clearly then, social behaviour and attempts to secure exclusive mating rights are not the only factors responsible for the spatial distribution of duiker at Weza.

Owen-Smith (1977) listed several other conditions favouring territoriality, including a) habitat seasonality, b) local population size, c) predation pressure, d) size, cohesion and mobility of female groups and d) food selection. His concept of habitat seasonality refers to Geist's (1974) suggestion that a vast seasonal superabundance of forage produced during temperate summers allows males to store extensive fat reserves which are later used to sustain them in a brief but intense rut. Owen-Smith (1977) proposes that territoriality, which is more prevalent among tropical ungulates, prevents such intense interactions since males are unable to deposit extensive fat reserves due to the fact that population levels in such climates usually approach the carrying capacity throughout the year. This proposal has been criticised by Spinage (1982) and it is probable that the major role of fat deposition is to ensure that individuals have sufficient reserves to survive the harsh winters. As Spinage (1982) points out, if fat reserves of tropical ungulates are depleted during the rut, the exhausted animal has a better chance of replenishing these than do temperate zone species where the rut often takes place at the onset of

winter. In any event, duiker breed throughout the year and are therefore unlikely to be subjected to intense periods of interaction and an associated decline in physiological condition for any length of time. Owen-Smith (1977) also considered that because tropical zone ungulates maintain higher local population densities than temperate zone species of similar size, conditions are less easy for individual recognition and it becomes more difficult to maintain dominance rankings without frequent contesting. Again, such conditions are unlikely to apply to duiker because of their solitary nature and relatively low population densities throughout Africa (see Chapter Nine). Because combat frequency is likely to be reduced in a territorial system, this level of organisation may be favoured in areas where predators are numerous (Owen-Smith 1977). However, reasons why duiker are territorial are unlikely to be due solely to predation pressure because solitary animals may in many respects be more vulnerable than individuals living in pairs (Dunbar and Dunbar 1980; Dunbar 1984) or groups (Bertram 1980) and furthermore such a level of organisation is not exhibited by bushbuck inhabiting the same areas. Owen-Smith (1977) further proposes that where females are wide ranging so that their location during the breeding season is unpredictable, this would favour the establishment of stable dominance rankings among males. But when females are associated in small cohesive groups that are sedentary, a territorial male can move within such a group and dominate its movements without excess expenditure. It would appear that duiker males are rarely, if ever, able to adopt such a strategy and from the arguments above their territories must have additional functional significance. Finally, Owen-Smith (1977) supports Jarman's (1974) suggestion that species with a highly selective diet feeding on discrete, limited food items that are in a relatively predictable (in time and space) supply would benefit by being territorial since exclusion of other conspecifics would significantly enhance the food available for the occupant(s). The results of this study support Jarman's (1974) conclusions regarding the classification of duiker in terms of both feeding style (Chapter Six) and social organisation. Thus not only is it

beneficial for duiker to feed by themselves but also to exclude others from removing discrete and highly nutritious food items that will not be replenished until the following year. The feeding strategy of this species may therefore more fully explain its level of social organisation than any other factor. Clearly more research is required before definitive conclusions regarding the proximate and ultimate factors explaining territorial behaviour in duiker can be made. Nevertheless, Leuthold (1977) also considers the role of territories in small solitary or monogamous species to apportion the habitat, and with it the food supply, among the social and/or reproductive units of the population. Spinage (1982) does not confine this function to solitary or pair bonding ungulates but suggests that territorial organisation, in contrast to the rank hierarchy, operates to select for the male which can hold his place in the environment. Consequently "he defends, first and foremost, a territory - a place in which to live. His mating activities become subordinate to this and thus do not lead to exaggerated development. In evolutionary terms this makes it the most efficient method, and we find it to be the most common" (Spinage 1982).

CHAPTER NINE

ABUNDANCE OF BUSHBUCK AND DUIKER

9.1 INTRODUCTION

Theoretically, there is no reason why large terrestrial mammals cannot be counted accurately to achieve a census, or sample counted to give estimates of population size or density (Mitchell et al. 1977). However, in practice, counting problems arise through movements and concealment; animals may be camouflaged or obscured by habitat or topographic features, or they may actively avoid the observers. Thus populations are generally more difficult to assess in woodlands than in open habitats, and in hilly terrain than on flat ground. Furthermore, animals that are widely dispersed are easy to miss, while large groups may be difficult to enumerate due to movements, and extensive areas of a continuous habitat type present different counting problems compared with smaller and more heterogeneous areas.

9.1.1 Methods Currently Employed In Monitoring Animal Abundance.

There is an extensive literature on estimating animal numbers but Overton (1969), Seber (1973), Caughley (1977), Eberhardt (1978), Norton-Griffiths (1978) and Collinson (1982) have classified and covered the main procedures together with their statistical backgrounds. Choice of method depends partly on the specific needs of the investigation which may vary from some form of density index capable of detecting population differences or changes to information on population size and composition. In addition to census objectives, choice of method may also be influenced by ecological and practical considerations, while problems are frequently encountered when attempting to assess the reliability of estimates made using any of these techniques (Mitchell et al. 1977).

Total or sample counts have frequently been conducted by aerial surveys (e.g. Bergerud 1963; Jolly 1969; Watson et al. 1969; Eltringham 1972; Sinclair 1972; Eltringham and Din 1977; Norton-Griffiths 1978; Floyd et al. 1979), although the popularity of this technique should not infer that the results obtained are exempt from any sources of error or bias (e.g. see Caughley and Goddard 1972; Pennycuick and Western 1972; Caughley 1974; Caughley et al. 1976; Norton-Griffiths 1976; Melton 1978b, 1978c; Beasom 1979; Beasom et al. 1981). Obvious advantages of operating from the air include speed of survey which may permit the coverage of more extensive areas, animals may be located in areas where access from the ground is difficult or impossible (Norton-Griffiths 1978), while bias from observer disturbances may be reduced (Caughley 1977). Disadvantages associated with aerial censusing have been listed by Collinson (1982), but the most serious of these is that a high proportion of animals may escape detection in moderately to densely wooded habitats (Caughley 1979a; Evans 1979). Animals that are inconspicuous by virtue of their size, colour, and/or posture tend to exacerbate this problem (Collinson 1982).

Total counts can rarely be accomplished on the ground unless study areas are small, although the entire region of interest may be surveyed at different times (e.g. Martinka 1969; Melton 1978a), albeit usually to determine distribution rather than abundance (e.g. Bayless 1969; Martinka 1968; Evans 1979). More frequently, sample counts are made using either direct or indirect methods. Some of the former methods include counts related to measurements of area that may be determined from transects, plots, strips or standard routes. Line transect methods (Kovner and Patil 1974; Sen et al. 1974; Anderson et al. 1979; Burnham et al. 1980, 1985) involve estimating density directly on a one dimensional sample line; densities are determined from the numbers of animals detected both on the sample line and at given perpendicular distances on either side of the line. They therefore differ from another form of plotless sampling, the line intercept method, where only animals encountered on the line are included; the accuracy and precision of this latter

method may be severely limited in many populations due to mobility and relatively low densities (Collinson 1982).

Block or plot sampling usually refers to the strategy of sampling irregularly shaped blocks that are demarcated on the ground by physical features such as roads, rivers, forest edges etc. Animals may be counted by any of several techniques within such blocks, the most common being the drive count where the area is systematically searched by a line of beaters spaced close enough to detect or disturb concealed animals. Animals are either counted by the beaters as they break back through the line, or by other observers placed at strategic points around the area as animals are flushed (e.g. Overton 1969; Pucek et al. 1975; Mitchell et al. 1977; Evans 1979; Odendaal et al. 1980; Schmidt 1983). Although the drive census is commonly recognised as the best technique for estimating deer numbers in temperate regions (see Dzieciolowski 1976) its use is often precluded by the high labour requirements and hence costs. Furthermore, the accuracy and precision of counts conducted in this manner have rarely been tested, but Anderson (1953) showed that drive counts may result in serious underestimates of population size when compared to results obtained from the elimination of the total stock.

Strip sampling methods may be based on either standard or modified strip transects. In standard strip transect sampling, the strip width, length and hence area is selected and fixed before the transect is sampled, and only those objects seen within the pre-selected fixed boundary of the strip are enumerated (Collinson 1982). Examples of standard strip sampling include the selection of a strip of uniform fixed width along the entire transect, where the investigator is certain he will locate all animals within that strip width (e.g. Wright 1960; Jarman 1982) or a variable fixed width which alters according to the structure of the habitat but again with the assurance that all animals within these strip widths will be detected (e.g. Western 1973 cited in Norton-Griffiths 1978; Leuthold and Leuthold 1976). Norton-Griffiths (1978) claims that no bias will occur with

either of these methods and that these are the only valid means of censusing populations using strip counts. Modified strip transect sampling involves the enumeration of all animals of interest seen while traversing (rather than pre-selecting and fixing) the strip width from field measurements taken from the line during, before and after the strip is sampled. There are numerous ways in which this effective strip width may be estimated. The fixed visibility profile method assures that the distance at which animals can be seen will vary along the length of the transect: this variable distance is mapped or calibrated either by measuring the perpendicular distance at which an object of similar height and colour to the subjects to be counted disappears from view (e.g. Hirst 1969b; Cumming 1975) or alternatively simply by measuring the distances from the transect of all animals seen and using the maximum distances to represent the edge of the transect strips (Norton-Griffiths 1978). Both of these methods of measuring the visibility profile have been criticised by Norton-Griffiths (1978) since the profile will change during the course of the year in response to plant growth etc., while if the maximum distance at which animals are detected is used, this limit will presumably be set by the largest and most conspicuous species or individuals. The variable visibility profile method of modified strip transect sampling may be conducted in several ways, all of which involve measurements each time a census is conducted. The simplest of these is the mean sighting distance or King's method where the distance of all observed animals is measured at right angles to the transect line (e.g. Robinette et al. 1974; Melton 1978a; Burnham et al. 1980). Norton-Griffiths (1978) found that this method consistently overestimated density when compared with standard strip transect sampling. An alternative approach, Kelker's method, involves a tally of the number of animals in belts of increasing distance away from the transect line; the distance at which sighting frequencies decline represents the effective strip width (e.g. Hirst 1969b; Jarman 1972; Robinette et al. 1974). The proportion of animals that are missed, and therefore the effective strip width, may also be calculated by regression analysis using Anderson and Pospahala's (1970) method (e.g.

Robinette et al. 1974). However, as Eberhardt (1968) cited in Norton-Griffiths (1978) points out, these methods are only suitable if sighting frequencies decline fairly abruptly. Data are more difficult to interpret where sightings decline gradually, or if they decline as a result of "dead" ground or dense vegetation, but then increase again. According to Norton-Griffiths (1978), variable visibility profile methods yield overestimates of density since they assume that the reason why animals are not detected is because they cannot be seen; the fact that they may be absent from the area is overlooked. Thus apart from Anderson and Pospahala's method, modified strip transect methods are based on models that are statistically invalid (Burnham et al. 1980). Other disadvantages of these methods include a) that their underlying assumptions (e.g. that disturbances do not cause animals to move out of range before being detected) are easily violated when the subjects are highly mobile and visibility is relatively restricted and/or variable (Collinson 1982) and b) the required field measurements are tedious and prone to observer error (Burnham et al. 1980).

Indirect methods of conducting sample counts may be based on a) single observations of animals, as in catch effort techniques, b) sightings of animals or animal signs, c) methods that involve repeated observations of individuals and d) mortality data (Eberhardt 1978). Few of the assumptions implicit in catch effort methods are biologically valid in ungulate populations and consequently the estimates that such methods provide are normally far less accurate than those provided by alternative means (Lewis and Farrar 1968; Caughley 1977; Collinson 1982). Examples of indices obtained from visual sightings include counts at artificial waterholes (e.g. Savory 1965; Young 1972), feeding sites or in natural, open, feeding areas where accuracy must partly depend on the behaviour of the animals as well as on local conditions (e.g. Mitchell et al. 1977) and counts made of animals detected by, or attracted to, audible signals (e.g. Kruuk 1972; Langvatn 1977). The most common types of animal signs used to estimate population size are faeces and tracks (e.g. Rogers et al. 1958; Neff 1968; Lautenschlager and Hennessey 1975;

McCaffery 1976; Mooty et al. 1984; Putman 1984). Potential problems associated with pellet counts include knowledge of the defaecation rate, locating all pellet groups within a prescribed area, the accurate identification and age determination of these signs, as well as other practical issues as outlined in Chapters Six and Seven.

Pucek et al. (1975) reported that track counts yielded lower and more variable estimates than drive counts, and the logical basis of some methods of track counts have been questioned (Mitchell et al. 1977). For example, if a density index is obtained from the difference between the number of tracks entering an area one day and those leaving the following day, such an index need not depend solely on animal numbers but may also be influenced by the size of the area surveyed and also by animal activity. Thus an area of prime habitat may have a resident population with little or no immigration/emigration (Mitchell et al. 1977). Similarly, density indices based on the numbers of tracks crossing transect lines in a day may be difficult to interpret (Dzieciolowski 1976). Track counts may therefore be most useful for detecting population trends in specific areas or for comparing numbers in similar habitats, while pellet counts may be better adapted to detecting large rather than small differences in population density (Mitchell et al. 1977).

Censuses that involve repeated observations of groups or individual animals include territory mapping methods, known group counts and mark-recapture techniques. Territory mapping methods use data from several visits to an area where the spatial distribution and activity of each animal is plotted on a map; this practice is repeated until distinct territories are identified (Overton 1969). Dawson (1981) has listed several problems associated with territory mapping and concluded that it frequently provides poor estimates of density. Known group counts also require a knowledge of the spatial distribution and social behaviour of the subjects (Mentis and Collinson 1977 cited in Collinson 1982) while the validity of the results rely on subjective decisions and are

suitable only when the species of interest forms stable groups that restrict their movements to localised and easily identifiable home ranges (Collinson 1982). Mark-recapture methods have received more attention from biologists than any other group of wildlife census strategies (Collinson 1982), with the result that there is a daunting number of options available (e.g. see Caughley 1977; Otis et al. 1978). However, all of these are based on the concept of estimating population numbers from the ratio of marked to unmarked individuals observed in a sample drawn from a population containing a known number of marked individuals (Collinson 1982). In its simplest form, the mark-recapture estimate of numbers involves marking on one occasion and recording the proportion of marked animals in a sample captured on a second occasion; this is commonly referred to as the Peterson estimate (e.g. Anderson 1961, 1962; Strandgaard 1967). Petersen estimates only yield accurate results when the following conditions are met:-

a) the probability of capturing an individual is the same for all individuals in the population, i.e. animals must be marked at random,

b) no births or immigration into the study area occurs between marking and recapturing,

c) emigration from or mortality rates within the study area are the same for marked and unmarked individuals and,

d) animals do not lose their marks in the time between marking and recapture (Caughley 1977).

Furthermore, marking should not affect the catchability of an animal, and both marked and unmarked animals should have an equal chance of being caught during the recapture phase of the operation (Seber 1973; Otis et al. 1978). The assumption that populations should be closed, i.e. no recruitment or losses (and thus population size remains constant during the period of investigation) is never completely true in a natural biological population (Otis et

al. 1978). Although minimizing the time between marking and recapture may partially obviate this problem, such a practice may violate other assumptions since marked animals may not have been given sufficient time to mix with unmarked members if this interval is of short duration (e.g. Norton-Griffiths 1978). However, Otis et al. (1978) have defined closure to mean that there are no unknown changes to the initial population; thus in practice, known losses do not violate this assumption and closure can be met at least approximately. Although the above review implies that it is necessary to trap or physically restrain animals during the capture phase of the census, visual sightings of marked and unmarked animals are perfectly adequate for data analysis (Anderson 1962; Strandgaard 1967; Kruuk 1972; Schaller 1972; Rice and Harder 1977; Otis et al. 1978; Gavin et al. 1984). Because the Petersen estimate is biased upward by birth and immigration or when the means of identification is lost, censuses will in time tend to overestimate the size of the population (Caughley 1977; Otis et al. 1978). Additional disadvantages are that a great deal of sampling effort and a high proportion of marked animals in the population are required to obtain a reliable estimate of population size (e.g. Anderson 1962; Strandgaard 1967). Offset against these limitations, the mark-recapture technique is frequently used simultaneously to measure mortality and/or movements (Overton 1969), growth rates and fecundity rates, albeit occasionally in a somewhat modified form (Caughley 1977). The Petersen estimate involves marking on a single occasion, but frequently such a design is impractical because insufficient numbers of animals can be marked at one time, resulting in an imprecise estimate of population size (Caughley 1977). The alternative strategy then necessitates marking on several occasions; in such instances the size of a population is estimated from the rate at which the proportion of marked individuals rises as progressively more are marked. Probably the simplest method involving multiple capture techniques is the Schnabel method which is a variant of the Petersen estimate (Overton 1969). Consequently it has several of the implicit assumptions (e.g. applicable to closed populations, equal catchability of both marked and

unmarked animals) of the latter method (Caughley 1977). Other multiple capture techniques available involve more complex assumptions and have been detailed in Overton (1969), Seber (1973), Caughley (1977) and Otis et al. (1978).

Selective removal methods based on mortalities or removals from the population are essentially based on the same model as mark-recapture methods and hence these two methods have similar underlying assumptions and disadvantages (Paulik and Robson 1969 cited in Collinson 1982). Basically, the approach in selective removal methods is to conduct an initial survey to determine the ratio of a specific class of individuals in the population. This is then followed by the selective removal of a known number of individuals from that specific class and a subsequent survey to determine the new ratio in the population (Caughley 1977). Because of the assumptions and limitations associated with this technique, selective removal methods are seldom worth considering (but see Paloheimo and Fraser 1981; Fraser 1984) unless animal removal is a common management practice (e.g. when only antlered males are hunted). Even then, the estimates obtained should be treated with caution and, if possible, tested against estimates derived from other means (Caughley 1977; Collinson 1982). Another population estimation technique that may involve mortality data is the catch-effort method, but as pointed out above, few biologists accept the implicit assumption of this method, which tends to yield less accurate results than those obtained from other methods (Lewis and Farrar 1968; Caughley 1977). Furthermore, unless animals have to be removed for other reasons, the effort, disturbance and reduction of stock can seldom be justified (Caughley 1977). A modification of this technique, the index-manipulation-index method, involves quantification or standardisation of the observation effort rather than removal (catch) effort, but suffers from the same, generally binding assumptions and disadvantages (Caughley 1977). In addition to providing potentially inaccurate results, index-manipulation-index methods are also inconvenient to apply where animals are not removed for other reasons, especially since the accuracy of the method requires a high

proportion of removal from the population. Finally, one other method of determining population size from mortality data may be through the total removal or extermination of a population. The best known example of a total removal programme is that of Andersen (1953, 1961, 1962) where the entire population of roe deer was replaced with animals of superior quality from elsewhere in Denmark. This non-sampling removal experiment yielded a population estimate (213 deer) three times greater than that obtained from "direct observations" (exact method unspecified, Andersen 1961). However, such a practice is rarely feasible elsewhere as it usually contradicts existing management and/or conservation policies. Population reconstruction has however, been attempted by recording the sex and age of all animals dying over the time of one maximum life-span (Lowe 1969, 1971) although the time required to do this is usually prohibitive in most studies of large animal populations.

9.1.2 Previous Studies of Bushbuck and Duiker Abundance

Bushbuck densities have been estimated in a variety of different habitats and areas (Table 9.1) but many of these resulted from general ungulate surveys where census design may not have incorporated considerations regarding the behaviour, activity patterns and habitat preferences of this antelope. Numerous census techniques have been used in counting bushbuck (Table 9.1), invariably during daylight hours, while distinction has not always been made between crude and ecological densities (Odum 1971). Consequently, the densities listed in Table 9.1 are not directly comparable but merely provide an indication of the relative abundance of bushbuck reported in different parts of Africa. The highest estimate of bushbuck density have resulted from specific studies of this species in natural habitats (e.g. Jacobsen 1974; Simpson 1974c; Waser 1975a; Allsopp 1978), while intermediate values of abundance have been recorded from intensive studies of bushbuck inhabiting indigenous forest and plantations on State land (von Gadow 1978; Odendaal et al. 1980; Seydack 1984).

TABLE 9.1 Density estimates of bushbuck (animals per km²) from various localities in Africa.

Density	Method of census *	Location	Source
0,04	?	Uganda	Petrides & Swank (1965)**
0,08	?	Ivory Coast	Geerling & Bokdam (1973)***
0,08	?	Niger	Poche (1975)***
0,09	?	Congo	Bouliere (1965)**
0,13-0,19	0	Nigeria	Milligan <u>et al.</u> (1982)
0,14	?	Nigeria	Milligan (1981)***
0,2	1	Kenya	Foster & Coe (1965)
0,23	?	Upper Volta	Heisterberg (1975)***
0,3	?	Zambia	Dowsett (1966)
0,35	?	Upper Volta	Sihvonen (1974)***
0,47	?	Cameroon	van Lavieren & Bosch (1977)***
0,74-2,75	?	Uganda	Field & Laws (1970)**
0,8	?	Upper Volta	Green (1981)***
0,8	0	Natal, S.A.	K. Zunckel (pers.comm.)
1,1	1/2	Zimbabwe	Dasmann & Mossman (1962b)
1,7	?	Natal, S.A.	Mentis (1970)
4,5-7,9	4/5	S.Cape, S.A.	Odendaal <u>et al.</u> (1980)
4,6+	6	East Africa	Kingdon (1982)
5-7	7	S.Cape, S.A.	Seydack (1984)
8,1-76,7	3	S.Cape, S.A.	von Gadow (1978)
9-26	8	Uganda	Waser (1975a)
10,9-43,3	1/8/9	Botswana	Simpson (1974c)
30,1	8	Kenya	Allsopp (1978)
66,7	8/10	Zimbabwe	Jacobsen (1974)

* ? = Not Known or stated; 0 = King's census; 1 = Road count; 2 = Strip count; 3 = Pellet count; 4 = Drive count; 5 = Track count; 6 = Culling; 7 = Photographic survey; 8 = Known individuals; 9 = River count; 10 = Transects.

** = cited in Waser (1975a)

*** = cited in Milligan et al. (1982)

As with many other aspects of their ecology, duiker have received less attention than bushbuck in terms of population abundance, and all of the published accounts of duiker densities have been estimated from general rather than specific or intensive surveys (Table 9.2). Several authors have remarked on the difficulties of counting duiker (and occasionally bushbuck) accurately and precisely either because of their relatively low abundance (e.g. Jarman 1972; Melton 1978b) or their behaviour (Dasmann and Mossman 1962c; Hirst 1969b) and it is highly probable that many of the densities derived from these general counts (Table 9.2) are underestimates.

TABLE 9.2 Density estimates of duiker (animals per km²) from various localities in Africa

Density	Method of census *	Location	Source
0,1-2,1	1/2	Zimbabwe	Dasmann & Mosmann (1962b)
0,11-0,34	0	Nigeria	Milligan <u>et al.</u> (1982)
0,32	?	Nigeria	Milligan (1981)**
0,52	?	Ivory Coast	Geerling & Bokdam(1973)**
0,77-1,16	?	Zimbabwe	Wilson & Roth (1967)
0,8	?	Zambia	Dowsett (1966)
0,88	?	Upper Volta	Sihvonen (1974)**
1,0-1,9	0/4	Cameroon	van Lavieren (1979)
1,03	?	Upper Volta	Heisterberg (1975)**
1,6	?	Natal, S.A.	Mentis (1970)
2,15	?	Upper Volta	Green (1981)**
2,2	0	Natal, S.A.	K. Zunckel (pers. comm.)
3,0	?	Cameroon	van Lavieren & Bosch (1977)**
15-950	3/4	Swaziland	R. Walter (pers. comm.)

* ? = Not known or stated; 0 = King's census; 1 = Road count; 2 = Strip count; 3 = Pellet count; 4 = Drive count.

** = cited in Milligan et al. (1982).

9.2 METHODS

The choice of census methods adopted in this study was largely dictated by the relatively low numbers of both bushbuck and duiker at Weza, their size, activity and behaviour, financial constraints and environmental factors (e.g. access, habitat diversity and the density and structure of the vegetation). For example, aerial surveying would have been quite impractical, due to visibility problems associated with the closed canopies of both indigenous forests and timbered areas, even if such resources had been available. Similarly, line transects were impractical because it was impossible to move silently through the majority of habitat types at Weza; disturbance and reduced visibility would have violated the assumptions inherent in such a method (see above). Thus several of the techniques tested at Weza were of an obligatory, rather than a random, systematic or necessarily representative design (Collinson 1982).

Indirect methods included surveys of animal signs (tracks and pellet counts) while direct observations were recorded during drive counts, road strip counts and mark-recapture methods. Track counts could not be readily accomplished in the various habitat categories at Weza because animals tended to travel along well-used game trails. Individual spoor could be detected on some dirt roads where the surface was not too compacted by heavy vehicle traffic, but rain in the summer and dust during the winter months tended to rapidly obliterate these or render estimates of track age virtually impossible. Clearing specific areas of all old tracks and resurveying them after a short time interval may have obviated some of these problems, but only if track densities warranted such efforts. To examine the feasibility of this, 100m sections of dirt road were surveyed on foot at 1km intervals (measured by an odometer) along a 15km route travelled by vehicle in May 1982. Two observers detected only five sets of distinct tracks over the 1,5km of searched road. Additional factors affecting track counts during this survey included variations in the surface of the

road (no spoor could be identified along stony sections of the route) and problems of identifying spoor where these intermingled with those of other species (e.g. horses and mules). Track counts were therefore abandoned in favour of alternative, usually more direct methods of census.

The feasibility of counting faecal pellet groups was examined in four habitats at Weza during June 1982 (see Schmidt 1983). For orientation purposes, each sample quadrat was 2,7m x 2,7m which conformed to the planting esplacement of unthinned pines. Marked rows of plots varying from 20 to 100 individual quadrats were arbitrarily selected in clearfelled areas, and compartments containing 4-12 year old pines where relatively high numbers of both antelope species had been seen at night earlier in the month. The counting and clearing of pellet groups was accomplished by two observers systematically searching each plot before commencing on the adjacent quadrat. The man-hours required to survey these plots, and the number of pellet groups detected were recorded and converted to effort and numbers per unit area. Initially, it was intended to resurvey these cleared areas at a later date but the time and financial costs, together with other constraints prevented the continuation of this work (see below). Defaecation rates were determined from a captive 14 month old female bushbuck that had been captured as a neonate and hand-reared by the author. Similar data were not available for duiker.

Drive counts were attempted during capture operations where up to 40 beaters were employed in two exercises in April and September 1981. Observers not involved in the actual beat were stationed at one end of the block where the nets were erected. Animals were prevented from escaping undetected at the sides of the block by opaque plastic sheeting that was hung on vegetation or wire stands at least two metres above ground level. Observers in the line of beaters controlled leashed beagles during the second exercise in September, and all members of the drive line were instructed to count only those animals that passed between them and the next member to their immediate right to avoid

duplication. On one occasion a small area of indigenous forest (1,0 ha) was entirely surrounded with nets before beaters and dogs were introduced into the area. Financial costs precluded the subsequent use of this method (see below).

All other censuses were conducted at night from a vehicle, and due to the structure of the vegetation and intensive management practices, were confined to the numerous roads and tracks within the two intensive study areas. A census route was selected in September 1980 which traversed the majority of habitat types at Weza (except indigenous forests where visibility rendered such surveys impractical). A minimum of three counts were made along this fixed route each month for one year, except in March 1981 when only one count was completed. Although assisted by several drivers, only three observers were employed, (two at any one time), one of which (the author) participated in every count. These were conducted from the open back of a four-wheel drive vehicle. Each of the two observers were equipped with a 200 000 c.p. spotlight and searched for animals on their respective sides of the vehicle. The numbers of both species seen were recorded and their positions noted with reference to a 1:12 000 management map with a 120m grid overlay. The habitat of each observed animal was also recorded along with group size and structure where known. Animals unidentified with respect to species, age or sex were listed accordingly. The time and ambient temperature at each observation site was also noted together with the activity of the animal when first observed. Distance of each observation from the start of the census route, which was always completed in the same direction, was recorded to the nearest 100m from the vehicle's odometer.

Visibility profiles were established along a 11,8 km section of the census route during daylight hours in November 1980. These were established at 100m intervals on either side of the road, and at each interval the shortest perpendicular distance at which a grain sack, held with its shorter edge trailing on the ground (see Cumming 1975),

disappeared from view was measured from the road by means of a range-finder. Sighting distances of observed animals were also recorded with a range-finder at night during the same month. Sighting angles were simultaneously measured using a 360° protractor (the magnetic field of a prismatic compass was influenced by the structure of the vehicle). Perpendicular sighting distances could then be calculated using the formula:

$$P = r \sin a$$

where P is the perpendicular distance to the road, r is the sighting distance and a is the sighting angle (Goodman 1975 cited in Venter 1979). The mean perpendicular sighting distance was subsequently determined for all sightings on each side of the road. The population estimate (N) could then be determined using King's method as follows:

$$N = nA/2LD$$

where n is the number of bushbuck or duiker seen, A is the total area of available habitats, L is the length of the census route and D is the mean perpendicular distance of all sightings of that species from the road (e.g. Overton 1969; Seber 1973; Melton 1978a). Due to the mosaic of heterogeneous habitats at Weza, population estimates were also stratified according to habitat type, with relevant adjustments to both mean sighting distance, the proportion of the area (A) occupied by that habitat and the length of the census route containing that vegetation type. Because compartments on either side of the road varied in size, the length of the census route bordering on to any one habitat type was totalled separately for left and right sides and then averaged. However, for reasons given below, these measurements were not repeated in subsequent months.

All attempts to census the bushbuck and duiker populations after 1981 were based on indirect methods of sampling. These involved either the use of simple indices relating the numbers of animals seen to the distance

travelled (in km) or the capture and subsequent resighting of marked animals using either the Petersen estimate or Schnabel's method. Capture and marking details have been detailed in Appendix D. Since the number of marked animals to be resighted was not decided prior to monitoring, Bailey's (1951,1952) formula (cited in Caughley 1977) was considered most appropriate:

$$N = M(n+1)/m+1$$

where M animals are marked in a population of unknown size N and m marked animals are recaptured or resighted in a subsequent sampling of n animals. This estimate has a formal standard error of approximately

$$S.E. = \sqrt{\frac{M^2 (n+1)(n-m)}{(m+1)^2 (m+2)}}$$

(Caughley 1977)

The size of the marked population M fluctuated within and between months because new animals were captured on subsequent occasions which increased M, while natural mortalities resulted in a decline of this total. Since many of the marked animals were fitted with radio transmitters, this facilitated the detection of lost (i.e. dead) subjects. In addition, the calculation of Petersen estimates was purposely delayed until the end of field work, so that animals marked and never subsequently observed or found (or observed for several months but then never seen again) could be omitted from the total of marked animals at the appropriate time (Allen-Rowlandson 1980). Thus although the Petersen estimate calls for marking on a single occasion, and assumes that the population is closed, some of these constraints were obviated by making relevant adjustments in this study (also see Seber 1973). Petersen estimates were commenced in July 1983, when 25 bushbuck had been marked in a 5 km² section of I.S.A.1, and continued until October 1984. A minimum of five counts were conducted each month except in October 1983 when only three surveys were completed. Mean monthly and overall estimates (Seber 1973; Eberhardt 1978)

were computed by taking the average value of M , m and n and calculating N as above rather than simply taking the mean value of N calculated independently after each census. In order to test the validity of this technique, estimates were compared to those obtained from Schnabel's method using the formula of Chapman and Overton (1966):

$$N = \lambda / x + 1$$

where $\lambda = \sum_{i=1}^k (n_i M_i)$ and $x = \sum_{i=1}^k x_i$

with N being the population estimate, M_i is the number of collared animals in the population and n_i and x_i are the total numbers of animals and collared animals respectively observed during census. The method of calculating confidence intervals for these estimates followed that of Chapman and Overton (1966) and to test for statistically significant differences in population levels between months or years, their z statistic was used (Chapman and Overton 1966: 175).

Remote censusing methods were also considered in this study. The feasibility of using a "Probeye" scanner (Hughes Aircraft Corporation) was examined during two trial censuses in June 1982, but the lateral cover in dense vegetation obscured the thermal infrared radiation emitted by both antelope species and domestic stock. Infrared scanning was therefore abandoned since it offered no advantages over simpler, less expensive census methods. Similar limitations of censusing deer populations by infrared scanning have been noted by Croon et al. (1968) and Wyatt et al. (1980). Consideration was also given to the feasibility of surveying these antelope photographically by means of automatic triggering (e.g. Seydack 1984) but the capital outlay proved to be prohibitive for the funds allocated to this study.

9.3 RESULTS AND DISCUSSION

The value of any censusing technique used at Weza was assessed not only on its merits in providing repeatable estimates of population size during the course of this study, but also in its practicability in future years when the personnel implementing it may be inexperienced and/or less motivated. Thus methods that potentially could provide reliable estimates but are prohibitively costly in terms of effort and/or time cannot be recommended, and the following discussion on the various census procedures attempted in this study includes aspects on their general utility in intensively managed timber plantations.

9.3.1 Pellet Group Counts

A total of 48 bushbuck and duiker pellet groups of unknown age were detected in 300 plots of 7,29 m², (219,5 pellet groups per ha). Overall, the time to search and clear these plots took 17 man-hours (77,8 man-hours per ha) but this varied according to habitat; the least amount of time was required to survey plots in 12 year pines (41,2 man-hours per ha) and the greatest time expended was in clearfelled areas and young pine compartments (102,9 - 109,7 man-hours per ha). As a census technique, all of these times should be doubled since it would take approximately the same time again to count pellets at a later date on these cleared plots (Schmidt 1983). Thus overall, a minimum of 157,5 man-hours would be expended per ha using this technique, but appreciably longer time would be required if sampling was stratified to include greater proportions of preferred habitats (see Chapter Seven). Schmidt (1983) calculated the costs of conducting three types of census in pine plantations, and based on the above results from Weza, estimated that pellet groups counts would amount to R266,00 per ha (unstratified sampling) compared to R0,84 per ha for spotlight counts and R1,53 per ha if drive counts were employed. Thus the effort required to survey 0,1% of the

total plantation area at Weza (10 989 ha) would be 1 731 man-hours, or assuming a working day of nine hours, 192 man-days which would result in a cost of R2 923. This was considered exorbitant for a short-term research study when compared to the costs and effort involved in other, more direct census methods. Although such costs could conceivably be defrayed by management budgets, it is argued (see below) that a 0,1% level of sampling intensity is totally inadequate for determining population trends in intensively managed timbered areas such as at Weza.

The major factor responsible for the inordinate amount of time (and hence expense) required for this technique was the structure and density of the ground cover or understory vegetation. As indicated in the times to count and clear pellet groups in the different habitat types (see above), plant density and diversity was greatest in clearfelled areas and least in 12 year pine compartments, the latter being in any case a less preferred habitat (see Chapter Seven). Problems were also encountered where plots contained dense stands of bramble; it was extremely difficult for observers to enter and move through these areas to count pellet groups, yet such areas were clearly used by both species of antelope. Several other limitations associated with this method have been detailed in Chapters Six and Seven, but additional disadvantages are also evident when it is employed as a census technique. For example, results from this study (also see Schmidt 1983) and those of von Gadow (1978) indicate a clumped distribution of pellet groups (particularly for duiker); this would require more intensive sampling if reliable estimates are to be achieved. In addition, the relatively low density of pellet groups observed in this study (which were of unknown age as no information was available on decomposition or disappearance rates of these faeces) would further increase the need for more intensive sampling (Neff 1968). Other considerations include the fact that pellets may be obscured by trash resulting from thinning and pruning, particularly in young compartments where these reductions are of no commercial value and the harvested trees and foliage are often left scattered over the compartment.

This last aspect also illustrates the need for stratified sampling because when such habitats are modified by management they tend to be avoided by both bushbuck and duiker (Chapter Seven). Another obvious disadvantage of the pellet group count method is that it only provides density data whereas more direct methods can also yield additional data such as population structure and social and spatial organisation. Finally, although von Gadow (1978) and Schmidt (1983) suggest that costs may be reduced by combining pellet group counts with other forest surveys, an obvious disadvantage with such a proposal is that decisions regarding the time to be devoted to counts as well as the actual areas to be counted may be largely determined by factors unrelated to the initial objectives of the census. This is inadvertently illustrated by von Gadow (1978) who coupled pellet group counts with a forest inventory and claimed the former was therefore practically cost-free, yet stated "Unfortunately the project had to be abandoned prematurely with the result that several aspects could not be studied in depth". Any estimate of population size that is conducted inadequately is probably little better than a guess, and could easily result in totally erroneous management decisions where such data are extrapolated to the entire area of interest. Schmidt (1983) makes the additional point that counting pellets may not be aesthetically pleasing to most labourers, which could result in a decline in motivation and/or accuracy when compared to other more direct methods. From the experiences of this study, it is strongly recommended that the task of counting and clearing pellet groups is not given to unqualified personnel if errors and biases regarding what constitutes a pellet group and whether that group falls within or outside the quadrat are to be minimized.

Pellet group counts were abandoned in 1982 when it was obvious from the manpower costs alone that such a technique was impractical at Weza. Defaecation rates had however been determined prior to this decision and were obtained from a female bushbuck that had been caught as a neonate and kept in captivity for 14 months. Pellet groups counted on seven

separate occasions in June yielded a mean daily defaecation rate of 16,4 groups per 24 hours ($\pm 3,9$ S.D.). This rate is appreciably higher than the five groups per 24 hours assumed by von Gadow (1978), which he subsequently used to calculate bushbuck densities ranging from 8,1 to 76,7 animals per km^2 . Assuming that the defaecation rate obtained in this study is more accurate by virtue of the fact that it was physically measured, then von Gadow's (1978) densities should be reduced to 0,30 (i.e. $5/16,4$) of their published values. This would yield corrected densities of 2,5 to 22,9 bushbuck per km^2 , which show closer agreement with bushbuck densities estimated by other means in similar habitats (Table 9.1). Similarly, R. Walter (pers. comm.) working on duiker in a Swaziland plantation assumed a defaecation rate of 2,5 groups per 24 hours. This rate yielded densities ranging from 70 to 950 duiker per km^2 , which are gross overestimates when compared to the mean density of 15,0 animals per km^2 determined from drive counts in the same area (R.Walter, pers. comm.). Errors in both these examples may have resulted from biased decomposition or disappearance rates as well as incorrect defaecation rates, and illustrate the need for accurate base-line data if such efforts are to be worthwhile. In view of all these limitations, results from this study support Schmidt's (1983) conclusions that pellet group counts cannot be recommended as a census technique for antelope inhabiting intensively managed plantations.

9.3.2 Drive Counts

Drive counts conducted during this study were largely unsuccessful because their costs made it necessary to combine counts with capture operations. Contrary to the suggestions of von Gadow (1978) and Schmidt (1983) given above, the two exercises were incompatible when conducted simultaneously for the following reasons. Firstly, insufficient numbers of experienced personnel were present and by necessity, were usually confined to the area where the nets were placed. Without adequate supervision, the beaters did not maintain equidistant positions and on occasions did not attempt to

penetrate the denser (and more preferred) stands of vegetation (also see Schmidt (1983)). Secondly, even when more experienced personnel were included in the drives, their range of visibility was often restricted and the accuracy of the method was still dependent on the ability of unskilled labourers to count, but not duplicate, the numbers of animals that broke back through the line of beaters. These labourers, when questioned by an interpreter, were reluctant to admit that any animals broke back if none had been caught in the nets, but if the drive was successful and animals were secured, the common answer was that animals were too numerous to count. These accounts were not substantiated by those more experienced and qualified members of the team of beaters. Thirdly, the disturbance caused in constructing the capture site (e.g. in erecting nets and plastic sheeting) may have caused local movements away from the area before the beaters were introduced, resulting in an underestimate of numbers. Movements away from the area to be surveyed may have been greater in the more open habitats since capture success was confined to patches of indigenous forest. The only reliable estimate obtained from these operations occurred when seven bushbuck emerged from a one ha patch of natural forest that had been completely surrounded with nets.

Several of these problems may have been obviated if drives had been designed specifically for census purposes, but the costs involved were so prohibitive (almost 50% of the annual budget allocated for research assistance was paid to 40 Forestry labourers for their services over four days) that attempts to use beaters and nets even for capture purposes were abandoned in September 1981 in favour of less haphazard methods (see Appendix D). Reducing the number of beaters may have alleviated some of this expense, but as van Lavieren (1979) points out, drive counts employing few beaters and observers should not be conducted in areas of dense or tall vegetation where limited visibility may be a major source of error. Such areas are preferred daytime habitats of bushbuck (Chapter Seven). It should not be inferred from these results that drive counts are unsuitable for censusing bushbuck and duiker in timbered areas. On the contrary, this

method has the potential to return absolute estimates with high accuracy particularly when animals, by virtue of their size, colour, behaviour and/or density are difficult to detect using other means (Collinson 1982) and has been used extensively in other areas (e.g. Pucek et al. 1975; Dzieciolowski 1976; Schmidt 1983). The success of such operations is however largely dependent on the resources available to the researcher, which in this study were somewhat limited. As Collinson (1982) points out, the drive count is generally inappropriate in situations where repeatable estimates are required because the costs of employing many reliable, well-instructed and highly disciplined observers can rarely be met. Furthermore, it may not always be possible to test the accuracy of such counts by comparing these with the results of other methods. Several biologists have failed to recognize this limitation. For example, Schmidt (1983) considered drive counts to yield more accurate results than spotlight counts, and found wide discrepancies in the numbers of animals detected by these two methods. He therefore inferred that animals not seen at night in dense habitats were in fact hidden, because such animals were detected during drive counts. The possibility that animals were not seen in dense vegetation at night simply because they were not there, was not considered. Results from this study indicate that bushbuck and duiker habitat selection differs markedly between day and night. Consequently, unless sampling intensity is substantially increased, and both methods of census are stratified according to habitat (with concomitant increases in cost), estimates obtained from drive and spotlight counts are not compatible and any attempt to compare these is based on highly spurious reasoning.

9.3.3 Road Strip Counts

A total of 37 counts were conducted along the 21 km fixed census route between September 1980 and August 1981. Of the 906 animals observed during these counts, bushbuck were recorded more frequently than duiker (50,2% and 41,5%

respectively while 8,3% of all sightings could not be identified to species. This trend was evident for much of the year but duiker were more frequently encountered than bushbuck during September and from November to February (Fig. 9.1), although this difference was significant only in January ($X^2=3,95$; $p<0,05$). Compared to the total number of sightings each month, significantly fewer duiker were observed in March and May ($X^2=3,98$ and $4,45$ respectively; both $p<0,05$). In contrast, there was a significant increase in the proportion of bushbuck observed in May and June ($X^2=4,10$ and $5,63$ respectively; both $p<0,05$; see Fig. 9.1) while the proportion of bushbuck observed in February was

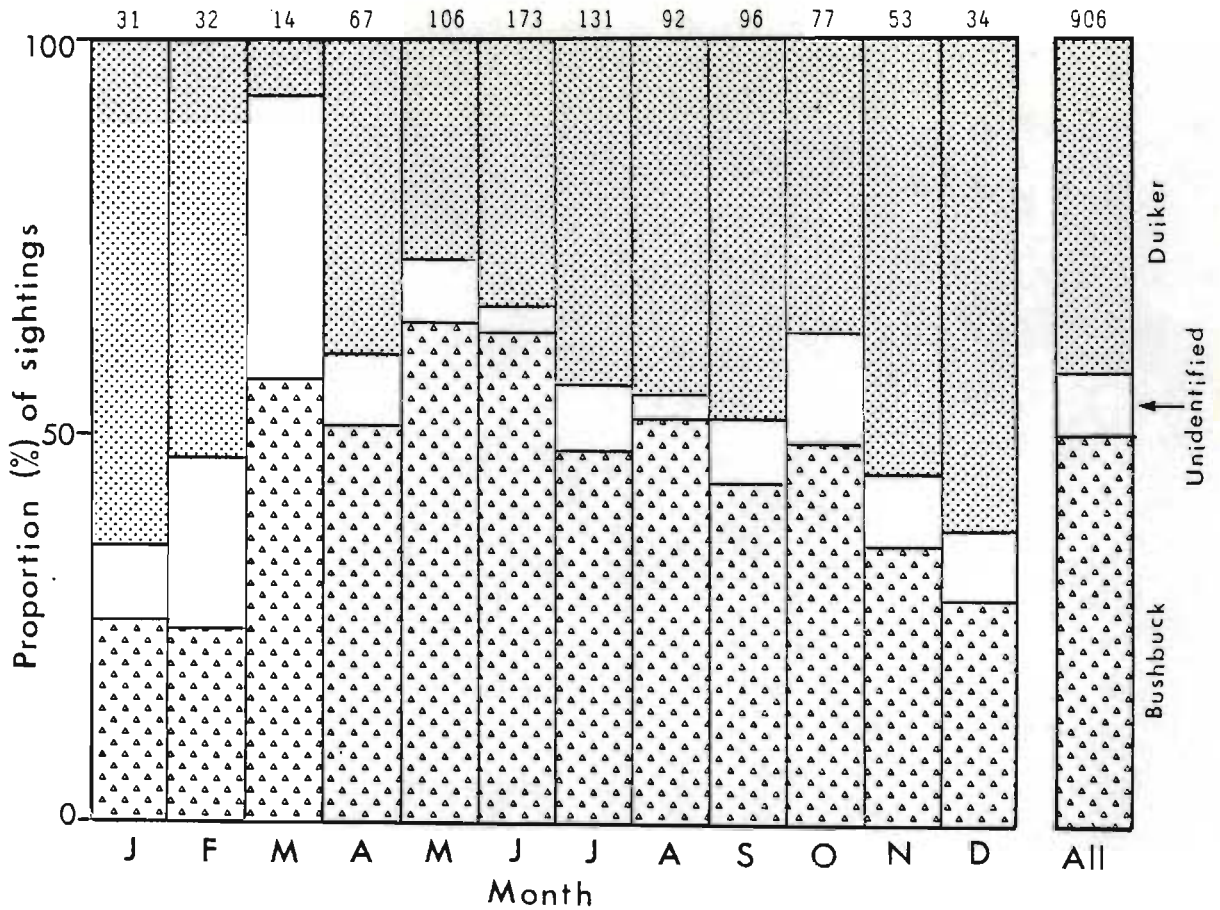


FIGURE 9.1 Monthly variation in the proportions of bushbuck, duiker and unidentified antelope observed along the 21km fixed census route at Weza. (Values at the top of the figure show the monthly totals of recorded sightings).

significantly lower than expected ($\chi^2 = 4,05$; $p < 0,05$). The proportion of unidentified animals recorded each month remained relatively constant for much of the year (Fig. 9.1) but increased significantly in February ($\chi^2 = 7,14$; $p < 0,01$) and March ($\chi^2 = 12,71$; $p < 0,001$) and was least in June ($\chi^2 = 4,83$; $p < 0,05$).

Sightings recorded during spotlight counts showed considerable seasonal variation, with mean numbers of animals observed each month ranging from 10,3 ($\pm 5,7$ S.D.) in January to 43,7 ($\pm 14,6$ S.D.) in July (Table 9.3). The average number of animals seen each month from December to March was significantly lower than the annual mean of 24,5 ($\pm 12,2$ S.D.)

TABLE 9.3 Monthly variations in the mean numbers of antelope counted along the fixed census route at Weza from September 1980 to August 1981.

Month (n)	Mean number of animals seen ($\pm$ S.D.)				
	Bushbuck	Duiker	Total *	χ^2	p
Sep (3)	14,0 $\pm$ 6,2	15,3 $\pm$ 5,0	32,0 $\pm$ 4,4	2,29	n.s.
Oct (3)	12,7 $\pm$ 3,1	9,3 $\pm$ 4,2	25,7 $\pm$ 9,5	0,06	n.s.
Nov (3)	6,3 $\pm$ 2,1	9,6 $\pm$ 4,0	17,7 $\pm$ 4,7	1,89	n.s.
Dec (3)	3,3 $\pm$ 2,5	7,0 $\pm$ 0,0	11,3 $\pm$ 3,2	7,11	$p < 0,01$
Jan (3)	2,7 $\pm$ 1,5	6,7 $\pm$ 3,5	10,3 $\pm$ 5,7	8,23	$p < 0,01$
Feb (3)	2,7 $\pm$ 2,5	5,7 $\pm$ 2,1	10,7 $\pm$ 0,6	7,77	$p < 0,01$
Mar (1)	8,0	1,0	14,0	4,50	$p < 0,05$
Apr (3)	11,3 $\pm$ 3,2	9,0 $\pm$ 7,6	22,3 $\pm$ 8,3	0,19	n.s.
May (4)	17,0 $\pm$ 3,6	7,5 $\pm$ 3,0	26,5 $\pm$ 6,6	0,16	n.s.
Jun (5)	21,8 $\pm$ 4,3	11,6 $\pm$ 3,1	34,6 $\pm$ 7,6	4,16	$p < 0,05$
Jul (3)	21,0 $\pm$ 5,3	19,3 $\pm$ 11,2	43,7 $\pm$ 14,6	15,04	$p < 0,001$
Aug (3)	16,0 $\pm$ 7,0	13,7 $\pm$ 3,2	30,7 $\pm$ 10,1	1,57	n.s.
Total (37)	12,3 $\pm$ 7,8	10,2 $\pm$ 5,8	24,5 $\pm$ 12,2		
95% C.L.	$\pm 2,5$	$\pm 1,9$	$\pm 3,9$		

* - includes unidentified animals.

animals per census, while significantly more animals were recorded in June and July (Table 9.3). This variability was due to fluctuations in the observed numbers of both bushbuck and duiker; fewer than 10 bushbuck sightings per census were recorded from November to March while duiker observations averaged less than nine animals per census from December to March (Table 9.3). Conversely, more than 15 bushbuck were seen per census during May to August while an average of more than 12 duiker per census was recorded in July, August and September.

Several factors were undoubtedly responsible for these variations in the mean number of animals seen each month. Although every effort was made to standardize census procedure throughout the year (e.g. maintaining the same vehicle speed, utilizing the same observers, conducting all counts at the same time of day and in the same direction etc.), conditions were inevitably influenced by climatic factors. The most obvious of these was rainfall, with approximately 80% of the annual precipitation falling between October and March (see Chapter Two). Censuses were rarely initiated during wet weather, but were frequently interrupted by either storms or mist. Counts were terminated and the results discarded whenever visibility was severely reduced by this precipitation, but occasionally summer counts were continued if the influence of rain or mist was considered to be slight, or if no other data had been collected during that month. In the latter instance, such results were subsequently ignored if at least three other counts could be completed in clear weather. Occasionally this also proved to be impractical (e.g. in January 1981 when it rained on 25 nights). An inverse relationship between the mean number of animals observed each month and the total rainfall for that month ($r = -0,694$; $p < 0,01$) indicates that sightings were affected either directly or indirectly (e.g. shelter seeking behaviour or other activities) by precipitation.

Results from this study suggest that rainfall had a much more pronounced influence on counting success by initiating and promoting plant growth during the spring, summer and

autumn months. The effect of this growth was not only evident in the height and density of the ground cover and understory vegetation, which resulted in a reduced range of visibility, but also affected forage production and hence diet, habitat selection and animal movements (Chapters Six, Seven and Eight). A highly significant inverse relationship between the monthly mean number of animals seen per census and the amount of rainfall received at Weza during the two preceding months ($r = -0,774$; $p < 0,001$) supports this conclusion. Evidence that plant growth and density reduced ranges of visibility resulting in fewer sightings during the summer rainfall period comes from the fact that the proportions of unidentified animals recorded during February and March were significantly higher than at other times of the year ($X^2 = 7,14$; $p < 0,01$ and $X^2 = 12,71$; $p < 0,001$). Conversely, fewer unidentified animals ($X^2 = 4,83$; $p < 0,05$) were observed during June when visibility was improved. Plant measurements and photographic records also demonstrated seasonal fluctuations in the density and height of the vegetation at Weza (Chapter Seven). Interestingly, surveys conducted along the census route at the peak of the growing season in January 1982 indicate that only three types of habitat (oaks, poplars and 19-30 year pines) had ground or understory vegetation that was, on average, shorter than the mean height of adult duiker (both sexes, see Tables 3.15 and 3.16) or adult female bushbuck (see Table 7.1). In addition to the above habitats, adult male bushbuck (mean shoulder height of 84,7 cm, see Table 3.13) could presumably be detected in most areas of grassland and 14-18 year pines at this time (Table 7.1), but the chances of seeing any animals in clearfelled compartments, 3-13 year pines, riverine vegetation, thickets and areas dominated by camphors would be slight.

Seasonal variations in the proportions of bushbuck and duiker observed in the various habitats at Weza during censuses have been detailed earlier (Chapter Seven, Figs. 7.1 and 7.2). Favoured nocturnal habitats of bushbuck during spring included clearfelled areas, riverine vegetation, thickets, gums and grasslands (Table 7.8). In addition to

these habitats, young pine compartments were selected in summer (Table 7.9) while there was a marked selection for grassland and oaks during the autumn (Table 7.10). Oaks remained a favoured habitat in winter, when the importance of clearfelled areas, grassland, riverine areas and gums notably declined (Table 7.11). These seasonal shifts in habitat selection were presumably influenced at least in part by the quality and quantity of available food resources (Chapter Seven), since animals generally moved over wider areas and had larger home ranges during spring and summer (Chapter Eight). Thus in addition to reduced ranges of visibility, a more dispersed pattern of distribution may have accounted for the fewer bushbuck and duiker seen along the fixed census route at these times. Conversely, both species tended to form aggregations at night during late autumn and winter (Chapter Eight), in response to localised food resources such as acorns and cultivated lands (Chapter Seven). Only 2,3% of the census route passed through oak stands, where the visibility remained constant throughout the year (Chapter Seven). The proportion of bushbuck sighted in these oaks each month varied from 0% in November to 32% in May, June and July (seasonal variations in the proportion of bushbuck observed in this habitat have been illustrated in Fig. 7.1). Therefore, in conclusion, these results indicate that bushbuck and duiker were less easily observed in late spring, summer and early autumn because ranges of visibility were reduced at this time and animals were more dispersed. During the drier periods of the year more animals were detected as a result of improved visibility, but differences in habitat selection and the formation of conspicuous aggregations in localised areas where discrete patches of food were available were also of considerable importance. These results therefore suggest that there is little point in attempting to census both populations throughout the year and efforts should rather be confined to the winter months when environmental conditions are most suitable. The design and siting of the census route also appears to be of crucial importance; for estimates of population size the route should include representative vegetation in proportion to the total area, but this is seldom possible to achieve

(Norton-Griffiths 1978). Alternatively, counts should be stratified, with numbers or density determined for each vegetation type and then multiplying these by the area of each vegetation type in the total area of interest. Caution should be given to those areas that are not necessarily representative of the entire study area (e.g. isolated oak stands, recently cultivated lands etc.) although since such sites are extremely attractive to both species they can provide a wealth of data concerning population structure, social behaviour etc.

Although some variability may be reduced by confining counts to the winter (when 44% of all counted animals were observed), variation in the numbers of animals counted during the months of June to August was still high and the differences between some successive counts was also high. For example, two successive counts conducted along the same route and under similar climatic conditions on 30th June and 15th July 1981 yielded totals of 23 and 60 animals respectively. Bushbuck counts completed during June to August yielded coefficients of variation (the standard error expressed as a percentage of the mean) ranging from 8,7 to 25,0; similar coefficients for duiker ranged from 12,1 to 33,7 while unidentified animal sightings had coefficients of variation from 50,0 to 72,7. These values were undoubtedly influenced by small sample sizes, as lower coefficients of variation were recorded when data from all winter sightings were pooled (Table 9.4). Greater precision may therefore have been achieved by increased sampling intensity either through conducting more counts each month or extending the length of the census route. Conducting more frequent counts was not feasible in this study due to other commitments (e.g. culling and capture exercises) and because this would have necessitated an increase in manpower and financial costs; a total of 356 man-hours were spent in counting 906 animals along 777 km of roads during the year. Similarly, extending the length of the census route would have resulted in increased expense while personal experience indicated that observer fatigue and discomfort (observers were frequently exposed to temperatures close to or below 0°C for periods

TABLE 9.4 Numbers of antelope counted at night along the fixed census route of 21km at Weza during winter 1981.

Date	Bushbuck	Duiker	Unidentified	Total
19/6/81	21	14	3	38
22/6/81	20	11	0	31
25/6/81	25	15	1	41
29/6/81	27	11	2	40
30/6/81	16	7	0	23
15/7/81	23	29	8	60
20/7/81	15	22	2	39
27/7/81	25	7	0	32
17/8/81	8	10	1	19
25/8/81	19	15	2	36
27/8/81	21	16	0	37
Total	220	157	19	396
Mean	20,0	14,3	1,7	36,0
S.E.	1,6	2,0	0,7	3,2
95% C.L.	$\pm 3,6$	$\pm 4,4$	$\pm 1,6$	$\pm 7,1$

ranging from 130 to 244 minutes; the mean time to complete a census was 192 minutes at an average speed of 6,6 km an hour) could become important sources of bias if censuses exceeded a period of four hours. Unless highly trained and motivated observers are employed, it is recommended that counts last no longer than two hours during winter nights otherwise greater effort may directed in trying to keep warm than in searching for animals (also see Schmidt 1983).

As a result of these restrictions, attempts were made to identify those factors that could potentially influence counting success during the limited number of censuses conducted each month. Variation in the numbers of animals seen was not due to observer errors as the same pair of observers were used throughout winter. Similarly, vehicle speed during counts remained relatively constant and rarely

exceeded 10 km per hour to ensure that both sides of the road were thoroughly searched. Counts in May were conducted at weekly intervals during clear nights to examine possible effects of the moon. During new moon a total of 35 animals were counted, while the count during the first quarter yielded a total of 28 animals. Further declines were evident during full moon and the last quarter (23 and 20 animals respectively) indicating that animals were more active or more easily detected on dark nights. However, no such relationship was evident during the remaining winter months (Table 9.4). Results regarding the effects of lunar phase on counting success of other herbivores are also inconclusive; Zagata and Haugen (1974) reported that the phase of the moon was of little consequence in counting deer but Progulske and Duerre (1964) and Fafarman and White (1979) observed more deer and rabbits respectively on dark nights.

The effect of temperature on counting success was also examined, but the correlation between the mean number of animals seen per census and the mean temperature (recorded at all observation sites) during that census was not significant. To examine this aspect further, particularly since minimum and maximum temperatures have been shown to be important variables affecting the counting success of deer (e.g. Progulske and Duerre 1964; Zagata and Haugen 1974; McCullough 1982), censuses were repeated on the same nights in June. Two censuses were conducted on 20th June and three were made on 24th June. Due to time constraints and observer comfort it was not feasible to count animals along the full 21 km route, and counts were instead confined to sections that traversed favoured habitats where relatively high numbers of both species were observed throughout winter. Because these were incomplete counts each obtained from a total of 5.5 km of roads (26% of the total route), results from these trials (Table 9.5) were not included with the remaining data obtained during June and were excluded from all other analyses. There was a general decline in the numbers of animals observed with decreasing temperature, although this relationship was only significant when total numbers of animals, rather than individual species, were

TABLE 9.5 Duplicated trial censuses conducted along selected sections of the fixed census route in June 1981.

Date	Time interval	Temp. °C $\bar{x} \pm$ S.D.	Number of animals counted			
			Bushbuck	Duiker	Unidentified	Total
20/6/81						
A	18.50-20.15	4,6 $\pm$ 1,2	9	8	0	17
B	21.25-22.50	2,4 $\pm$ 0,7	6	6	1	13
24/6/81						
A	18.50-20.15	10,5 $\pm$ 1,9	13	14	0	27
B	21.55-23.15	9,2 $\pm$ 2,8	15	9	0	24
C	23.45-00.55	5,0 $\pm$ 1,1	15	7	0	22

considered ($r = 0,933$; $p < 0,05$). This trend may however have been influenced by other factors (e.g. disturbance, animal activity etc.) as counts repeated later the same night always yielded fewer sightings. Whatever the cause, these results indicate that the best time for censusing is approximately two hours after sunset and that the longer counts are delayed at night, the fewer animals will be observed (also see Progulske and Duerre 1964). Counts commencing after midnight were not attempted on the grounds that few observers would be enthusiastic about starting work at this time.

All counts made along the 21 km census route in this study were commenced within three hours after sunset, and thus the variation between and within months could not be ascribed to temporal differences. Failure to identify any environmental factors (with the exception of rainfall) responsible for the wide differences in the number of animal sightings indicates that behavioral factors such as habitat selection, movements and activity may have been largely responsible for this variation (also see Progulske and Duerre 1964; Zagata and Haugen 1974; Downing *et al.* 1977; McCullough 1982; Sage *et al.* 1983). If so, then the only means of producing more reliable estimates would involve more intensive sampling confined to optimal periods of the year

(i.e. winter), albeit with concomitant additional costs.

The road count data presented above do not provide any estimate of population size because no attempt was made to incorporate measurements of the area covered in these surveys (the initial objective being to identify the optimum conditions for census at Weza). Nevertheless, if the mean number of animals counted each month is related to the distance travelled, this provides a convenient count index for comparative purposes (Table 9.6). A similar monthly index was calculated for all the bushbuck sightings recorded in an intensive study area of 5 km² that was regularly

TABLE 9.6 Count indices (animals per kilometre travelled) recorded (a) along the 21km fixed census route between September 1980 and August 1981 and (b) within a 5km² section of I.S.A.1 between November 1983 and October 1984.

Month	n	Count index ($\bar{x}$ no. of animals/km $\pm$ S.E.)				
		(a) Fixed census route			(b) I.S.A.1	
		Bushbuck	Duiker	Total *	n	Bushbuck
Jan	3	0,13 $\pm$ 0,04	0,32 $\pm$ 0,10	0,49 $\pm$ 0,16	8	0,27 $\pm$ 0,04
Feb	3	0,13 $\pm$ 0,07	0,27 $\pm$ 0,06	0,51 $\pm$ 0,01	7	0,28 $\pm$ 0,09
Mar	1	0,38	0,05	0,67	4	0,29 $\pm$ 0,03
Apr	3	0,54 $\pm$ 0,09	0,43 $\pm$ 0,21	1,06 $\pm$ 0,23	6	0,70 $\pm$ 0,13
May	4	0,81 $\pm$ 0,09	0,36 $\pm$ 0,07	1,26 $\pm$ 0,16	11	1,08 $\pm$ 0,08
Jun	5	1,04 $\pm$ 0,09	0,55 $\pm$ 0,07	1,65 $\pm$ 0,16	12	1,52 $\pm$ 0,17
Jul	3	1,00 $\pm$ 0,15	0,92 $\pm$ 0,31	2,08 $\pm$ 0,40	6	1,65 $\pm$ 0,24
Aug	3	0,76 $\pm$ 0,19	0,65 $\pm$ 0,09	1,46 $\pm$ 0,28	5	1,77 $\pm$ 0,30
Sep	3	0,67 $\pm$ 0,17	0,73 $\pm$ 0,14	1,52 $\pm$ 0,12	7	1,03 $\pm$ 0,13
Oct	3	0,61 $\pm$ 0,09	0,44 $\pm$ 0,11	1,22 $\pm$ 0,26	9	0,51 $\pm$ 0,07
Nov	3	0,30 $\pm$ 0,06	0,46 $\pm$ 0,11	0,84 $\pm$ 0,13	7	0,38 $\pm$ 0,06
Dec	3	0,16 $\pm$ 0,07	0,33 $\pm$ 0,00	0,54 $\pm$ 0,09	4	0,34 $\pm$ 0,05
All	37	0,59 $\pm$ 0,06	0,48 $\pm$ 0,05	1,17 $\pm$ 0,10	86	0,84 $\pm$ 0,07

* - includes unidentified animals.

surveyed from July 1983 to October 1984. This area was visited on 121 occasions to determine the ratio of marked to unmarked animals, and hence to provide an indication of population size using the Petersen estimate (see below). Count indices were recorded from November 1983 to October 1984 and incorporated 86 separate censuses. Although the numbers of animals seen per km travelled were considerably higher than along the 21 km fixed census route, the same trends (increased sightings in winter and least numbers of bushbuck seen during summer) were evident. This area included highly preferred bushbuck habitat throughout the year, but duiker were rarely encountered in this region and count indices were not calculated for this latter species.

Estimates of bushbuck and duiker densities were calculated from separate counts which incorporated measurements of the areas that were surveyed in November 1980. Visibility profiles measured at 100m intervals along an 11,8km section of road rendered an average range of visibility of 43,4m ($\pm 37,5$ m S.D.). This however excluded 21 sites on the left side of the road where topography prevented the measurement of distance (and hence where no animals could be observed) or in sections where the habitat was considered to be totally unsuitable (e.g. on the perimeter of the village) or inaccessible (e.g. securely fenced gardens and camps in rural areas) to both species. The effective area covered by these counts was therefore 93,40ha (11 800 x 43,4m + 9 700m x 43,4m). The number of bushbuck and duiker seen during the four surveys of this area ranged from 1 to 8 and 2 to 10 respectively. Consequently, densities ranged from 1,1 to 8,6 ($\bar{x}=4,8$) bushbuck per km² and 2,1 to 10,7 ($\bar{x}=7,5$) duiker per km² which by extrapolation yielded mean estimates ($\pm$ 95% confidence limits) of 533(± 541) bushbuck and 821 (± 592) duiker for the total plantation area of 10 989 ha at Weza (see Chapter Two). The estimated size of the bushbuck population showed even wider confidence limits when the counts were stratified, but less variation was evident from the duiker data when analysed in a similar manner. Stratification details are presented in Table 9.7 and the estimated densities of bushbuck and duiker derived from these

counts are listed in Table 9.8; neither species were observed in clearfelled areas during these counts. The estimated size

TABLE 9.7 Stratification of the census route used for visibility profile analysis

Vegetation type	$\bar{x}$ range of visibility $\pm$ S.D. (m)	Area surveyed during census (ha)
Grassland	60,0 $\pm$ 39,6	50,43
3-30yr pines	27,8 $\pm$ 28,8	27,24
Clearfelled	47,5 $\pm$ 36,9	10,45
Hardwoods	48,0 $\pm$ 39,6	5,28
Total	43,4 $\pm$ 37,5	93,40

of each population ($\pm$ 95% confidence limits) was 606 ($\pm$ 1 064) bushbuck and 727 ($\pm$ 140) duiker. Inadequate sampling was obviously responsible for the imprecise estimate of the bushbuck population, but the variable number of animals seen during each census at any one time of the year suggests that more precise estimates could rarely be achieved without a substantial increase in both effort and costs.

The visibility profile method of determining antelope density and hence population size had several other major disadvantages and limitations. Firstly, visibility profiles would require revision each month during the growing and dormant seasons if areas were to be measured with any degree of accuracy. This would necessitate considerable additional costs, since more time was spent "unproductively" measuring visibility profiles than in actual counting. Secondly, measuring the range of visibility at 100m intervals provides a somewhat crude estimate of area, particularly in heterogeneous environments where there is a mosaic of small but discrete habitat patches, but measurements at every 20m interval (for example) would be impractical. Finally, the range of visibility may vary considerably within any one

TABLE 9.8 Estimated densities of bushbuck and duiker (animals per km²) determined from stratified visibility profile and King's census results at Weza.

Species and method of census	Habitat type		
	3-30yr pines	Grassland	Hardwoods
Bushbuck			
Visibility profile			
census 1	3,7	13,9	0,0
census 2	0,0	7,9	0,0
census 3	3,7	0,0	0,0
census 4	18,4	0,0	0,0
$\bar{x}$ sighting distance			
census A	20,8	0,0	0,0
census B	0,0	9,2	0,0
Duiker			
Visibility profile			
census 1	3,7	7,9	0,0
census 2	7,3	13,9	0,0
census 3	7,3	13,9	18,9
census 4	11,0	0,0	0,0
$\bar{x}$ sighting distance			
census A	2,0	13,7	100,0
census B	6,3	16,7	0,0

habitat type (Table 9.7), depending on the composition of the understory, management history etc. and hence average values may not be particularly meaningful. In view of these sources of variation, together with the variable numbers of animals that were observed during successive counts, the visibility profile method must be regarded as a totally unsuitable means of estimating population size in timbered areas. Other limitations and biases associated with this method, (even when used in more suitable habitats), have been detailed by Norton-Griffiths (1978).

Estimates based on mean sighting distances obviated the need to measure ranges of visibility prior to the census, but unfortunately, inadequate numbers of animals seen each count led to imprecise measurements of the areas surveyed. Overall, the mean sighting distance recorded from 18 observations of duiker was 49,9m ($\pm 30,9$ m S.D.) while only five bushbuck were seen during two counts along 11,8km of the fixed census route; these provided a mean sighting distance of 42,6m ($\pm 24,4$ m S.D.). Sample sizes decreased even further when results were stratified, and the density estimates presented in Table 9.8 are included merely for comparative purposes; no reliance should be given to these values in terms of estimating population size. As with the visibility profile method, because so few bushbuck and duiker were encountered during any one census, reliable estimates would require many more surveys than could be accomplished in this study. Furthermore, if population estimates are required, then more extensive areas should be surveyed; only 1% of the total study area was covered by the visibility profile and King's census methods which is considered to be totally inadequate for extrapolation purposes in a region with such diverse habitats. Again this would involve considerable additional expense.

King's method has another inherent limitation that was encountered in this study. No bushbuck or duiker were seen in clearfelled areas, consequently sighting distances could not be recorded, and thus no estimate of the clearfelled area that was surveyed could be made. Such omissions are likely to result in gross overestimates of density or population size, particularly where actual ranges of visibility are large in habitats that are consistently avoided by the species of interest. This limitation does not appear to have been commonly encountered or recognised in other studies, although Norton-Griffiths (1978) states that censuses based on mean sighting distances generally produce highly biased results and his own trials consistently produced overestimates of density.

While several of the densities listed in Table 9.8 were

obvious overestimates (see below), it is highly likely that population estimates derived from either the visibility profile or King's census method were too low. This is because spotlight counts were largely ineffective in regions of dense vegetation, yet such areas were highly preferred habitats at all times of the year (Chapter Seven). Similar restrictions regarding visibility ranges in dense cover have been noted in numerous other studies (e.g. Zagata and Haugen 1974; McCullough 1982; Sage *et al.* 1983). Drive counts may overcome this problem of restricted visibility, but in addition to their expense, they must be conducted during the day; results from these drives are not comparable with those obtained from spotlight counts in more open areas because of marked differences in diurnal and nocturnal habitat selection (see above) and because the same animals may be counted twice using these two methods.

The few animals observed in November 1980 resulted in meaningless estimates of population size irrespective of census method. Reasons why area measurements were abandoned in subsequent months are given below, but both methods indicated that the effective strip width during counts averaged approximately 100m ($2 \times 50\text{m}$). A crude approximation of the area covered during each of the 37 counts along the 21km route was therefore $2,1\text{km}^2$. Since the mean numbers of bushbuck and duiker seen along this route during the year were 12,3 and 10,2 respectively (Table 9.1), these observations yielded crude densities of 5,9 bushbuck per km^2 and 4,8 duiker per km^2 where 1,9% of the total plantation area was sampled. Therefore, by extrapolation, estimates of animal numbers ($\pm 95\%$ confidence limits) for the $109,9\text{km}^2$ plantation area were 648 (± 131) bushbuck and 527 (± 99) duiker. Again these are probably underestimates as substantial areas of preferred habitats (e.g. indigenous forests, grasslands) were not surveyed in this study, but these can be regarded as the most reliable estimates from road count data.

Attempts to overcome the serious limitations associated with road counts involved mark-recapture methods where it was assumed that the chances of sighting marked or unmarked

animals were the same in any given habitat. All other forms of census, with the exception of the count index (number of animals seen per kilometre travelled) were abandoned after 1981 on the grounds that they produced totally inadequate results in the time and with the funds that were available to this study; additional reasons for rejecting these conventional census methods at Weza are given below.

9.3.4 Counts Based on Mark-Recapture Methods

Mark-recapture methods involving bushbuck were confined to a relatively small (5km^2) section of I.S.A.1. The size of this area was chosen because any larger region would have been monitored less intensively or effectively and thus would have resulted in less precise assessments of movements (immigration and/or emigration) and mortality rates. Following consultations with Forestry personnel, and for reasons given below, the locality of the area was selected on the understanding that it would remain relatively undisturbed by management during the course of this study.

A total of 121 counts were conducted in this area between July 1983 and October 1984, with a minimum of three counts completed each month. The proportion of marked animals each observed at least once during any one month (expressed as a percentage of the total marked population during that month) varied from 42% in March 1984 to 77% in August 1983 and exceeded 50% for 10 months of the year (45% were observed in January 1984). Losses of marked animals as a result of mortality or emigration were partially offset by continuous capture operations, and the monthly proportions of marked animals expressed as a percentage of the total estimated population during that month remained relatively high throughout the year ($\bar{x} = 60\% \pm 6\%$ S.D.; range = 48-75%). This proportion of marked animals in the population approximates that recommended by Andersen (1962) and Strandgaard (1967) and thus can be considered as adequate for a reliable measure of population size.

Based on data from the 121 censuses, the mean number of animals seen each count was 10,3 bushbuck, of which 5,6 were marked, while the mean number of marked animals in the population was 29,9 bushbuck. These values yielded a mean population estimate of 51,2 bushbuck ($\pm 12,1$ S.E.) in the 5km² study area. As predicted by Caughley (1977), monthly mean Petersen estimates showed a slight increase with time, although these monthly differences were not significant (Fig. 9.2), presumably because capture and marking operations continued throughout the period of census. The lowest

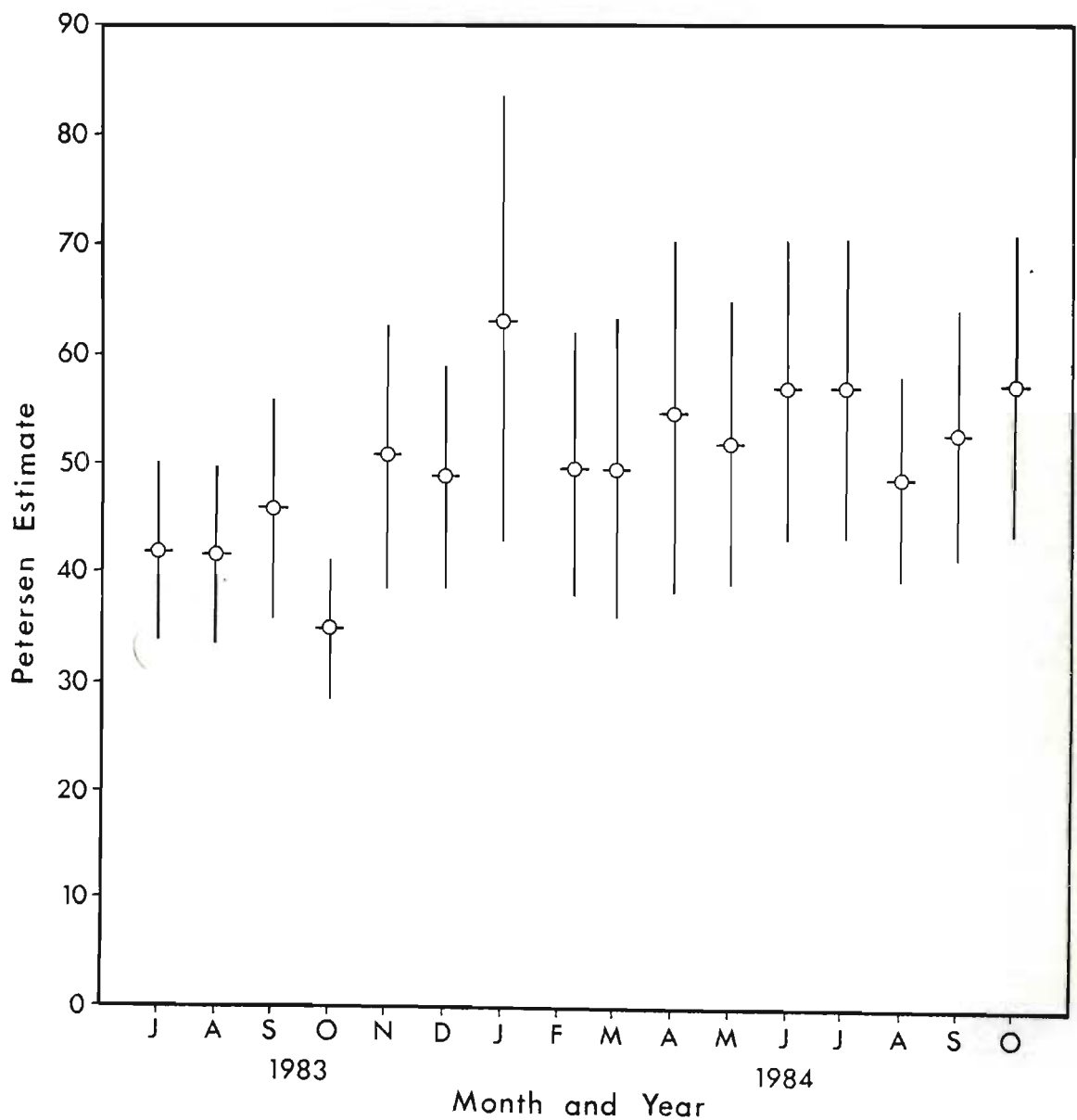


FIGURE 9.2 Mean monthly bushbuck population estimates (+ one standard error) within a 5km² section of I.S.A.1 from July 1983 to October 1984.

monthly mean population estimate was recorded in October 1983 ($\bar{x}=34,9$ bushbuck $\pm 6,2$ S.E.). This estimate may have been influenced by inadequate sampling (only three counts were made in this month compared to a minimum of five censuses completed each month for the remaining period). However, since the mean probability of observing a collared bushbuck in October (0,229) did not differ significantly from the mean probability of seeing a marked animal in either September (0,264) or November (0,210), this suggests that the population decline in October was real. The high proportion of marked bushbuck (and therefore presumably unmarked animals as well) that died of natural causes during the previous six months (see Fig. 9.3 and Chapter Four) supports this conclusion. The highest monthly mean estimate of 63,2 bushbuck ($\pm 20,5$ S.E.) was recorded in January 1984 (Fig. 9.2). Although the mean probability of observing any of the marked bushbuck in January was lower (0,100) than in either December (0,240) or February (0,123), these differences were not significant. Similarly, the mean population estimate in January was not significantly higher than the estimates obtained for the preceding and succeeding months and was probably an artefact of sampling, particularly since the coefficient of variation of 32,4% in January was the highest value determined during any of the 16 months of census (also see Fig. 9.2).

As with other road counts, the number of both marked and unmarked bushbuck sightings showed considerable seasonal variation. Although the total number of marked animals within the population remained relatively constant during the last year of field work (Fig. 9.3), the chances of observing a collared individual were considerably greater in winter and spring than in autumn and summer (Table 9.9). Similarly, bushbuck (both marked and unmarked) were more commonly encountered during censuses in winter and spring than in autumn and summer (Table 9.9), with the result that there was a highly significant relationship between the mean number of marked animal sightings and the mean number of all bushbuck observations ($r = 0,995$; $p < 0,001$). These results infer that Petersen estimates of population size were unaffected by

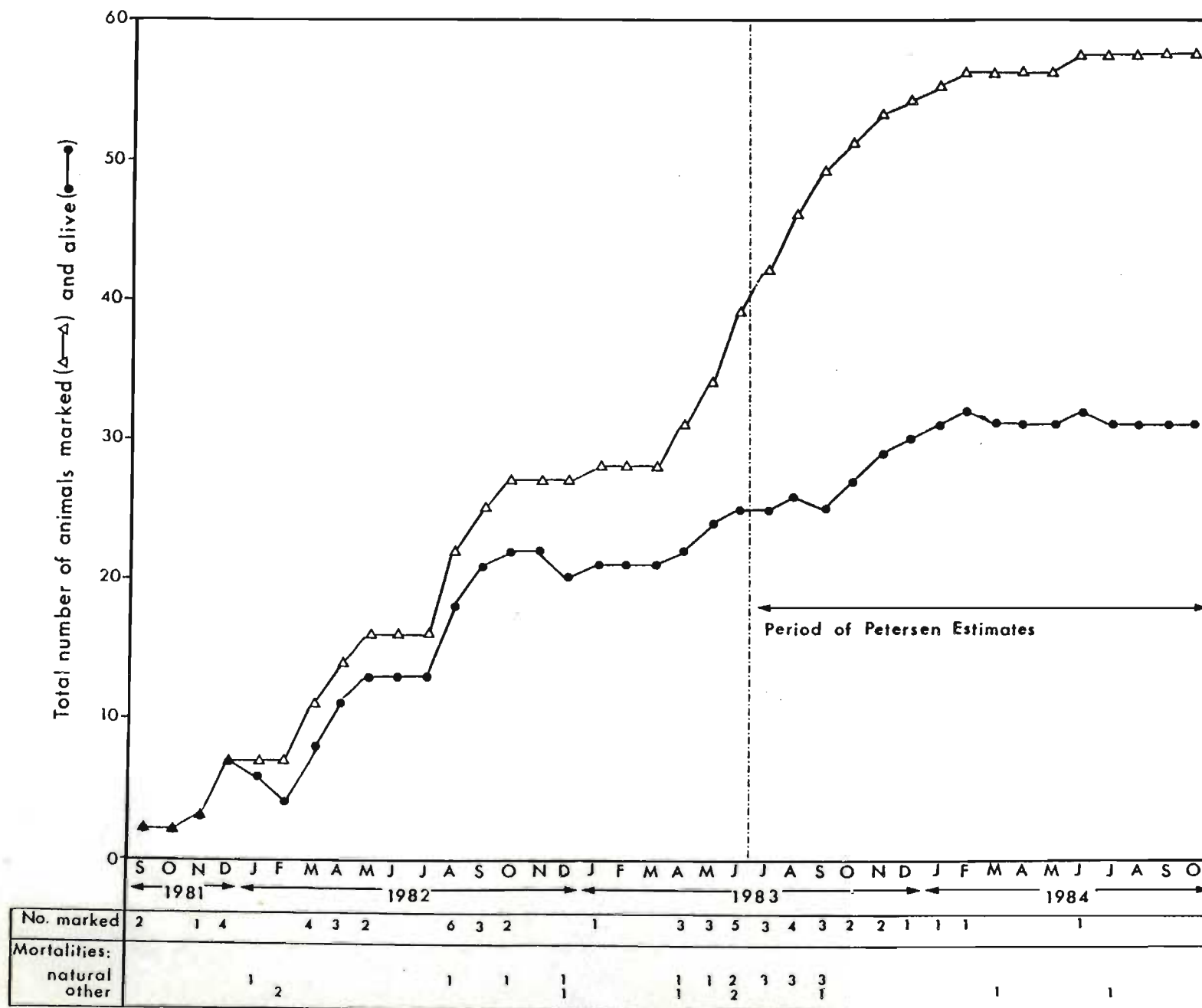


FIGURE 9.3 Changes in the number of marked bushbuck within I.S.A.1 from September 1981 to October 1984.

TABLE 9.9 Seasonal variations in the mean number of bushbuck seen each census within the 5km² section of I.S.A.1.

Period of census	No. of counts	$\bar{x}$ no. of marked bushbuck seen (m)	$\bar{x}$ no. of marked bushbuck in the population (M)	Probability of seeing a marked bushbuck (m/M)	$\bar{x}$ no. of bushbuck seen (n)
Winter 1983	10	9,1	25,3	0,360	15,8
Spring 1983	18	6,3	26,8	0,235	11,7
Summer 1984	28	4,6	30,4	0,151	8,8
Autumn 1984	27	3,6	31,1	0,116	6,7
Winter 1984	23	6,2	31,4	0,197	11,5
Spring 1984	15	6,5	31,0	0,210	12,3

variations in visibility during the course of the year, although if censuses are designed to include supplementary data pertinent to other aspects (e.g. group size, structure and activity) then obviously these should be conducted in winter and spring when animals are more frequently observed than at other times of the year.

Schnabel estimates obtained for bushbuck were generally slightly higher (overall estimate = 54,6 animals; 95% confidence interval of 50,6 to 59,1 bushbuck) than those determined from the Petersen estimate, but showed identical monthly trends in population size (Table 9.10). To test for a difference in population levels between years, Schnabel estimates were calculated for each month from July to October 1983 and compared with the corresponding months in 1984. In none of these instances were the resultant z values significant (range = 0,572 to 1,813; see Chapman and Overton 1966). All the available evidence therefore suggests that bushbuck numbers remained relatively constant during the monitoring period. However, 33% of the marked population died of natural causes during April- September 1983, and it

TABLE 9.10 Monthly Schnabel estimates of bushbuck in a 5km² section of I.S.A.1, Weza State Forest, from July 1983 to October 1984.

Month	λ *	x+1 *	N	95% confidence intervals
Jul '83	1992	46	43,3	32,0-59,1
Aug '83	2015	47	42,8	31,8-58,3
Sep '83	2704	56	48,3	37,6-64,3
Oct '83	654	19	34,4	21,1-57,6
Nov '83	2261	42	53,8	39,2-74,6
Dec '83	3263	64	50,9	40,3-66,6
Jan '84	2023	28	72,3	48,7-109,0
Feb '84	2130	40	51,9	38,4-74,6
Mar '84	1259	23	54,7	35,3-86,7
Apr '84	1054	18	58,6	35,4-99,6
May '84	3286	60	54,8	42,9-72,7
Jun '84	4295	71	60,5	48,4-77,9
Jul '84	2036	34	59,9	42,0-86,5
Aug '84	1984	40	49,6	35,8-69,4
Sep '84	2635	48	54,9	40,8-74,4
Oct '84	3100	51	60,8	45,7-81,4
Overall	36691	672	54,6	50,6-59,1

* - see Section 9.2 for definitions of these symbols

is reasonable to assume that a similar proportion of unmarked animals also succumbed at this time. Since these deaths did not result in an appreciable decline in population numbers, these findings infer that losses from natural (and unnatural) causes were partially offset by immigration. Some of these immigrants presumably remained in the study area and were subsequently captured with the result that the proportion of marked animals during the last year of study also remained relatively constant (Fig. 9.3). This aspect is discussed further in Chapter Ten.

Mark-recapture techniques involving duiker were limited to an area of $2,9\text{km}^2$ within I.S.A.2. A minimum of three counts per month were completed from July to November 1981 when the minimum number of marked animals in the population varied from eight to ten individuals (known mortalities and animals never seen after their release were excluded from this total). Petersen estimates for this area varied from 20 duiker ($\pm 8,9$ S.E.) in July and November to 40 duiker ($\pm 20,0$ S.E.) with an overall estimate of 26,9 ($\pm 12,9$ S.E.) animals. The proportion of the population that was marked during any one month ranged from 25% to 40% (average = 31,3%) which was considerably less than the corresponding proportion of marked bushbuck in I.S.A.1. This lower proportion of marked duiker may have accounted for the higher variance associated with each monthly mean estimate; coefficients of variation exceeded 40% for all five months and thus the estimates are less reliable than those obtained for bushbuck. Counts were not continued after November 1981 because of the few animals seen during the summer months, and although counts were initially scheduled to continue during the winter of 1982, this lapse in monitoring made it extremely difficult to assess natural mortalities (and hence to make relevant adjustments to the total number of marked animals in the population). None of the duiker marked in 1981 were fitted with radio transmitters, and even when these were fitted in 1982, radio tracking efforts met with limited success (Appendix D). As a consequence, all attempts to capture, mark and fit radio collars were abandoned at the end of 1982. Because (a) natural mortality rates could not be monitored with any degree of temporal precision in 1982 (when the highest proportion of marked animal deaths were recorded (see Chapter Four)) and (b) several other assumptions inherent in the Petersen estimate were also violated, attempts to continue monitoring this species by mark-recapture methods were also abandoned at this time.

Although Caughley (1977) stated that mark-recapture methods should only be used when no other census method will suffice, and despite the problems associated with capturing, marking and observing duiker, the Petersen estimate provided

the most reliable means of censusing both antelope populations at Weza. Many of the limitations of this technique detailed by Caughley (1977) and Otis et al. (1978) were obviated by continuous capture and marking exercises, while radio tracking greatly facilitated the detection (and hence omission) of marked bushbuck that had died, and emigration, had it occurred within the bushbuck population (see Chapter Eight), could have been quantified through regular monitoring. One way in which estimates could have been biased concerns the loss of marks, but there was no evidence from this study that any of the marked animals lost their collars, which were made from machine belting and fastened with either rivets or nuts and bolts (Appendix D). Absolute estimates may also have been biased if marked subjects were more conspicuous than unmarked animals, but this is considered unlikely as all mark-recapture exercises were conducted at night, and animals were usually initially detected in the beam of the spotlight by eye-shine (light reflected from the tapetum). Even if marked animals were indeed more conspicuous, they presumably would have been so throughout the duration of this study, and hence comparisons between relative densities at different times of the year, or between the same seasons in different years, would remain valid.

The value of the Petersen estimate as a census technique at Weza was largely attributable to the intensive capture, marking and monitoring operations that continued until field work was completed. Unfortunately, such exercises were extremely expensive and time-consuming (Appendix D) but were justified because marked animals were also essential to many other aspects of this study (e.g. Chapters Five, Seven and Eight). However, it is highly improbable that management staff will incur such costs on capture and marking (to ensure that at least 50% of the population is marked) and expend such efforts on monitoring (during regular censuses as well as in detecting deaths and animal movements) solely for census purposes in future years. Because less intensive efforts are likely to diminish the value and reliability of the Petersen estimate, and thus render it more prone to the

limitations listed by Caughley (1977) and Otis et al. (1978), this technique cannot be recommended as a suitable or practical means of censusing bushbuck and duiker in Weza State Forest and other timbered areas where the importance of wildlife is always secondary to plantation management.

9.3.5 Absolute estimates and indices of bushbuck and duiker numbers

The problems of censusing antelope in plantations and indigenous forests are not unique to Weza - they have also been experienced and reported by several other biologists (e.g. Odendaal et al. 1980; Schmidt 1983; Seydack 1984), all of whom have stressed the necessity of increased sampling in order to detect fluctuations in population size. The only reliable and repeatable means of censusing antelope in this study involved the Petersen estimate, but because these counts were made in prime bushbuck and duiker habitats, extrapolation of these estimates to the entire plantation area would result in gross overestimates of population size. Relative densities of six bushbuck per km² and five duiker per km² determined from counts along the 21km fixed census route (assuming an effective strip width of 100m) must be regarded as mere approximations, although they compare favourably with estimates obtained in similar habitats elsewhere (Odendaal 1977; Odendaal et al. 1980; Schmidt 1983; Seydack 1984; K. Zunkel pers. comm.; see Table 9.1), but are considerably lower than densities recorded in more natural (and presumably superior) habitats (e.g. Jacobsen 1974; Waser 1975a; Allsopp 1978). It is therefore highly improbable that absolute numbers of bushbuck and duiker will ever be estimated with any degree of accuracy or precision without substantially more funds and manpower than was available for this study. Despite the obvious advantages of accurate estimates particularly when a population is to be reduced by culling or when proposals regarding hunting are submitted to management and administration staff (Stearns 1969; Norton-Griffiths 1978), the need for absolute

estimates is often questionable and such estimates may even be regarded as unnecessary luxuries (Caughley 1977, 1979a). However, although less costly, the alternative approach of estimating indices of density is also restricted by many of the limitations experienced in estimating absolute numbers. Three important factors affecting the precision of counts at Weza, namely (a) the structure and variability of the vegetation occurring within a mosaic of heterogeneous habitats, (b) the relatively low densities of animals which resulted in inadequate sampling and (c) the enormous variability in animal sightings within any one month, have already been considered. There is yet another extremely serious constraint inherent in plantation wildlife census techniques. Management activities involved in silviculture and timber exploitation (e.g. burning, cleaning, pruning, thinning and felling) often result in widespread and drastic alterations to localised habitats. These activities affect the quality, availability and distribution of food resources and cover that are already fluctuating naturally on a seasonal basis (see Chapter Seven). Bushbuck and duiker may respond to these activities in different ways, but it is extremely important that the potentially adverse or beneficial results of such management actions are recognised and incorporated in census designs. Failure to "dilute" the effects of intensive, localised timber management practices on animal distributions by extensive sampling will result in highly erroneous conclusions regarding population trend. Consequently fixed census routes are totally unsuitable; counts conducted during one winter are not comparable with those obtained during the following winter if extensive habitat alterations have occurred along that route during the interim period. It is for this reason that area measurements along the 21km fixed census route were abandoned in November 1980; counts were merely continued in an attempt to identify the optimum conditions and periods for census. The potential effects of habitat modification on the accuracy, precision and repeatability of forest wildlife population estimates have frequently been neglected in other studies conducted in South Africa (e.g. Odendaal 1977; von Gadow 1978; Odendaal et al. 1980), while these presumably are of less consequence

in more temperate areas where timber growth rates are slower, rotation cycles are longer and hence management practices are less intensive (e.g. Peek et al. 1976; Schoen et al. 1981; Rose 1982).

All future attempts to census both bushbuck and duiker populations should be as extensive as possible to ensure that all the available habitats are monitored and that these are monitored at all stages of succession and management, and in relation to their juxtaposition with less preferred or more favoured habitats. Provided that counts are conducted over extensive areas, such sampling will obviate the need to stratify these habitats, which is difficult to achieve in plantation areas. Counts should be confined to the winter months, and because of the limitations of road counts detailed above and in Norton-Griffiths (1978), a simple but standardised (with regards to vehicle speed, choice of observers, time of census etc.) count index would be adequate for assessments of population trend. Indirect methods of estimating population trends during the course of this study are detailed in Chapter Ten.

CHAPTER TEN

POPULATION PERFORMANCE AND MANAGEMENT

10.1 POPULATION PERFORMANCE

A detailed analysis of the population dynamics of bushbuck and duiker using life table data was not possible in this study because of the unequal intervals of time separating each adult age class. However, several inferences regarding the performance of these two species at Weza may be made by examining the structure of the populations and comparing these to the productivity data detailed in Chapter Five.

10.1.1 Population Structure

The structure of both bushbuck and duiker populations was determined in two independent ways. Firstly, all animals seen during the first year of study were classified by sex and age (wherever possible) using the criteria presented in Chapter Three. These records were not maintained after 1981 as field work from 1982 to 1984 was concentrated in the two intensive study areas where the chances of duplicating sightings of the same individuals were much greater than during the first year of study. The second approach involved recording the sex and age of all the animals that were culled randomly within the extensive study area from 1980 to 1984 (as detailed in Chapters Three to Six). Ages were determined using tooth eruption and replacement sequences and patterns and thus were more comprehensive and allocated more accurately than was possible during field classification.

10.1.1.1 Bushbuck

A total of 944 bushbuck were observed during the first year of study, and of these 927 (98,2%) were classified by sex and age. Adult females comprised 44,7% of the population; this proportion increased to 49,7% during autumn and was lowest during winter (40,8%), when most bushbuck

sightings were recorded (Table 10.1). Adult males constituted 38,9% of the population throughout the year, but were most frequently observed during the winter (41,3%) and comprised 33,5% of the observed population in autumn (Table 10.1). Subadult males and females and unsexed infants showed less seasonal variation, and overall constituted 3,7%, 6,9% and 5,8% of the population respectively.

TABLE 10.1 The population structure of bushbuck at Weza State Forest determined from (a) field sightings and (b) culled specimens.

	Adult males	Subadult males	Adult females	Subadult females	Infants
(a) sightings					
Spring (n=220)	38,6%	3,6%	46,8%	5,9%	5,0%
Summer (n=106)	40,6%	3,8%	45,3%	4,7%	5,7%
Autumn (n=197)	33,5%	3,6%	49,7%	6,6%	6,6%
Winter (n=404)	41,3%	3,7%	40,8%	8,2%	5,9%
All year (n=927)	38,9%	3,7%	44,7%	6,9%	5,8%
(b) culled					
All year (n=132)	44,7%	6,1%	38,6%	6,8%	3,8%

The population sex ratio (adults and subadults) calculated from these observations was 82,6 males : 100 females, which differed significantly from parity ($\chi^2 = 7,89$; $p < 0,01$), but the adult sex ratio of 87,2 males : 100 females did not differ significantly from unity.

The population structure derived from culled bushbuck showed a similar trend, with the exception that adult males (44,7% of the sample) were slightly more numerous than adult females (38,6%), while the five infants collected (one male and four females under 8 months of age) comprised 3,8% of the population (Table 10.1). The sample size was inadequate for any meaningful comparison on a seasonal basis. Neither the

population sex ratio (106,3 males : 100 females) or the adult sex ratio (115,7 males : 100 females) derived from culling differed significantly from parity. The age structure of all of the bushbuck culled at Weza is detailed in Fig. 10.1).

These findings concur with the general trend that has emerged from other studies (Table 10.2) and although Mentis (1970) and Dasmann and Mossman (1962b) recorded disproportionate sex ratios in favour of females, these were derived from culling and small sample sizes respectively, while both included juvenile or subadult animals. Care should be given in interpreting sex ratios obtained from other general ungulate surveys as authors not familiar with

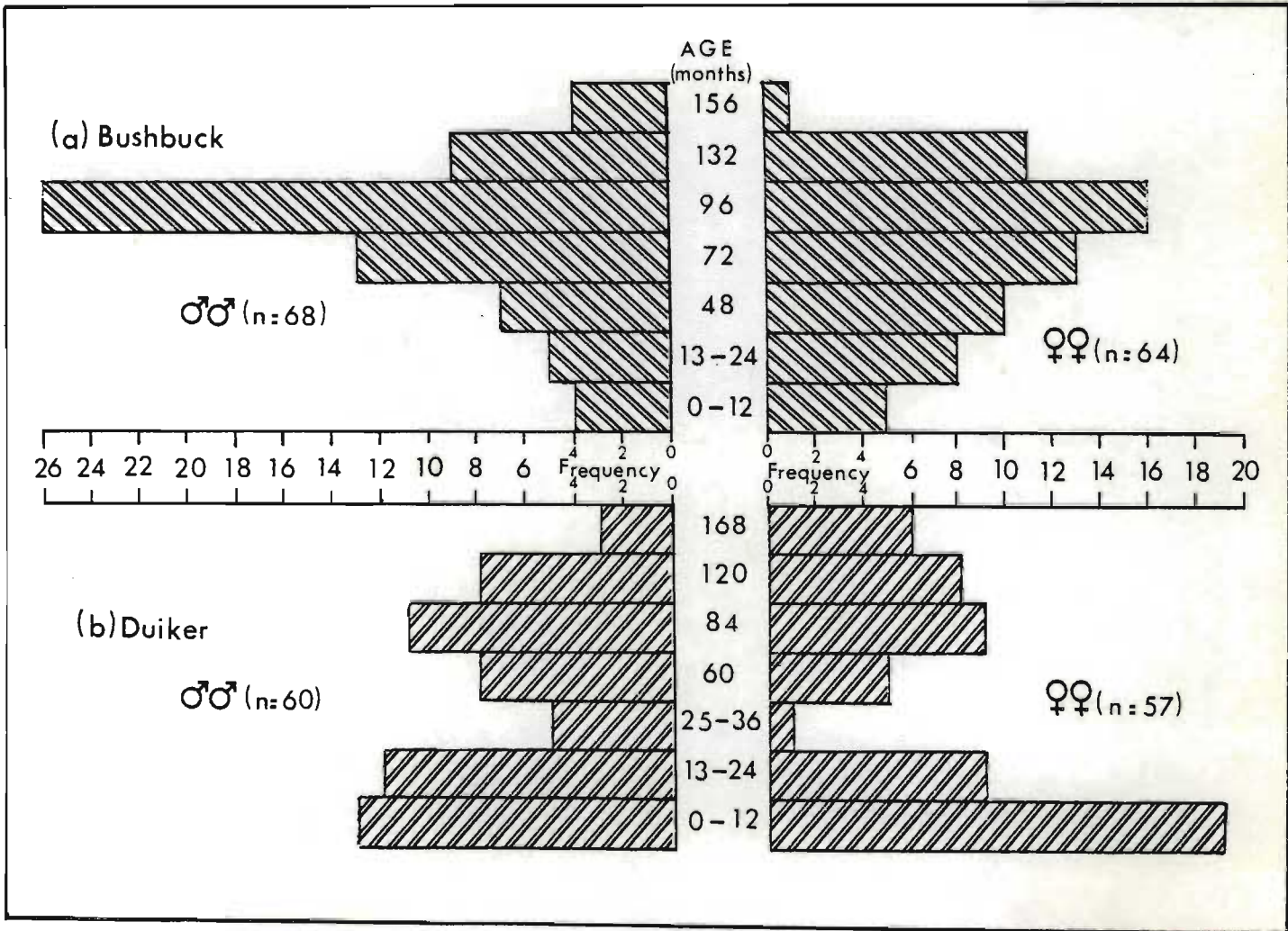


FIGURE 10.1 The age structure of a) bushbuck and b) duiker culled at Weza State Forest.

TABLE 10.2 Comparative population sex ratios of bushbuck in southern Arica calculated to a base of 100 females.

Number sexed		Ratio males:100 females	χ^2	P value	Source
Males	Females				
740	587	126,1	17,64	$p<0,001$	Odendaal (1977)
N/A	N/A	120,0	N/A	N/A	Jacobsen (1974)
39	35	111,4	0,22	n.s.	Wilson & Child (1964)
388	359	108,1	1,13	n.s.	Odendaal (1977)
68	64	106,3	0,50	n.s.	This study - culled sample
84	83	101,2	0,01	n.s.	Elder & Elder (1970)
38	40	95,0	0,05	n.s.	Allsopp (1978)
78	83	93,9	0,16	n.s.	Thomson (1972) *
249	281	88,6	1,93	n.s.	Morris (1973)
16	19	84,2	0,26	n.s.	Mason (pers. comm.)
395	478	82,6	7,89	$p<0,01$	This study - field observations
19	25	76,0	0,82	n.s.	Bouliere & Verschuren (1960) **
1416	2119	66,8	139,80	$p<0,001$	Mentis (1970)
N/A	N/A	66,0	N/A	N/A	Simpson (1974c)
11	19	57,9	2,13	n.s.	Walther (1964)
12	25	48,0	4,57	$p<0,05$	Dasmann & Mossman (1962b)
26	61	42,6	14,08	$p<0,001$	Dasmann & Mossman (1962b)
* - cited in Odendaal (1977)					
** - cited in Elder and Elder (1970)					

bushbuck could inadvertently include younger animals, which would bias the results in favour of females because young "red" males cannot be easily distinguished from females until they are at least 14 months old (Chapter Three). Such errors undoubtedly occurred even in this detailed study when animals were classified at night, and probably account for the significantly higher proportions of females recorded during field observations which was not evident in the randomly culled samples.

10.1.1.2 Duiker

Of the 708 duiker observed during the first year of study, only 418 (59,0%) could be classified by sex and age. Adult females constituted 44,0% of the classified population throughout the year, and this proportion fluctuated from 40,8% in winter to 48,8% during the summer months (Table

10.3). Adult male duiker comprised 27,8% of all sightings, and varied from 20,4% in autumn to 35,4% in spring; these wide fluctuations infer that considerable errors were made during classification in the field. The proportions of recorded infants and subadults also showed considerably more seasonal variance than for bushbuck (Table 10.3). The population sex ratio derived from these sightings was 74,9 males : 100 females which departed significantly from parity ($X^2 = 8,18$; $p < 0,01$); this ratio differed even more significantly when only the adult section of the population was considered (63 males: 100 females, $X^2 = 15,41$; $p < 0,001$).

TABLE 10.3 The population structure of duiker at Weza State Forest determined from (a) field sightings and (b) culled specimens.

	Adult males	Subadult males	Adult females	Subadult females	Infants
(a) sightings					
Spring (n=130)	35,4%	10,8%	43,8%	7,7%	2,3%
Summer (n=82)	32,9%	4,9%	48,8%	3,7%	9,8%
Autumn (n=54)	20,4%	13,0%	46,3%	18,5%	1,9%
Winter (n=152)	21,1%	19,1%	40,8%	13,2%	5,9%
All year (n=418)	27,8%	12,9%	44,0%	10,3%	5,0%
(b) culled					
All year (n=117)	27,4%	20,5%	23,9%	16,2%	12,0%

The population structure obtained from the culled sample reveals higher proportions of subadults and infants, and a much lower proportion of adult females (23,9%) in the population. These data are considered to be a much more accurate reflection of the duiker population at Weza, because they were derived from more refined methods of age estimation. The only source of error that might have biased

the culled material concerns the selection of certain individuals, but since the majority of duiker seen at Weza were solitary animals (Chapter Eight), culling must have been conducted randomly in most instances. Younger animals may have been less conspicuous, but the rapid rate of growth attained by this species (Chapter Three) suggests that differential visibility was of negligible importance. The similar proportions of adult males determined from both sightings and culled specimens indicates that little error was made in classifying these animals in the field, presumably because their horns were conspicuous. However the culled sample infers that subadult males and subadult females were inadvertently classified as adult females on numerous occasions, and consequently field observations of this species cannot be recommended as a reliable means of determining population structure. The fact that the population sex ratio and adult sex ratio derived from culling (105,3 males : 100 females and 114,3 males : 100 females respectively, neither differing significantly from parity) shows close accord with the same ratios determined elsewhere, while the population sex ratio obtained from sightings is the only significant deviation from unity in all these studies (Table 10.4), supports this conclusion. Similar problems and biases associated with sex and age ratio data have been noted by several other authors studying species with less rapid rates of growth and more pronounced sexual dimorphism (e.g. Progulske & Duerre 1964; Zagata & Haugen 1974; Downing et al. 1977; McCulloch 1982; Sage et al. 1983).

The age structure of the duiker population culled at Weza is detailed for comparative purposes in Fig. 10.1.

10.1.2 Fecundity and Juvenile Mortality

Both mature bushbuck and duiker females were producing approximately 1,6 young per annum during the course of this study, and were thus virtually breeding at their full reproductive potential (Chapter Five). The stark differences in the proportions of infant and juvenile animals in the

TABLE 10.4 Comparative population sex ratios of duiker in southern Arica calculated to a base of 100 females.

Number sexed		Ratio males:100 females	X ²	p value	Source
Males	Females				
35	26	134,6	1,33	n.s.	Child & Wilson (1964)
25	22	113,6	0,19	n.s.	Mason (pers. comm.)
83	77	107,8	0,23	n.s.	Mentis (1972)
99	94	105,3	0,13	n.s.	Wilson & Clarke (1962)
60	57	105,3	0,08	n.s.	This study - culled sample
29	29	100,0	0,00	n.s.	Dasmann & Mossman (1962b)
114	115	99,1	0,00	n.s.	Wilson & Roth (1967)
1676	1743	96,2	1,31	n.s.	Mentis (1970)
9	11	81,8	0,20	n.s.	Dasmann & Mossman (1962b)
8	10	80,0	0,22	n.s.	Dasmann & Mossman (1962b)
170	227	74,9	8,18	p<0,01	This study - field observations
15	22	68,2	1,32	n.s.	Dasmann & Mossman (1962b)
17	26	65,4	1,88	n.s.	Dasmann & Mossman (1962b)

bushbuck and duiker populations (Table 10.5) are therefore cause for concern since they indicate much higher mortality rates and thus depressed recruitment in the population of bushbuck. Several independent methods were employed to examine this aspect further.

TABLE 10.5 The proportions of juvenile and subadult bushbuck and duiker in culled samples from Weza.

	Age class (months)		
	0-12	13-24	0-24
No. of bushbuck culled	9	13	22
% of total sample (n=132)	6,8%	9,9%	16,7%
No. of duiker culled	32	21	53
% of total sample (n=117)	27,4%	17,9%	45,3%

A common means of determining juvenile mortality is by evaluating conception rates from a culled sample, or recording adult female:infant ratios shortly after the peak calving season, and then following the survival of those infants by repeated female:juvenile ratio counts in the field (e.g. Martinka 1967; LeResche 1968; Parker 1972; Beasom 1974; Woodard et al. 1974; Wegge 1975; Carroll and Brown 1977; Staines 1978; Smith and LeCount 1979; Attwell 1982; Hamlin et al. 1984; Skogland 1984). Such an approach assumes that adult females and juveniles are equally visible, that animals under a certain predetermined age (e.g. 12 months) can be readily distinguished from older members and that adult female:juvenile ratios below that expected from birth rate data must be due to juvenile mortality. The technique is therefore best suited to highly seasonal breeders occupying open habitats whose young are "followers" rather than "hiders", and is consequently less applicable to both bushbuck and duiker (see Chapters Five and Seven). Nevertheless, since all postpubertal females of both species were fertile and bred throughout the year, the ratio of infants to adult females should be 1,6 : 1,0 assuming a mean length between each generation of 7,5 months for both bushbuck and duiker (Chapter Five). Any departure from this ratio can, theoretically at least, be attributed to mortality. The ratio of infant to adult female bushbuck recorded during field observations was 1 : 7,7 (Table 10.1) which suggests that for every 12,3 infants born ($1,6 \times 7,7$), only one survives. This can be expressed as percentage mortality, following Spinae (1970), as:

$$100 - (1/6,6 \times 100) = 84,8\%$$

The mortality rate determined from the infant:adult female ratio obtained from the culled sample (1:10,2) was even higher at 93,5%. Mortality rates computed in an identical manner from infant:adult female duiker ratios observed in the field (1:8,8) and collected during culling operations (1:2,0 see Table 10.3) were 92,3% and 54,6% respectively. The former rate was undoubtedly biased by inaccurate age estimations of both infants and adult females in the field

(see above) and the rate determined from the culled sample should be considered as a more realistic value. These mortality rates were also probably overestimates due to the concealment and lying out behaviour of both antelope species.

Another independent method of determining infant mortality is the weaning ratio (Spinage 1982) which does not involve any measure of infant numbers and is thus not subject to any possible bias from lying out behaviour. In a continuously breeding animal it is expected that the adult female will be permanently lactating except when she stops feeding the lamb at heel in order to produce colostrum for the next birth (Spinage 1982). Colostrum is produced by bushbuck during the last ten days before parturition (Chapter Five) and so the infant should normally be weaned when the foetus has a gestational age of approximately 170 days. Of the 61 female bushbuck examined older than 30 months, 28 were lactating (animals producing colostrum not included) and thus the average length of lactation was

$$\frac{28}{61} \times \text{gestation period (180 days)} = 83 \text{ days}$$

Infant mortality up to weaning can therefore be calculated as

$$\frac{(180-10) - 83}{(180-10)} \times 100 = 51,1\%$$

The average length of lactation in duiker (17 of the 44 females at least 20 months of age were lactating), assuming that colostrum is produced during the last ten days of pregnancy (Fig. 5.27) and a gestation period of 191 days (Chapter Five) was 74 days and infant mortality up to weaning was therefore 59,1%.

The weaning ratio therefore provides a slightly higher mortality rate among infant duiker than for infant bushbuck, and yet infant:adult female ratios based on culled specimens

indicates that infant bushbuck losses are considerably greater than those for infant duiker (infants in these instances being any animal younger than 8 months of age). Reasons for these anomalous results are not obvious, but the age structure of the bushbuck population and the infant:adult female ratios tend to suggest that infant mortality prior to weaning may be underestimated using Spinage's (1982) method.

The age structure of the culled duiker sample suggests that either the population is expanding, or that adult mortality is much higher than in the bushbuck population (Fig. 10.1). Duiker observations recorded during censuses and routine fieldwork do not support the suggestion that the population was expanding, and to examine this aspect further the population mortality rate and life expectancy were calculated for both populations from the ratio of juveniles to adults, being the method described by Caughley (1967). Because both species breed throughout the year, the population mortality rate per year was estimated from six months of age and life expectancy was estimated from a base age of six months (Caughley 1967). Insufficient bushbuck data were obtained for the calculation of population mortality rate per year during 1982 to 1984, and animals dying from accidental causes have been included to increase sample sizes (Table 10.6). Since it is unlikely that either population had a stable age distribution (See Chapter Four), only the means of these estimates will have biological significance. The calculations give estimates of population mortality rate per year for bushbuck as 0,12 and life expectancy at 6 months as 15,5 years. The corresponding values for duiker are 0,32 and 2,9 years respectively (Table 10.6). While these must be considered as extremely crude estimates due to the small sample sizes involved, they nevertheless indicate that life expectancy for 6 month old bushbuck is considerably longer than that for duiker. Possible reasons for this difference are considered below.

TABLE 10.6 Calculations of mortality rate and life expectancy from (a) two samples of female bushbuck and (b) five samples of female duiker at Weza.

Sampling period	No. of females 0-12 months old (j)	Total females (n)	Population mortality rate per year (j/n)	Life expectancy in years at 6 months (2n-j/2j)
a) Bushbuck				
1980	1	27	0,04	26,5
1981	5	25	0,20	4,5
			Mean 0,12	15,5
b) Duiker				
1980	5	21	0,24	3,7
1981	7	20	0,35	2,4
1982	3	12	0,25	3,5
1983	3	11	0,27	3,2
1984	3	6	0,50	1,5
			Mean 0,32	2,9

10.1.3 Performance

Reasons for the higher mortality among bushbuck infants than in juvenile duiker are probably directly related to the different causes of mortality in the adult segment of these two populations. All the available evidence obtained in this study, including seasonal fluctuations in physiological condition indices, differences in deposited fat reserves between populations under different management regimes, seasonal fluctuations in diet, and the temporal distribution of natural mortalities strongly suggest that food quantity and/or quality are limiting for bushbuck during winter and early spring. Young animals are likely to be much more susceptible to starvation and exposure at this time because of their less extensive fat reserves (de Calesta *et al.* 1975, also see Chapter Four), and because if their mother's have severely depleted fat deposits, they may delay or cease producing milk. (Verme 1963, 1965, 1967, 1969, 1977; Klein 1970, 1981; Eberhardt 1977; Hanks 1981; also see Chapter Five). Furthermore, the mother's nutrition during pregnancy

may have a direct bearing on the growth and development of the foetus, and consequently on the post-natal survival of that infant. Animals born during mid-winter may be considerably smaller than infants born in summer, and even if winter infants survive, they experience two winters by the age of 12 months, and presumably are less healthy or vigorous than animals of similar age born during summer. Since the onset of puberty is directly influenced by body mass, animals born at different times of the year may account for the differences in the ages at first parturition observed in this study (Chapter Five). Further, since the nutrition of the female can directly influence the age at which she conceives for the first time (Klein 1970, 1981; Eberhardt 1977), the later age at which female bushbuck attained sexual maturity in this study compared to several other wild and captive populations indicates that the nutritional resources at Weza may be substantially inferior to those available in other bushbuck habitats. Relative densities and home range sizes (see Chapter Seven and Nine) support this conclusion. Another factor, fecundity, may also decline in response to inadequate food resources, (Klein 1970, 1981; Eberhardt 1977; also see Chapter Five), while Verme (1983) has demonstrated that nutrition may influence foetal sex ratios in deer, with undernourished females tending to produce a surplus of males whereas more females are born to mothers in healthy condition. Neither of these indications of nutritional stress were evident in this study, presumably because food resources were limiting for relatively short periods of time. Other more subtle aspects that may influence neonatal mortality, such as overcrowding at localised food resources (see Ozoga *et al.* 1982a), could not be monitored in this study, but warrant attention in the future.

The aseasonal breeding strategy of the bushbuck may therefore appear somewhat incongruous in an environment such as Weza where there are pronounced seasonal changes in temperature, distribution of rainfall and hence plant production during the year, but plantations are a totally artificial and relatively recent environment that has been exploited by this species; the natural habitats selected by

bushbuck elsewhere (indigenous evergreen forests, natural thickets and riparian communities, see Chapter One and Seven) are presumably much more stable and therefore capable of supporting animals of all ages throughout the year, and bushbuck have responded to these conditions by breeding continuously.

In contrast to bushbuck, adult duiker showed much smaller seasonal differences in deposited fat reserves, but had most extensive perinephric fat reserves during autumn (Chapter Four). The winter diet of duiker consisted largely of fungi and fruits, which are rich sources of protein and energy, and are readily digestible (Chapter Six); these dietary items were rarely consumed by bushbuck. These results, together with the fact that far fewer duiker died of natural causes during the winter months, suggest that this time of the year is nutritionally less stressful for duiker. If adults, particularly females, are in reasonable condition during the winter, then it follows from the reasoning above that infant survival will be enhanced. Resource partitioning by territorial behaviour would also reduce intraspecific competition among the juvenile segment of the population, while the social and spatial organisation exhibited by this species (Chapter Eight) suggests that animals may be subjected to more stress as they reach puberty and are evicted from their natal range by the parent of the same sex. However, the age structure of the duiker culled at Weza infers that mortalities are more pronounced among the 25 - 60 month old segment of the population. Reasons for this are not immediately obvious, but the high proportion of duiker deaths recorded in 1982 provides some indication of what factors may be responsible. A greater proportion of the extensive study area was influenced by Forestry management practices during 1982 than at any other year in this study (Chapter Two). Since duiker are territorial, their reactions to disturbance and habitat modifications resulting from felling, cleaning, pruning and thinning may not be the same as those of bushbuck, where the latter species simply avoids the affected area by moving into adjacent compartments until forage and/or cover is restored. A duiker's response to

disturbance and changes to the habitat will presumably depend on the proportion of his territory that has been affected, but movement into adjacent areas will largely depend on whether such areas are occupied by other territorial duiker. Territory sizes in I.S.A.1 and I.S.A.2 suggest that the latter area is the more suitable and productive for duiker (Chapter Eight), but the average size of compartments in I.S.A.2 is more than double that in I.S.A.1 (Chapter Two), and considerably larger than the size of the average territory there. Precisely how duiker react to these perturbations could not be determined in this study, but I suggest that these changes were causal factors in the "disappearance" (either deaths or extensive emigration) of many of the duiker marked at Weza. Interestingly, Boshe (1984) found that Kirk's dikdik, which establish territories in more open areas and generally avoid areas of dense thickets and shrubs (and thus show similar habitat selection patterns to duiker), either extended their territory boundaries or simply abandoned them in response to reduced shrub density and cover. Either action is likely to involve additional contact with conspecifics, and will only be beneficial in the long term if the benefits (e.g. assured supply of food and cover, and mate acquisition) exceed the costs (time and energy expenditure, exposure to harassment and/or injury, risk of predation etc) irrespective of which strategy is adopted. Finally even where vegetation is not affected by management activities, forage and suitable habitat availability may alter drastically as a result of plant succession (see Klein 1970, 1981) with the result that certain communities may become totally unsuitable with time, and duiker may be forced to seek new territories in more suitable habitats.

Because the field data obtained from duiker were less comprehensive than for bushbuck, these conclusions regarding population performance are obviously tentative and need to be substantiated or refuted by additional research. However, this study had demonstrated that food, on a seasonal basis, is not limiting duiker at Weza. It is extremely difficult to envisage how stable territories can be established in an area

that receives highly variable precipitation, has highly pronounced seasons of plant growth and dormancy, and is intensively managed and manipulated for timber production. Prepubertal animals presumably experience less stress, or evoke fewer responses from conspecifics, than adults when dispersal and/or abandonment of a territory is necessary, and thus the greatest turn over in the population is among young adults competing with prime animals when new territories are sought. In contrast, bushbuck are limited by food quality and/or quantity, show fidelity to specific areas, but are tolerated by conspecifics provided that they act submissively when such behaviour is warranted. Habitat modifications due to management or plant succession may be detrimental over relatively short periods of time, and such areas are avoided, but these invariably alter and provide varying amounts of food and/or cover depending on their levels of subsequent management. If we assume that food resources limit the bushbuck population during winter, and space (in terms of habitats suitable for the development and maintenance of functional territories) limits the duiker population, then the latter is likely to show greater fluctuations in population size under the present management regime at Weza; numbers with will vary according to the availability of suitable and undisturbed habitats. Bushbuck number will be more stable, and food resources (dependant on the rainfall during the previous wet season) will influence the deposition of fat reserves and directly affect the numbers of bushbuck that can survive through the most nutritionally stressful period, namely winter and early spring. In years of adequate rainfall, mortalities are probably confined to the infant and old adult portions of the population, but adults are likely to succumb to starvation and/or exposure during winters when rainfall is below average and food resources are more limiting (see Chapter Four).

Mortality patterns of duiker at Weza may therefore be density independent, and population size is likely to be variable with time. These factors, together with several other attributes such as rapid growth, short generation times, rapid colonization of suitable (albeit perhaps

ephemeral) habitats, and relatively small body size are generally exhibited by species favouring *r* selection (Pianka 1970). In contrast, bushbuck mortality is almost certainly more density dependent, and population size is likely to remain more constant in time at or near the carrying capacity (see below) of the environment, while the species showed a low level of dispersal at Weza, had slower rates of development and selected those habitats that were most stable. All of these aspects are associated with species exhibiting *K* selection. (Pianka 1970). There are obvious difficulties in subdividing a continuum and the listing of the above attributes should not imply that there are no similarities between bushbuck and duiker; an obvious aspect shared by both species is their reproductive potential. However, the above discussion serves to demonstrate their contrasting strategies to habitat and forage utilization and their differing life cycles. Consequently, habitat modifications and management practices aimed at stabilizing or enhancing the population growth of duiker may not necessarily be beneficial to bushbuck, and vice versa. Similarly, the fact that the size of the duiker population at Weza is likely to fluctuate more than bushbuck numbers will should not imply that neither of these populations can, and should be, exploited on a limited scale. Both of these aspects are considered below.

10.2 MANAGEMENT

The aims of population management are few and circumscribed, and can usually be achieved by specific action. Caughley (1976, 1977) notes that there are only three problems of population management:

- (a) the treatment of a small or declining population to raise its density,
- (b) the treatment of a population that is too dense, or which has an unacceptably high rate of increase, to stabilize or reduce its density, and

- (c) the exploitation of a population such that it provides an optimum or maximum sustained yield.

These three problems are commonly termed conservation, control and sustained yield harvesting respectively (Caughley 1977). All of these problems can be solved by manipulating the dynamics of the population to be managed, but the way in which the manipulation is effected may vary considerably according to circumstances. In certain instances direct manipulation may be necessary (e.g. Giles 1969) but occasionally a modification of available cover, food or water supply (e.g. Yoakum and Dasmann 1969) may be adequate to produce the desired effect on the population's rate of increase (Caughley 1976). However, it should be noted that a problem only arises when a relationship or situation develops that is not suited to the manager's purposes, whatever these might be, and no management decision is possible until we know what it is that we want (Caughley 1977).

For the last 30 years or so, the wildlife within Weza State Forest has been managed on a policy of total preservation. Forestry staff, perhaps unwittingly, opted for an ecological carrying capacity equilibrium (in the sense of Caughley 1979b) where little or no management was necessary. Thus if populations were forced off that equilibrium by an unusually harsh drought followed by a severe winter, when many animals may have died, the system would have returned to equilibrium in time without any interference from management. Conversely, if plant production was stimulated by a warm spring and a wet summer, plant biomass would have increased and the vegetation would have moved off its equilibrium density. Antelope numbers would have increased in response to these changes, and the added foraging pressure would have pulled the plant density down again until ecological equilibrium was maintained once more. There would have been interference from management however in that silvicultural and exploitation practices would have affected forage density and production in localised areas each year. Consequently, bushbuck and duiker numbers have undoubtedly fluctuated over

the last three decades, but these changes were probably unnoticed and certainly have not been recorded by field staff.

This same policy of non-intervention (with the exception of management practices associated with timber production) could be adopted in future years. However, Forestry's concern regarding the amount of damage antelope cause to pine seedlings, and their interest in the potential and feasibility of offering limited sport hunting on State land indicate intentions that depart significantly from the management policy currently employed. (See Chapter One). The objectives of this study were not directed at any one specific management problem, but were aimed at providing base-line data concerning population abundance, trends, distribution, feeding ecology, habitat preferences and animal movements. Assessments could then be made of the extent to which these movements, habitat preferences and feeding strategies may effect, and be influenced by forestry management practices, followed by an evaluation of the proportions of both populations that could be utilized for sport hunting and/or meat production on a sustained yield basis. It is within these conditions of reference that the following management recommendations are based. I appreciate that the primary management aim at Weza is to produce timber; any revenue obtained from wildlife will be insignificant compared to that received from the sale of timber (Chapter Two). Consequently some of the following recommendations regarding wildlife may appear totally impractical, inappropriate or may be diametrically opposed to the aims and objectives of timber production: they are included here however because if forests are to become areas of multiple land use, then wildlife and timber management should become more compatible (see Ryle 1967; Staines 1967) and thus policies and values (either economic or aesthetic) should change accordingly.

Compared to Europe and North America, wildlife management and utilization in plantations in this country are at a very early stage of development. Much can be learnt

from the history and present state of wildlife management in the temperate areas of the northern hemisphere, even though there are obvious differences in the biotic and abiotic environments of such areas compared to South Africa. The most obvious of these include the more severe climatic conditions, slower growth rates and rotation times of timber species and less pronounced temporal changes in plant succession in the northern hemisphere, where the majority of ungulates are cervids that have pronounced annual cycles of growth and reproduction. Nevertheless, there are numerous similarities among certain aspects of the ecology of forest antelope and cervids. Bushbuck mortality during winter can be an important factor affecting populations inhabiting plantations, just as it is in reducing deer numbers on northern ranges (Bartmann 1984). Within the timbered habitats at Weza, bushbuck and duiker select the early successional stages of vegetation in a similar way to North American deer (Klein 1970; Short 1972; Gavin et al. 1984), while there are further similarities in the diurnal and nocturnal selection by deer and bushbuck of habitats classified by their structural composition (see Loft et al. 1984). Numerous other similarities have been noted throughout this thesis in such aspects as seasonal variations in deposited fat reserves, diet quality and composition, and social and spatial organisation (with bushbuck and duiker resembling the behaviour exhibited by white-tailed and roe deer respectively) and indeed Walker (1975) has stated that the general habits of bushbuck "are much like those of the North American white-tailed deer (*Odocoileus*) and the form is similar". Previous studies concerning the conservation, (including habitat improvements), control (including the reduction of damage caused by browsing where this is warranted) and even the exploitation of deer populations in the northern hemisphere can therefore be of direct relevance to the future management of these two antelope populations, particularly as guides where base-line data are lacking, and the more pertinent of these will be referred to under the appropriate sections of management.

10.2.1 Conservation

I see no cause for concern regarding the sizes and trends of both bushbuck and duiker populations at Weza. All the available evidence gathered in this applied study indicate that winter food resources are limiting the bushbuck population, while additional research (see below) is required before it can be unequivocally demonstrated what the effects of timber management are on duiker, although the finding of this study suggest that duiker may be limited by the availability of suitable habitats. The concept of managing both these populations at or just below ecological carrying capacity are discussed below, but mention must first be given to those strategies that can assist in increasing the numbers of both species (if either are found to be decreasing, or for any other reason) in future years. These include the continued control against poaching, habitat modifications, the provision of supplementary food and, where possible, the reduction of man-made disturbances.

10.2.1.1 The control of poaching

Data obtained from marked animals killed by poachers indicate that illegal hunting using either dogs or snares may be more serious than is currently realized. Methods of control employed at present should be maintained; these include restricting access to only those people that work or live in the plantations and indigenous forests and to those who are utilizing these areas for legitimate recreational purposes, controlling feral and hunting dogs, and searching for and removing snares, particularly during and immediately after the Christmas period when there is a large influx of people returning to their traditional homes during this annual holiday season. If manpower and expenses permit, field staff should be encouraged to patrol random sections of the forest at night with a vehicle and spotlights; personal observations indicate that the chances of encountering dogs or apprehending poachers will be greater at such times, while the mere knowledge that the plantations are randomly

patrolled at night may act as a further deterrent. These activities could be incorporated into routine surveys to obtain indices of abundance etc.

10.2.1.2 Habitat modifications

In the North American conception of wildlife management, the amount of wildlife is primarily related to both the amount and quality of available habitat (Dasmann 1964 cited in Geist 1971b). It follows that, "to maintain or increase wildlife populations, it is necessary to conserve habitat, or create more and improve the existing one. That this is the essential first and major step in the management of all ungulates, is a conclusion with which it is impossible to quarrel" (Geist 1971b).

Unfortunately, although bushbuck and duiker both utilize some of the habitats available at Weza, their contrasting patterns of selection (Chapter Seven) indicate that both species will not necessarily benefit from improvements made to every habitat type. For example, bushbuck are likely to respond positively to increased areas of indigenous forests and riverine areas (both of which are protected areas) as well as thickets, but such habitats are of less importance to duiker (except possibly around the edges of these communities) and therefore their response will be less marked. Bushbuck require areas of dense cover, particularly during the day, and patches of bugweed, wattles and other shrubs and trees that form thickets should be left undisturbed wherever these are not competing with timber species. From the forester's outlook, such patches may appear "untidy" or should be utilized as sources of firewood (as occurred in I.S.A.1 after the completion of field work). However, offset against these "improvements" or financial benefits is the destruction of highly favoured and/or essential habitats for bushbuck, the loss of which will almost certainly cause disturbance and localised changes in distribution that may lead to additional pressures elsewhere. It is difficult to generalise on the long term effects of

habitat destruction in a forest environment because the reduction of dense vegetation and overstories inevitably leads to an increased availability of forage through the early stages of succession, but adequate food resources are not sufficient to ensure thriving populations of bushbuck (see Chapter Seven). Therefore decisions regarding the promotion or destruction of densely structured habitats should be made after an appraisal of what other suitable habitats are locally available (also see Harestad 1985).

It is not necessary to list all of the habitats that should be retained or improved at Weza; these should be evident from the results and discussion in Chapter Seven. Consideration here will be given to those practices that can enhance the value of certain habitats for bushbuck and/or duiker. Those specifically geared towards providing forage are considered under supplementary feeding (10.2.1.3) although it should perhaps be noted here that manipulating winter habitats by increasing "preferred" foods will not be justified when the "preferred" designation is an artefact of data analysis (see Chapter Six). In such instances, management practices will be more beneficially directed towards the physical structure of winter habitats (Nudds 1980).

I suggest that one of the reasons duiker and bushbuck are able to survive entirely within plantations is due to the diversity of cover and forage that is available within these habitats. This diversity is a result of even-aged management, where intensive activities such as planting, weeding, pruning, thinning and felling are limited both temporally and spatially. Such diversity could therefore be increased by a reduction in the size of some of the larger compartments, which would create an even greater mosaic of heterogeneous habitats. Reducing the size of the larger compartments would also ameliorate the detrimental effects of such activities. If compartment size reduction is not possible, then mitigation procedures (Patton et al. 1985) may be beneficial, particularly for duiker by virtue of their smaller ranges (Chapter Eight). Such procedures could

include partial stand, group-selection or alternate-strip cleaning, thinning and felling (Wallmo 1969; Wallmo et al. 1972; Decker et al. 1983), which if staggered over relatively short periods of time, would not alter the objectives of even-aged management. All of these activities would also increase the amount of habitat edge. The influence of edge could not be assessed in this study, but it is generally considered that ecotones are favoured habitats that promote species diversity (Decker et al. 1983; see Chapter Six) although it cannot be broadly assumed that forest edge is always of value to ungulates (Clarke and Gilbert 1982; Hanley 1983; Kirchhoff et al. 1983; Melchior et al. 1985).

Results from this study have demonstrated that advancing forest succession frequently results in declining habitat quality, and similar findings have been recorded in numerous other studies (e.g. Irwin and Peek 1983; see Chapter Seven). Intensive timber management tends to promote this advancement. Young compartments are selected for the forage that is available, and 3-8 year pines provide cover. Compartments of 9-13 year pines tend to be avoided, presumably because of the intensive pruning and thinning regimes that are implemented at this stage, while greater use is made of 14-18 year pines that are left relatively undisturbed. Canopy closure in 19-30 year pines usually results in little understory growth and hence limited forage and cover. Several other studies have demonstrated the value of thinning in stimulating understory and ground cover growth (e.g. Conroy et al. 1982; see Chapters Six and Seven), and Shaw (1970) suggests that 90% of habitat manipulations required by forest wildlife can be achieved by properly planned cutting operations. However, the current practice of cleaning all compartments to be pruned and thinned tend to offset the immediate benefits of tree density reductions. Consideration should therefore be given to the judiciousness of cleaning prior to every other management activity, particularly where alternative sources of cover and/or forage may be locally scarce.

Clearfelled areas are the most important timber habitats for bushbuck and duiker, and the value of clearfelled areas to deer in temperate forests has also been recognised (Hooven 1962; Wallmo et al. 1972; Regelin et al. 1974; Davis 1977; Lyon and Jensen 1980; McNicol and Gilbert 1980; Irwin and Peek 1983; Monthey 1984; Sweeney et al. 1984). Several of the above authors have discussed the effective or maximum size of clearfelled areas that will be fully utilized, although deer use of forest openings is not only influenced by their size but also their distance from the forest edge and the forage and cover conditions within the openings (Short et al. 1977; Lyon and Jensen 1980; Kirchhoff et al. 1983; Melchior et al. 1985). Thus the configuration of clearfelled areas may also be important; if such openings are long and narrow they will provide readily accessible cover to foraging animals and will offer more forest edge (Halls 1973a; Witmer and deCalesta 1983; Loft and Menke 1984), but it has also been argued that increased damage to commercially important species may result from this configuration (Harper 1969 cited in Witmer and deCalesta 1983). Alternatively, large uniform clearfelled areas may result in a severe lack of food and cover immediately after felling, and although the area might produce an abundance of food in the next few years, much of this might not be utilized (Halls 1973a; McNicol and Gilbert 1980) or be available because of widespread cleaning activities.

The timber management activities practiced at Weza are obviously geared towards maximum production. But if there is an intention to increase bushbuck and duiker numbers in future years, this may well be achieved by altering compartment size and shape, considering the alternative and locally available areas of food and cover before indiscriminately altering compartment composition and structure, and reducing the sizes of areas affected by such management by temporally staggering these activities. Any of these integrated approaches may have the desired effect without resorting to more expensive forms of habitat improvement.

10.2.1.3 Supplementary feeding

The widely divergent differences in the diets consumed by bushbuck and duiker (Chapter Six) infer that there is little interspecific competition at Weza. Although both species are considered to be concentrate selectors (Hoffman 1973), duiker at Weza predominantly consumed generative plant parts while bushbuck selected large quantities of browse. Bushbuck may therefore have obtained their nutritional requirements by consuming less nutritious foods but relying on a fast turnover resulting from rapid excretion rather than rapid digestion, as has been proposed for mule deer by Hobbs et al. (1983). Whatever dietary strategies are employed by these antelope, these findings need not infer that localised habitat improvements specifically directed at increasing forage quantity and/or quality will benefit only bushbuck or duiker. Both antelope utilized cultivated areas, oaks, Mexican hawthorns and clearfelled sites, and although the majority of bushbuck rumen contents were unidentified and presumably of indigenous plant origin, many of the identified plants were consumed more frequently and in greater quantities by duiker.

Supplementary feeding may be implemented in a number of ways, the most common being the provision of pelleted rations or the distribution of forage that has been grown, harvested and transported from other areas. However, supplementary feeding is used here in its widest sense and also includes plantings, the promotion of mast and any other method that increases the quantity and/or quality of other living forage (natural or exotic) during the critically important periods of the year, which for bushbuck are winter and early spring. Providing living forage obviates the problems of animals adapting to novel sources of food or in making errors in the timing of introducing such resources (see Anderson et al. 1975; Ullrey et al. 1975; Hubert et al. 1980; Barrett 1982). Furthermore, living plants are less likely to (a) evoke the same digestive disorders caused by feeding low quality forage or (b) cause ruminal acidosis and even death resulting from the provision of high-energy concentrates

(Wobeser and Runge 1975; Woolfe 1977 cited in Baker and Hobbs 1985). Several other problems associated with winter feeding have been addressed by Giles (1978), Thorne et al. (1979) and Lyon and Ward (1982), all cited in Reese and Kadlec (1984) and include the further destruction of available habitat by promoting overcrowding at areas where food is provided (Anderson et al. 1975; Mitchell et al. 1977; Mautz 1978; Barrett 1982) and the fact that certain dominant individuals may monopolize the provisions, thus making them available to only a small segment of the population (Mitchell et al. 1977). Another reason why supplementary feeding may fail is because deer commonly decrease their food consumption during winter even when high quality feed is available (Ozoga and Verme 1970; see Chapter Four). However, Ullrey et al. (1975) reported that white-tailed deer fed a protein-energy supplement block increased their dry matter intake of traditional browse. Again, the timing of providing supplementary food may be crucial; de Calesta et al. (1975) suggest that once deer have lost approximately 30% of pre-starvation mass, some animals are in such a depressed physiological state that they cannot be saved by refeeding, and postulated that supplementary feeding could save a portion of the population which was not already close to death (de Calesta et al. 1977).

These problems and observations have led to the widespread belief that wild deer in particular cannot be fed supplementally, or that the provision of supplements has little effect on the production and mortality of wild populations (see Barrett 1982; Baker and Hobbs 1985). Other criticisms leveled at this procedure include a reduction in the "wildness" of animals (Wolfe 1978), and by preventing the culling effects of winter on weak animals, feeding may harm the genetic quality of the fed population. However, as Baker and Hobbs (1985) point out, no matter how strong and articulated such arguments are, few have data supporting them. Perhaps the major argument against winter feeding is the artificiality which it creates, but the magnitude and implications of this are debatable (Mautz 1978), particularly where populations exist in totally artificial environments

anyway. The controversy continues however (see Hubert et al. 1980; Ozoga and Verme 1982; Baker and Hobbs 1985) and although most biologists do not consider supplementary feeding as a logical substitute for habitat restoration or a panacea for unpopular herd management measures, there are occasions when provision of feed may be justified (Wolfe 1978); when properly administered it can serve as a valuable tool in the current state of the art (Mautz 1978) provided that its limited range of efficacy is appreciated (Baker and Hobbs 1985).

As pointed out by Ozoga and Verme (1982), feeding programmes must be conducted in an ecologically sound manner if they are to be reasonably successful and economical. Thus the objectives (as with any wildlife management aim) must be clearly defined. Supplementary feeding (in its widest sense) may be used for any of a number of purposes. The provision of localised food resources may facilitate capture operations (Sauer and Boyce 1983), and censusing or hunting effort (Halls and Stransky 1968). Supplementary feed may also be offered to promote production, physiological condition (especially mass), antler quality and survival (Magruder et al. 1957 cited in Halls and Stransky 1968; Jenkins and Reusz 1969; Hungerford 1970; Short 1972; Robinette et al. 1973; Mitchell et al. 1977; Ozoga and Verme 1982). Alternative foods may also be provided to alleviate damage by attracting ungulates to other areas (Jenkins and Reusz 1969, see below) and to improve relations between landowners, game managers and sportsmen (Halls and Stransky 1968). In addition to these density-dependent and public relations factors, supplementary feeding may frequently be used to try and prevent catastrophic die-offs during severe winters (Wolfe 1978; Ozoga and Verme 1982; Baker and Hobbs 1985). If such actions are successful in increasing winter survival, increased production may occur during the following year, and thus there will be more animals to feed during the next winter. Proper management would dictate harvest of this surplus, otherwise the ungulate-plant equilibrium would become more extreme and the damage to future natural browse supplies would be even more serious (Anderson et al. 1975;

Mautz 1978; Ozoga and Verme 1982; Ozoga et al. 1982a). These problems 'are likely to be greatly aggravated if, for economic or sociological reasons, supplementary feeding is terminated (Fanter 1977 cited in Ozoga and Verme 1982; Mitchell et al. 1977). Supplemental feeding of deer to provide hunting stock has been done in Europe and the United States (Jenkins and Reusz 1977; Woolf and Harder 1979) and as ever-increasing demands are placed on wildlife resources for hunting and other uses, winter feeding possibly holds the key to increasing or maintaining some populations and providing a huntable surplus in the face of increased destruction of natural habitats (Mautz 1978; Wolfe 1978).

Clearly, determining whether such costs are commensurate with the benefits requires 'careful analyses rather than empirical or emotional decisions, as have been frequently made in the past (and are probably responsible for much of the ensuing controversy, see Halls and Stransky 1968). The most recent costs of supplementing feed for deer have been analysed by Ozoga and Verme (1982) and Baker and Hobbs (1985); such costs will obviously depend on the kind of supplement provided, transport and manpower costs, etc. Ozoga and Verme (1982) spent \$37.00 on each deer fed between 37% and 61% of their total diet (depending on herd composition and density) for 127 days during winter. Baker and Hobbs (1985) spent \$34.80 feeding each deer 0,9kg of supplement each day for 100 days and estimated that 995 deer were saved by feeding 5 000 animals. Thus it cost \$174.87 to save each deer fed at this rate and consequently deer needed to have a value exceeding this amount for the exercise to be economical.

The above discussion serves to demonstrate that the success of supplementary feeding depends on the initial objectives of such an exercise; if feeding programmes are to be initiated, they should be planned and executed with purposeful, not incidental, benefits in mind. Such benefits are considered to be low at Weza. The type of hunting and quality of harvested animals envisaged in this area (see below) does not warrant the expense and effort of providing

food. Unlike antler growth in cervids, which may be enhanced by nutritional factors (Bobek 1977b; Ozoga and Verme 1982), there is no evidence to suggest that horn growth (and hence trophy size) is influenced by environmental conditions; antelope horn growth is apparently influenced by genotypic factors although the ultimate size of horns may be affected by such factors as wear (Spinage 1969d). Supplementary feeding could, in theory at least, reduce annual variations in bushbuck and duiker numbers by mitigating the effects of occasionally severe winters. But since bushbuck are overabundant for the food resources that are available in winter, methods should be directed at reducing the population rather than in providing more food and stimulating survival and production (with the result that numbers are even greater the following year). In contrast, duiker may benefit from additional food resources that might prevent abandonment of territories that have been drastically modified by timber management, but such food resources would only be beneficial if other habitat requirements such as cover are available.

There are however two aspects of supplementary feeding that warrant further consideration. Results from this study have demonstrated that localised food resources may be particularly valuable in facilitating censuses and capture operations, and such areas should be maintained and increased if future populations are to be monitored. Secondly, additional feed may attract animals away from areas potentially vulnerable to damage from browsing. Providing food for these two purposes need not involve the planting of annual crops, as is conscientiously done on surrounding farms (where the populations are utilized); in any event such an approach is not acceptable to Forestry staff (P.J. le Roux pers. comm.). Sources of attraction could include open grassland areas that are simply ploughed during autumn to ensure that winter forage is available in the form of early stages of seral vegetation (e.g. palatable pioneer species and herbaceous weeds, see Appendix C). Long narrow plots would ensure adjacent cover (see above) and could act as fire breaks during the winter, while the costs of establishing such belts would be minimal.

Alternatively, dicotyledenous species could be planted to provide food during the winter months (Halls and Stransky 1968; Yoakum and Dasmann 1969; Halls 1973a). Lists have been made of the plants that can improve wildlife habitats in North America (e.g. Dawson and Decker 1978; Decker et al. 1983) and although forest habitat procedures are much less advanced in South Africa, the diets of both bushbuck and duiker in timbered areas show many similarities with those of temperate cervids (Chapter Six), and thus such lists may be useful guides. Forestry should propagate the same indigenous trees that are currently available as seedlings for public purchase in their nurseries, but because many of these require shade and are slow-growing, more immediate success may be achieved by planting other trees, particularly those that provide mast which is an important autumn and winter food to many species of wildlife (Chapter Six). Efforts to increase food supplies can be most effective in open areas (Lay 1966; Halls and Alcaniz 1968) where forage dry matter per hectare can equal that produced in 100 ha of intensively managed pine plantation (Short 1972), although planting shrub and tree species in thinned areas can also mitigate the effects of forage and cover reduction resulting from thinning and cleaning (Ertz 1982). Palatable browse species intended to provide mast in future years should be protected while at a vulnerable age. Obvious choices in this latter category include oaks and Mexican hawthorns, both of which provide extremely valuable sources of highly nutritious food during autumn and winter, and which are heavily utilized by both bushbuck and duiker. By virtue of their territorial behaviour, duiker are more likely to benefit from small, isolated patches of available food resources rather than from one large stand, and wherever possible such resources should be well distributed throughout the area of interest. It should be noted that individual oak trees differ in their ability to produce acorns, and thus it is better to plant a surplus of trees and then thin out those that are less proficient or that dominate good mast producers (Decker et al. 1983). Acorn production may also be influenced by a number of environmental factors such as frost (Wolgast and

Trout 1979) while fertilization of certain age classes can significantly increase acorn yields (Wolgast and Stout 1977). Because annual yields from oaks may be highly variable, those species that are largely dependent on acorns as a winter food must change to other sources during years of mast failure (Segelquist and Green 1968; Harlow et al. 1975); this can have dire consequences in terms of damage to conifers (Dunkeson 1955) or severe mortality (Segelquist et al. 1969). Decker et al. (1983) have estimated that acorn yields of 112 kg/ha would be adequate to meet the food needs of all mast-using wildlife in the United States, which could be provided at a stocking density of 54-62 large oaks per hectare. Other independent studies have indicated acorn yields of 1,3 kg (fresh mass) per tree (Goodrum et al. 1975), or average yields of 142 kg/ha to 550 kg/ha, depending on species of oak, age and application of fertilizers (Segelquist and Green 1968; Segelquist et al. 1969; Quilkin and Musbach 1977; Wolgast and Stout 1977; and using the data from Burns and Viers 1973 where dry mass values were given). Even higher yields of 813 kg/ha have been recorded during good years (Segelquist et al. 1969).

These data are only of value if the requirements and intake of the foraging animal are known; no such information is available for bushbuck and duiker. However, as an approximate guide, Duvendeck (1962) calculated that deer ate 0,013 kg of acorns per kg of body mass daily. Adult bushbuck males, eating acorns at the same rate, would require 0,8 kg per day while 0,4 kg and 0,2 kg would be consumed by adult female bushbuck and duiker respectively. Adult male and adult female bushbuck would therefore each require 144 kg and 72 kg of acorns for a period of 180 days. At relatively high stocking rates of 12 animals per km² (Chapter Nine), and assuming an even adult sex ratio (see above), then the total amount of acorns needed to feed this density for 180 days would be 12,96 kg/ha which is well within the yields reported in northern temperate areas. Alternatively, Goodrum et al. (1975) calculated that the mass of acorns required to feed deer at a density of one animal per 20 acres (12,4 deer/km²) for 180 days assuming that each deer consumed 2,27

kg of forage each day and that acorns formed 50% of the diet, would be 204 kg or a yield of 25,2 kg/ha. If bushbuck dietary requirements were the same, it can be seen that just a few hectares of oaks could support and attract a considerable number of animals. Duiker requirements are likely to be considerably smaller, and this species would benefit from several isolated stands of just a few trees scattered wherever suitable habitats for this species exist.

Finally, supplementary feed need not only be important in providing resources rich in protein or energy, but may also provide nutrients such as phosphorus that may be limiting in forest habitats (Lay 1957; Halls and Stransky 1968; see Chapter Six). Licks could be provided in those instances where essential elements are lacking. However, since fungi are particularly nutritious and contain high levels of phosphorus (Halls 1973a; Blair et al. 1977; Jones and Weeks 1985), the wisdom of allowing mushrooms to be commercially harvested at Weza, without any detailed consideration as to the potential effects such exploitation may have on consumers, is highly debatable. This example and the destruction of prime bushbuck habitat due to the harvesting and sale of firewood demonstrate that management is presently geared towards economic returns rather than any consideration of wildlife and habitat conservation. In future, it is recommended that management techniques that attempt to maintain or increase the quality as well as the quantity of available habitats and forage (e.g. prescribed burning and fertilization) should be of special importance. Those management efforts that do not appreciably increase habitat quality have limited potential for measurably improving carrying capacity (Short 1972).

10.2.1.4 Disturbance

It is a cardinal principle in wildlife management that animals develop best in a "predictable environment" (Geist 1971a,b; Cowan 1974). Any influence that reduces predictability, i.e. any form of disturbance, is likely to

impair the performance of a population in terms of energetic efficiency. This may manifest itself in animals losing physiological condition, in loss of appetite, neurosis, susceptibility to predators, reduced rates of reproduction and/or recruitment, in higher mortality or in a combination of these factors (Geist 1971b, 1978).

Theoretically, any disturbance must have an undesirable effect in that it raises metabolism and thus the "energy cost of living" (Geist 1971b). However, the overall effect depends on the quality of the other features of the environment. Even minor disturbances may impose a significant energy cost if the animal is already under energy stress from other causes. Disturbance is inevitable in an intensively managed timber plantation, and all the available evidence obtained in this study indicates that bushbuck have habituated to such activities. Nevertheless, avoidance of areas being disturbed results in a reduction of available habitat, and conversely may increase the use of habitats not affected by disturbances (Edge and Marcum 1985). Avoidance of disturbed areas appears even more pronounced in duiker, although it was not possible to isolate the effects of actual disturbance from the modified habitats resulting from such activities. Any activity that is known to have a negative effect should be carried out in the shortest time possible (Geist 1971b) but as mentioned above, the long-lasting effects of disturbances such as thinning and felling may be minimised if such practices are staggered, so that some suitable habitat is always available.

Although not evident in this study, avoidance of roads (e.g. Schultz and Bailey 1978) may also result in a considerable reduction in the availability of habitats (Lyon 1979; Rost and Bailey 1979). Roads may however have an indirect impact on another form of disturbance, namely hunting, since road access may influence the distribution of hunters (Basile and Lonner 1979). Hunting can become a major source of disturbance, and it should be carried out in such a way that game find it impossible to associate it with specific stimuli such as cars, people etc. so as not to

interfere with the general process of habituation to such objects. The impact of hunting as a disturbance can be further reduced by restricting it in time. This could best be achieved by allowing organised beats in specific areas; the number of animals to be harvested could be taken over a much shorter period of time than if animals were individually stalked. However, the latter form of hunting appears to be more popular with non-landowners (see below). Nevertheless, careful consideration should be given to the type and duration of hunting as well as to the age and sex structure of the animals to be harvested; performance may be influenced by a reduction in the prime male (trophy) segment in the population while harvesting females may cause additional disturbances due to orphaning etc. (see Woodson et al. 1980; Ozoga and Verme 1984). These aspects are considered further in section 10.2.3, but it should be noted that the disturbance caused by hunting may alter the behaviour of the harvested population, and males and females may respond differently to these activities, resulting in divergent patterns of habitat selection or range use. Females frequently become more wary than males (e.g. Mitchell et al. 1977) and this trait was noticed among bushbuck during capture operations at Weza. Alternatively, males may react to disturbances by either enlarging their home ranges or abandoning them for varying periods of time (Hood and Inglis 1974). Although movements away from such disturbances as hunting may be of short duration, with animals maintaining fidelity to their home ranges (Progulske and Baskett 1958; Sweeney et al. 1971; Hood and Inglis 1974), subsequent behavioural changes such as flight distances and activity patterns may be substantial (Roseberry and Klimstra 1974; Sage et al. 1983) and may affect observability which in turn could significantly influence recreational viewing, censusing etc. (Behrend and Lubek 1968). These aspects have been highlighted by Batcheler's (1968) study (cited in Mitchell et al. 1977) where deer that were intensively hunted moved to a less preferred habitat and became more secretive and nocturnal in habits. Animal performance then declined, with animals in poorer condition and having lower reproductive rates. Barren hinds became evident in one population and the

females apparently became smaller after several years. Geist (1971b) predicted that in addition to an increase in the average age of sexual maturity, antler growth in males would be retarded, the average birth mass of fawns would decline and maternal behaviour may have degenerated. In this instance a reduction in the controlled population was desired, but it is worthwhile noting how disturbance may affect the non-harvested members of a hunted population. Similar changes in behaviour, including increased wariness and alterations in activity patterns during hunting have been noted by numerous other authors cited in Mitchell et al. (1977) and interestingly, both bushbuck and duiker have reacted to continuous hunting in a similar manner (Wilson and Roth 1967; Morris 1973). This is one of the very reasons that game eradication schemes designed to combat trypanosomiasis have never been completely successful (Leuthold 1977).

10.2.2 Control

The control of populations can be divided into two distinct categories (Caughley 1976). The first involves a set of problems relating to displaced equilibria, the treatment being aimed at moving the vegetation-herbivore system back to equilibrium with a minimum of trauma. However, at any given time the biomass of ungulates and the biomass of their food supply are unlikely to be at equilibrium with each other, and unless the imbalance is more than 30% away from equilibrium, it is better to let natural events find this equilibrium; attempts to help them on their way may create problems that did not exist before intervention (Caughley 1976). Thus winter mortality is one such event, while intensive timber management serve as another means of controlling antelope numbers, even though this is not its intended function.

The second category involves problems of unwanted equilibria where the task of control is to impose an alternative equilibrium appropriate to management's

requirements (Caughley 1976). It is to this second category that the following discussion is addressed. When the carrying capacity equilibrium level of ungulates is unacceptably high for what is considered the optimum level, the system can be shifted to a more convenient equilibrium by killing a quota of animals each year. Control by hunting is simply an exercise in sustained yield harvesting, whether or not the yield is utilized, and the techniques and analyses appropriate to its planning are the same as those used in a harvesting programme: direct control and harvesting are operationally identical (Caughley 1976).

Direct action on the herbivore is not the only form of control - this may also be achieved by protection or modification of the habitat or resource with which the herbivore has become imbalanced with (Garthwaite 1967). This latter approach may be more successful, but also more expensive to implement, and may not provide the required results as rapidly as a direct reduction of herbivore numbers. As Caughley (1977) points out, attempts to control or exterminate populations directly have often failed (for the reasons given above, see 10.1.2.4), while exterminations have usually been accidental events resulting from adverse habitat changes. Populations are therefore frequently more vulnerable to a manipulation of their habitat than they are to a direct manipulation of their numbers.

Under the current conditions and trends at Weza, the only justification for controlling bushbuck and/or duiker numbers would be to reduce the amount of damage caused by these antelope browsing on commercially important timber seedlings. The results of this study have not only shown that pines are non-preferred species of forage, but that Forestry's concern regarding the level of damage caused by antelope at Weza (a primary factor prompting this study) were unfounded. Possible reasons why reports of damage were overstated have been listed in Chapter Six, and added to this could be observations confined to the periphery of compartments; such an edge effect has been noted in this study and in other surveys of damage (e.g. Stickley et al.

1979). Damage resulting in a loss of revenue is obviously an emotive issue, but could have been more thoroughly assessed and evaluated by Forestry personnel without resorting to the services of an outside agency, as happened in this project.

Damage from browsing was more frequent, but not necessarily more severe, in certain compartments. If such levels of damage either increase or become intolerable in future years, then decisions may be made to initiate control measures. There are numerous methods that could be effective in controlling such damage, but whether any of these would be cost-effective should be considered carefully before they are applied. Mechanical barriers could be used to either protect entire compartments or individual seedlings. The costs of erecting conventional fencing would be prohibitive, particularly since protection would only be necessary for the first year after planting (Chapter Six). Electric fencing provides a more temporary barrier and has been used to protect young poplar trees with some success at Weza. However, costs are also high with this form of fencing and observations at Weza and elsewhere (Tierson 1969) indicate that the efficiency of such a barrier may be questioned. Protection for individual seedlings may be afforded by tubes of plastic netting as described by Campbell (1969), Anthony et al. (1978) and Larson et al. (1979); Campbell and Evans (1975b) estimated the total material-labour costs to be from \$13.00 to \$15.50 for the protection of 100 seedlings. However at today's prices and the level of damage at Weza, it is highly improbable that the costs of such protection would be commensurate with the benefits. Developing and testing the efficiency of repellents continues to be researched (e.g. Campbell and Bullard 1972; Campbell and Evans 1977; Caslick and Decker 1980; Harris et al. 1983) but studies in South Africa have demonstrated that the effects of antelope repellents used to date were inconsistent, adversely affected seedling growth or did not justify the costs (Wright and Bourquin 1977; Schutz et al. 1978; Novellie and Bigalke 1981). Instead of repelling antelope, damage may be alleviated by attracting animals to alternative, more preferred forage (Dasmann et al. 1967; Halls and Stransky

1968; Campbell 1974). If native vegetation is established, then not only can damage be reduced, but such measures also lead to wildlife habitat enhancement and thus integrate timber and wildlife objectives (Campbell and Evans 1975a, 1978). In direct contrast to this approach, damage may be lowered by reducing the cover and food resources of habitats where damage is likely to occur (Borrecco 1976 cited in Evans 1976). Finally, the most practical means of preventing damage to seedlings is to reduce herbivore numbers, either by cropping or hunting, or by live removals through capture and translocation (Carpenter 1967).

Probably the most effective control measures at Weza, if and where justified, are habitat modifications and population reductions. For either of these approaches to be worthwhile, they should be initiated before damage becomes severe; the areas where and periods when damage is most likely to occur have been identified (see Chapter Six). All the available evidence gathered in this study indicates that pine damage is inversely related to alternative food resources, and that pine consumption (apart from incidental ingestion when animals are foraging on other plants) is indicative of an inadequate diet. Providing alternative, more preferred forage therefore has great potential in reducing this damage. The time required to establish more preferred browse would be too great to offset browsing on seedlings during their first year after planting, but forbs could readily be established within or adjacent to young pine compartments by ploughing (and possibly fertilizing) areas during late summer and autumn. Since duiker are considered to be the major culprits, such alternative forage is unlikely to attract a large number of animals, because of territorial behaviour, and thus increased pressure on the compartment as a result of such attraction sites is unlikely to occur. Areas most susceptible to damage are those that are afforested rather than reforested, so that cultivating land is likely to pose fewer problems. In reforested areas compartments are frequently cleaned of all natural and exotic vegetation during autumn or winter in order to reduce competition and promote seedling growth at the onset of the spring rains.

Such effects are of short duration however; many weeds have more rapid growth rates than pine seedlings and are frequently the dominant vegetation in late spring and early summer, when cleaning is again deemed necessary. Since damage in uncleaned compartments is substantially less than in those where the early seral communities have been removed, the possible benefits of promoting early growth at the expense of increased browsing should be carefully assessed. Cleaning operations in clearfelled compartment during the winter, when food is most limiting, is a form of habitat destruction which is ineffective in controlling damage, and cannot be supported. Indeed, many timber management activities result in cover and forage destruction (albeit inadvertently), which are likely to induce additional pressures on both favoured and marginal habitats (including compartments planted with seedlings), and so greater consideration should be given to the duration, extent and location of these at critical times of the year. In addition, and wherever possible, those pines that are the most resistant or least palatable to bushbuck and duiker should be planted in areas likely to receive the greatest pressures. Patula pines should therefore be planted in recently established compartments, or where winter cleaning is likely to continue. Where slash pine planting is obligatory on silvicultural grounds in such areas, additional precautions should be taken, as recommended by Garthwaite (1967) for lodgepole pines (*Pinus contorta*) that are particularly vulnerable to deer damage in Britain (Yanchinski 1982).

The capture and removal of live animals to reduce damage will seldom, if ever, be warranted at Weza. Apart from the enormous costs involved, bushbuck would have to be translocated over considerable distances to ensure that animals did not return to their original ranges (see Chapter Eight), while introducing duiker into new areas that are already occupied by others may be tantamount to, but less humane, than culling. Any decision to reduce antelope densities should therefore involve cropping or hunting. Since areas potentially susceptible to browsing damage can be

predicted, reductions should occur before the onset of winter, when damage and intraspecific competition for localised resources are most pronounced. If animals are to be hunted, this would necessitate special permits (also see Evans 1976) to hunt outside the regular and legal hunting season (31st May to 31st August). Cropping would be most effective at night, using spotlights, when animals are most active, while home range and territory sizes (Chapter Eight) provide some guide as to the areas (beyond the compartment to be protected) that should be patrolled. Hunting such areas during the day by stalking would undoubtedly be highly ineffective, but organised beats using trained hounds and experienced hunters could provide an efficient means of control. Local hunt clubs, with established members conversant with such important factors as fire risks, safety and control of the hounds, would be willing to provide this facility where reductions were warranted (B. Lund, pers. comm.). Both parties would benefit from such an arrangement: Forestry would have antelope numbers reduced quickly, humanely and with a minimum of disturbance, while recreational sport hunting would be provided to the hunt club. Provided that all carcasses remained the property of Forestry (to be disposed of in any way senior administrators see fit), no charge should be levied against the hunters assisting in the control of antelope numbers. All the available evidence suggests that most damage is caused by duiker, and efforts should therefore be concentrated on this species. This type of control is considered to have a negligible effect on subsequent numbers. Relatively few animals would be harvested in such areas, while any dispersion that might occur as a result of disturbance might simply be promoting movements that would otherwise occur as a result of plant succession and management activities; 3-13 year pines compartments are generally avoided by duiker (see Chapter Seven).

10.2.3 Sustained Yield Harvesting

Many people regard harvesting as a practice carried out by professionals for profit (e.g. whaling, commercial

fishing) but as Caughley (1977) points out , most harvesting effort is expended by sportsmen. According to statistics published by the U.S. Department of the Interior (cited in Shaw 1970) there were more than 13,5 million hunters in the United States alone during 1966, and there is every indication that this form of recreation is increasing in popularity.

The same management principles apply whether a population is managed for commercial harvesting or for recreational hunting; management is aimed at providing a sustained yield - a crop that can be taken year after year without forcing the population into decline. There can be one of any number of sustained values depending on management objectives and treatments. Efficient management aims at developing the treatment to provide the largest possible sustained yield (the maximum sustained yield) or more commonly, to provide an optimum sustained yield that maximises revenue or recreational values (Caughley 1977).

There are several methods that can be used to estimate sustained yield values and these have been comprehensively reviewed by Caughley (1976,1977). Theoretically, the rate of harvesting that holds the population rate of increase at zero is that rate at which a population would increase if it were not harvested. Hence a population increasing at a finite rate of 0,20 and therefore at an exponential rate of 0,182 can be harvested at an instantaneous rate of 0,182. An isolated rate of harvesting is used to calculate sustained yield values when hunting is confined to certain months of the year (see Caughley 1976). However most populations, although experiencing annual fluctuations, have a rate of increase which averaged over several years is close to zero. Thus if rate of harvesting depended solely on the population's rate of increase , as in the above example, a population with an average rate of increase of zero has an appropriate instantaneous harvesting rate of zero and therefore a sustained yield also of zero. Consequently, a population that is stable in the absence of harvesting can only be harvested after the vegetation-herbivore system has

been manipulated to raise the rate of increase above zero. In theory there are two means of achieving this: by treating the vegetation to raise its density or production, or much more commonly, by reducing the density of the animals. Both have the effect of raising the amount of available food per animal which in turn improves production and survival to generate a positive rate of increase. When this positive rate of increase is generated by reduced density, the population is then harvested at this rate to stabilize numbers at the lowered density.

It therefore follows that, within limits, the farther a population is reduced below its unharvested density then the higher will be its increased rate of increase and thus the higher will be the rate of harvesting needed to hold numbers at the reduced density (Caughley 1977). Using this approach, the sustained yield must be calculated from the size to which the population is initially reduced, not from the steady size at ecological carrying capacity. Questions such as "what percentage of the population can be harvested each year?" are meaningless and should be rephrased as "if the population is reduced by $x\%$, what fraction of the reduced population must be harvested each year to hold it stable at that size?" Such questions presuppose that the original and reduced sizes of the population are known (see below).

These theoretical aspects of sustained yield harvesting have rarely been utilized in the practical management of wildlife. Instead, harvesting is based on the assumption that at least after the first year of life, hunting mortality and natural mortality are exactly compensatory, i.e. harvesting one individual reduces natural mortality by one. It is then deduced that (a) maximum sustained yield of animals older than one year of age is obtained by harvesting at a rate identical to the percentage of yearlings in the post-calf population, (b) harvesting of a population at ecological carrying capacity density at a rate less than this will not lower density and/or (c) the sustained yield can therefore be calculated as the appropriate rate of harvesting multiplied by the size of the post-calf population at

ecological carrying capacity. Thus harvesting the entire population at the rate represented by the proportion of calves or yearlings in the post-calf population may be recommended (e.g. Mitchell et al. 1977). However as Caughley (1976) points out, the characteristics of this assumption have never been recorded for any population. For example, the rate of natural mortality at densities below carrying capacity is certainly less than that at steady density, but it is not negligible (Caughley 1976).

Sinclair and Grimsdell (1982) describe an alternative approach where, if the growth form of a population is logistic, it is possible to estimate the sustained yield that a population of a particular size can withstand. Necessary for this calculation is a knowledge of three parameters; the maximum rate of increase of the population under stated conditions and at very low density, the size of the population at which the sustained yield is to be taken and the size of the population at ecological carrying capacity. Although both bushbuck and duiker were breeding at their full reproductive potential, and may thus give an indication of the maximum or intrinsic rate of increase, measurements of population size were extremely difficult to obtain with any degree of precision (see Chapter Nine). Furthermore there are several means of assessing ecological carrying capacity, the most recent of which favour a nutritional approach (e.g. Bobek 1977a; Wallmo et al. 1977; Mautz 1978; Hobbs et al. 1982) which was beyond the scope of this study. Problems of estimating carrying capacity have been experienced in many studies (e.g. Nicholson 1974) especially where estimates are based on animal densities without also considering the density and composition of the vegetation (Caughley 1979b). Estimates are further compounded where climatic parameters and plant production vary annually (Wallmo et al. 1977; Hobbs et al. 1982) and in such instances managers must occasionally accept high levels of mortality even on the best managed ranges (Crowe and Strickland 1984 cited in Baker and Hobbs 1985) unless populations are maintained well below maximum carrying capacity (Hobbs et al. 1982). Carrying capacities may fluctuate even further where forage and

habitat quality is also directly influenced by management practices, not just by the interaction of herbivores and plants. Under such conditions, which are prevalent at Weza, the dynamics of both bushbuck and duiker populations are artificial and may contribute much less to the interactive models of the plant-herbivore interface than in the more natural systems described by Caughley (1976, 1979b, 1981). Thus, in conclusion, carrying capacity should be regarded as a labile rather than a static characteristic of the habitat (Hobbs et al. 1982) and recognition of this fact is particularly relevant when considering the management of such areas as Weza.

The above discussion serves to demonstrate that reliable estimates of maximum sustained yield values are extremely difficult, if not totally impractical to obtain at Weza. This need not imply that hunting could not or, or should not, occur at Weza. Despite all the theory surrounding game harvesting, the actual approach is very much more pragmatic. Most ungulate populations hunted by sportsmen are harvested without the administering agency having more than the slightest notion of population size or current harvesting rate (Caughley 1976). The yield is usually known however, and is frequently regulated by the issue of hunting licences or permits. If hunting pressure remains fairly constant, the exploited population and its food supply will move to an equilibrium with the unknown rate of harvesting, while the proportion of the maximum sustained yield represented by the harvested animals will remain unknown. Most hunted populations in North America and Africa are managed in this way (Caughley 1976).

The fact that estimates of ecological carrying capacity and absolute numbers could not be determined with any degree of precision in this study therefore does not necessarily diminish the feasibility or practicability of implementing hunting at Weza. However, the decision whether to allow hunting in such an area rests not with wildlife biologists but with senior administrators who would obviously prefer to have finite numbers at their disposal. And if hunting is to

be permitted then decisions must be made regarding a wide variety of issues, one of the most important being the annual harvest. This can best be made by regarding the function of hunting as hunting and not disguising or confusing that function with ecological principles (Caughley 1979b, Caro 1984). Thus consideration of the area to be hunted and the planned number of hunters to be catered for can facilitate decisions on the level of harvesting.

It is recommended that not more than 20% of the total plantation area at Weza is hunted (2 200ha), and that initially, approximately 20% of the population in this hunting area can be utilized. From the densities detailed in Chapter Nine, this hunting area would have approximately 130 bushbuck and 106 duiker of which 26 and 21 respectively could be harvested if a hunting allocation of 20% was implemented. Results from other studies indicate that this level of utilization is unlikely to have any adverse effect on population sizes at Weza. A total of 422 duiker were shot during tsetse fly control operations in an area of 518 km² over a period of two years, and apparently this population in eastern Zambia was not significantly reduced (Wilson and Roth 1967). These authors concluded that shooting appeared to remove the annual increment, which they estimated to be in the order of 0,4-0,8 duiker per km². Similarly, Mentis (1970) reported that common duiker and bushbuck were little affected by 7,5 years of tsetse fly control shooting in Umfolozi Game Reserve and the surrounding area. In an area of nearly 1 200 km², 20 461 duiker were shot at an average rate of 2 728 animals per year or 2,3 duiker per km² per annum. The bushbuck kill was 22 232 at an average rate of 2 964 per annum or 2,5 per km² each year. At the end of the campaign both species were reported to be "very numerous". Du Toit (1954), cited in Mentis (1970) assessed the degree of eradication achieved: "game observers reported large numbers of the smaller species of antelopes and evidence of the presence of a considerable numbers of the nocturnal bushpig, when to the casual observer, all game appeared to have been eliminated. In fact a balance appeared to have been struck whereby natural increase in the thicket-inhabiting species

balanced the rate at which they were being destroyed". More locally, Harding Hunt Club has maintained records of the localities and numbers of all the bushbuck and duiker shot during the last 13 years. A total of 538 male bushbuck and 388 duiker (both sexes) have been harvested during 267 hunts. Normally only one farm, or specific section of that farm is hunted each year, and the mean number of bushbuck shot per hunt per year has ranged from 1,45 in 1981 to 2,75 animals in 1977. The mean number of duiker shot per hunt varied from 0,88 in 1984 to 2,75 animals in 1977. An average of 41,4 bushbuck ($\pm 2,0$ S.E.) and 29,9 duiker ($\pm 2,3$ S.E.) have been harvested per annum over this 13 year period at Harding (N.Lund, pers. comm.). Finally, a total of 132 bushbuck and 117 duiker have been culled at Weza from September 1980 to August 1984, at an annual rate of 33 bushbuck and 29 duiker, without any obvious, adverse effects on either population.

Provisional recommendations that hunters be allowed to harvest 20 bushbuck and 20 duiker on an experimental basis were accepted by the Directorate of Forestry in 1985, but unfortunately the delay in adopting these proposals led to hunting outside of the recommended period, when five animals were harvested by a total of eight fee-paying hunters. This exercise was aimed primarily at examining (a) the feasibility of hunting in plantations and (b) the potential conflict between hunters' requirements and timber management objectives that had emerged during earlier discussions. Insofar that Forestry personnel were inexperienced in the implementation, control and supervision of any form of hunting, the exercise was undoubtedly successful. Earlier recommendations that had been made by a sub-committee to the Weza Bushbuck and Duiker Project Steering Committee (1983, unpublished report) were also implemented in part during this experimental hunting exercise. Aspects of this report, to which I contributed, included an examination of possible hunting methods, allocation and supervision of the hunts, hunting regulations, accommodation and fees. Many of these issues attempted to integrate the practicality of hunting with standard plantation management practices, and need not be considered in detail here. However several important

aspects emerged from these discussions. It was decided to restrict hunts to those members of recognised hunting associations that held an accepted proficiency test, and that hunting parties should consist of a maximum of two hunters. Hunting would be permitted only at weekends so that timber management operations would not be prejudiced, and hunting would be allowed for a maximum of three months of the year (see below). Animals were to be hunted on foot (stalking) or from hides, but the sub-committee would not accept the hunting of bushbuck and duiker by drives (using hounds) on the grounds that this is not an ethical hunting method; a view that I do not share. Hunting fees were also considered and hunters were charged a fee of R200.00 each per weekend, which included the costs of accommodation (R50.00) and the non-refundable fee (R150.00) for shooting a male bushbuck. Additional fees for shooting a female bushbuck and a duiker (either sex) were R100.00 and R50.00 respectively. Although the allocation of hunting prices is beyond my jurisdiction, I strongly recommend that fees paid in advance do not include the price of an animal that has yet to be shot - this is likely to encourage hunters to shoot at animals because they have paid for them rather than because they can be sure of a killing and humane shot. Hunters should therefore initially pay only for their accommodation and for the services of a guide (forest guard) and other supervisory staff; any animal they shoot at Weza should only be paid for once it has been despatched or wounded. An earlier recommendation that has yet to be adopted concerns the detection of wounded animals with the minimum of delay. At least one hound should be trained and housed at Weza throughout the hunting season if hunting is to become a regular event; the services of such a trained animal would be invaluable in following and finding any antelope that is wounded and cannot be despatched after more conventional tracking methods. Other recommendations pertinent to the future utilization and management of both antelope populations are detailed below.

10.2.3.1 Harvest levels

The proposed yield of 20 bushbuck and 20 duiker per annum is considered to be an extremely conservative level of harvest, representing less than 4% of the estimated sizes of both populations. However, because hunting on State land is likely to be a contentious issue with certain sectors of the public, it is considered expedient that harvest levels are well below rather than greater than the (unknown) maximum sustained yield. If hunting is confined to 20% of the total plantation area, and decisions regarding the timing of hunting and the numbers of hunters permitted at Weza do not alter, then it is unlikely that this level of harvesting will need to be revised. A maximum of two hunters per weekend over a period of 12 weeks could harvest 24 bushbuck and 24 duiker if bag limits of one of each species are imposed on each hunter. Assuming a hunter success rate of 62,5% (achieved in 1985), then 15 bushbuck would be harvested each season; this success rate is likely to decline if the same area is hunted regularly and animals become increasingly aware of hunting activities and react to the disturbance (see above). No duiker were harvested in 1985 (the R1 600.00 Forestry received from the eight hunters was for accommodation and a prepaid fee for eight male bushbuck) and consequently actual yields in future years may be substantially less than the limit of 20 animals. If however demand for hunting increases, Forestry may either allocate additional areas and increase the number of animals to be hunted accordingly, or intensify hunting within the proposed area. Both strategies have merits and disadvantages, but the latter approach would facilitate monitoring the impact of hunting (see below).

10.2.3.2 Proposed localities for hunting

If the recommendation that 20% of Weza be set aside for hunting is accepted, the siting of this area needs careful consideration. Following discussions with the Control Forester at Weza (J.T. Nel, pers. comm.), four blocks were

selected with a total plantation area of 2 066ha. These blocks (E, F, H and J) form one continuous area, thus facilitating monitoring, and are situated in the western section where the Ingeli range forms a natural and distinct boundary. Private farms to the west of this region are not timbered and it is highly improbable that any wounded animal would leave the vicinity, thus obviating the need to request the landowner's permission to enter his farm and track over unfamiliar areas. Because of the quality of the habitat (which is largely grassland), farmers to the west of Weza do not hunt bushbuck and duiker on their land, which again makes these bordering areas suitable. Elsewhere to the north and east, farmers believe that Weza acts as a reservoir and provides them with surplus animals, and although these views were not substantiated in this study, confining hunting to areas far removed from boundaries where there are common interests is likely to promote public relations.

It is strongly recommended that no hunting be permitted within indigenous forests, irrespective of size, as these are areas of prime habitat for bushbuck and are considered as important natural refuge sites. Despite making this recommendation in 1983, it has obviously been ignored; accounts of hunting experiences at Weza are clear evidence of this (White 1985a, 1985b; Balcomb 1985). Furthermore hunting should not be permitted in the vicinity of hiking trails. Recommendations that areas one km either side of trails should be protected were made in 1983, and more recent and comprehensive data on home range sizes (Chapter Eight) indicate that this area of protection should be increased to 1,5 km on each side of the trail, so that nonconsumptive wildlife recreation is not influenced directly by hunting activities. In spite of these recommendations to Forestry, one hunter "standing on a hiking trail" describes how he killed a male bushbuck at Weza that had just emerged from natural bush 100 m away (Balcomb 1985). Clearly if these recommendations are accepted, then much stricter supervision is required to ensure that they are enforced. Precise locations and boundaries for each hunt should be clearly defined by management staff at the commencement of every

hunting excursion, to both hunter and forest guard (who acts as a guide and should accompany the hunters at all times). Finally, it is recommended that management staff reserve the right to modify or alter the proposed areas for hunting at any time. Such modifications may be necessary due to silviculture or exploitation activities, environmental conditions or simply for reasons of safety.

10.2.3.3 Recommended season for hunting

All the available evidence gathered in this study indicate that food quantity and/or quality are limiting bushbuck numbers during the winter months. The removal of animals harvested in August and September, as occurred in 1985, is unlikely to have any benefit (in terms of reducing intraspecific competition or increasing forage availability) to non-hunted animals at this time. Duiker do not appear to be limited by seasonally-induced fluctuations in food resources, presumably because of their contrasting level of spatial and social organisation, and thus the timing of hunting appears less important to this species. Hunting seasons are frequently identified and determined at times when hunting activities will have the least negative effects on reproduction, and consequently ungulates are commonly protected during the rutting and calving seasons. Because both bushbuck and duiker breed throughout the year, it is not possible to identify periods when animals should be protected, but by the same reasoning the removal of a small proportion of these populations by hunting is unlikely to impair the reproductive performance of more than a few individuals. Consequently, it is recommended that hunting at Weza takes place from mid-autumn to early winter (April to June inclusive). For convenience, duiker as well as bushbuck should be hunted during this time, when the risks of inadvertently causing fires is considerably less than in late winter and early spring.

10.2.3.4 Selective or nonselective harvesting

The impact of selective harvesting depends largely on the initial objectives of that harvesting programme. If animals are to be culled or hunted for meat production, then the results of this study indicate that young animals should be selected; maximum productivity was attained by duiker and female bushbuck during their first year of life, and by male bushbuck until they were two years of age (Chapter Four). However, the behavioural attributes of both species make them better suited to sport hunting than to exploitation for meat production (also see Bigalke 1974), particularly in view of the limited harvest recommended at Weza. If the objective of hunting is, at any stage, to help control numbers where densities are considered to be excessive, then animals should be harvested with the minimum levels of disturbance (see above) and removals should be nonselective. If only males are harvested then this is unlikely to reduce population numbers significantly, unless exploitation is severe (see Caughley 1977), and may have the exact opposite effect in promoting population growth (e.g. Bergerud 1971c). Unselective harvests have been used to control or reduce ungulate numbers in many temperate areas (Roseberry et al. 1969; Short 1972; Holsworth 1973; Mitchell et al. 1977; Coe et al. 1980; Ozoga and Verme 1984).

However, if the objective is to allow limited sport hunting, as recommended in this study, then it is highly probable that the majority (if not all) the bushbuck selected by hunters will be adult males. Reasons for this and the wisdom of sex-selective bushbuck harvests have been reviewed by Mentis (1973c) and Allen-Rowlandson (1985) and will only be briefly outlined here.

In Natal, male bushbuck are classified as ordinary game and are hunted for three months of the year while females are protected game and can be legally harvested only by special permit. Traditionally, hunters in Natal have also practiced age-selective harvesting of male bushbuck, with protection generally being afforded to animals with horns shorter than

the ears. Irrespective of their legal protection, reasons why the hunting of female bushbuck is considered to be unethical or unwise include:

a) females are less wary than males, particularly when being chased and therefore offer easier targets,

b) because only females bear young, any shot this year will lead to fewer juveniles the following year, and

c) one male may mate with several females and so fewer males are required in the population.

Such reasoning, while undoubtedly resulting from sincere concern for the welfare of this species, is however somewhat spurious (Mentis 1973c; Allen-Rowlandson 1985). Admittedly the flight behaviour of females may differ markedly from that of males during organised beats, but as Mentis (1973c) points out, this may be due in part to conditions where many generations of females have been protected. Elsewhere in game eradication schemes females have proved more difficult to shoot than males, and personal experiences revealed that females were equally as wary during capture operations. These findings therefore suggest that a more sporting means of hunting females would be by stalking, which is the method Forestry and consulted hunting associations wish to implement at Weza.

The second argument regarding productivity is not substantiated by all our knowledge of population dynamics and performance, and does not warrant further discussion. But the third argument that fewer males are needed in a population is debatable. In most of the bushbuck populations that have been studied, including this one, there are approximately equal numbers of males and females. This might infer that males are more expendable but if so, which males should be harvested? It is commonly claimed that old males are sterile and therefore should be culled because they cause a decline in recruitment by preventing younger males from breeding. Such claims of sterility were unfounded at Weza

and have yet to be substantiated for any other bushbuck population. If males have managed to survive to an old age and are still capable of breeding, then presumably this is a trait which should be encouraged and preserved so that it can be passed on to future generations.

By the same argument, it would be unwise to remove those males that are the most successful in mate acquisition. Since the social organisation of bushbuck is based on a dominance hierarchy (Chapter Eight), such animals are likely to be the largest and heaviest. (Subordinate males would rarely be able to acquire mates because breeding is aseasonal and therefore the competition between males for the relatively few females in oestrus at any given time would be severe). Some prime males are undoubtedly shot whenever the common policy of shooting males with horns longer than the ears is adopted. During drives in dense vegetation this is usually the only distinction that is made; hunters rarely have time to appreciate the full magnitude of every adult male that is shot at (i.e. before it is killed and inspected). Conversely, stalkers have the opportunity to assess the size and head of their quarry before despatching it, and are frequently much more selective. At low levels of utilization the effects of removing the very males that nature has selected for breeding are probably negligible but may be quite drastic as the intensity of hunting for trophies or for meat increases. Consequently heavy hunting pressure on adult male bushbuck alone is an extremist policy (Mentis 1973c) and should be regarded as a highly dubious practice (Allen-Rowlandson 1985); possible methods of preventing it are considered below.

In contrast to bushbuck, the law regarding the hunting of duiker does not distinguish between males and females, and hunters generally do not show the same reluctance to shoot female duiker, presumably because of the lack of sexual dimorphism (other than horns) exhibited by this species. Thus all the reasons why female bushbuck should not be hunted are ignored for female duiker because of the difficulties in sexing this animal in the field. As a result, approximately

equal proportions of males and females (both adults and subadults because of additional difficulties in determining age in the field) are harvested. There have been no published accounts of such a practice having a deleterious effect on any duiker population, while extremely heavy but random culling operations during the game eradication programmes in Zambia had quite the opposite effect resulting in duiker breeding at an earlier age and having shorter intervals between pregnancies (Child and Wilson 1964; Wilson and Roth 1967). More locally, and despite this exploitation of females, duiker are more common than bushbuck in Natal (Mentis 1973c). Reasons why the hunting of female bushbuck should remain such a controversial issue are therefore not obvious, particularly since laws regarding the hunting of many other female ungulates ecologically similar to bushbuck were amended years ago.

10.2.3.4.1 Trophy hunting

Concern over trophy hunters selecting prime males is not restricted to bushbuck - several biologists have pointed out how the genetic composition and fitness of ungulate populations may be adversely affected by intensive and selective harvesting (Geist 1971b; Jarman and Jarman 1974; Leuthold 1977; Caro 1984). These warnings have generally been unheeded by hunters who, having paid their fee, consider that the choice of the animal that they want is theirs and theirs alone. It is therefore the responsibility of management to ensure that hunting conforms to the intended strategy of harvesting.

It may be argued that with the limited level of utilization proposed for Weza, sex- and age-selective harvesting will have little effect on the population in future years. The fact that bushbuck numbers remained relatively stable in I.S.A.1 even following the loss of more than 30% of the marked population during the winter of 1983 tends to support this, as some degree of immigration must have occurred. However, the area where animals were intensively monitored contained prime bushbuck habitat that

presumably was highly attractive to these immigrants. In more marginal areas there may have been more mortalities and less rapid recolonization. Furthermore, although numbers were replaced, the "quality" of the immigrants may not have been the same as those that died; some aspect prevented those immigrants from occupying this prime habitat prior to 1983. It therefore follows that the removal of prime males does not lead to their immediate replacement by other males of the same age or social status, as some hunters like to believe. If the same areas are repeatedly hunted at Weza, and each of 20 hunters every year selects a prime male, this could have a considerable impact on the age structure of the local male population over a period of five or ten years, particularly in areas where there is a high proportion of nonpreferred or marginal habitat. Differing age structures as a result of hunting or harvesting have been noted in many exploited populations (e.g. Wilson and Roth 1967; Cordero and Ojasti 1981) and it is particularly interesting to note the lower average age of adult male bushbuck hunted on surrounding farms (where approximately 40 per annum are harvested) compared to the males culled randomly in Weza State Forest (see Chapter Four).

The minimum trophy horn length to qualify for Rowland Ward is 15 inches (38,1 cm) measured in the manner described by Bryant (1984). Of the 71 adult male skulls from Weza examined in this study, six (8,5%) would have qualified had the animals been hunted ethically. Ages of these trophy animals ranged from 72 months to 132 months, with an average age of 108 months. The proportions of trophy animals within each adult age class are detailed in Table 10.7. Since horn growth continues throughout life (Chapter Four), it is worthwhile considering what proportion of the males in each age class had horns approximating the qualifying length (i.e. within 1 cm or 2,6% of the minimum trophy size). These proportions increased with age, ranging from 0,0% in 48 month old males to 60,0% in the oldest males of 156 months, and overall 12 males (16,9% of the adult sample) had horn lengths within 1 cm of the minimum qualification (Table 10.7). Although the sample size in the oldest age class was

small, the fact that 60,0% of these males had horns approaching trophy size but that none qualified suggests that horn wear may exceed growth at this age. Among the younger age classes several males may have developed trophy horns had they lived.

TABLE 10.7 The proportion of trophy animals in the sample of adult bushbuck males measured at Weza.

	Age Class (months)					
	48	72	96	132	156	Total
No. of males culled	8	14	32	12	5	71
No. of trophy males	0	1	3	2	0	6
% of trophy males	0,0	7,1	9,4	16,7	0,0	8,5
No. of males with horns within 2,6% of trophy *	0	1	5	3	3	12
% of males with horns within 2,6% of trophy	0,0	7,1	15,6	25,0	60,0	16,9

* - i.e with horn lengths of 37,1 - 38,0 cm

Comparisons between the mean body mass (and condition indices) of trophy animals and all other adult males were not considered valid due to the seasonal fluctuations in these parameters exhibited by bushbuck at Weza (Chapter Four). Three (10%) of the 30 adult bushbuck males immobilized at Weza had trophy horns, but the ages of these animals could not be determined accurately in the field. Similarly, two (4,1%) of the 49 adult males I examined during hunts on surrounding farms had horns longer than 38,1 cm but these skulls were not available for age determination purposes. The difference in the proportions of trophy animals at Weza and on surrounding farms may be greater than that revealed in this study since the former group was culled randomly whereas on the farms hunters selected adult males.

The minimum length of duiker horns to qualify for Rowland Ward is 4,5 inches or 11,4 cm (Bryant 1984). Ten (26,3%) of the 38 adult (at least 27 months of age) males examined at Weza had horns equal to or exceeding this length. Although this is a much higher proportion than trophy bushbuck, this need not imply that trophy duiker are more numerous; almost half the duiker population at Weza consisted of animals under 30 months of age. However, assuming that culling operations were conducted at random, then the proportion of trophy duiker within the culled sample of males of all ages (15,2%) was more than double that within the culled sample of male bushbuck (7,0%). Trophy duiker had an average age of 90 months (range 60-168 months) and 60 month old males had a higher proportion of trophy horns than any other age class (Table 10.8). With the exception of the small sample of 168 month old males, the proportion of trophies declined with increasing age in animals older than 60 months. Since duiker attain 99,8% of their asymptotic horn growth by the age of 36 months (Chapter Three), these results suggest that in some instances horn size decreases

TABLE 10.8 The proportion of trophy animals in the sample of adult duiker males measured at Weza.

	Age Class (months)					
	27-36	60	84	120	168	Total
No. of males culled	5	9	12	9	3	38
No. of trophy males	0	4	3	2	1	10
% of trophy males	0,0	44,4	25,0	22,2	33,3	26,3
No. of males with horns within 2,6% of trophy *	1	1	4	2	0	8
% of males with horns within 2,6% of trophy	20,0	11,1	33,3	22,2	0,0	21,0

* - i.e. with horn lengths < 11,3cm but > 11,1 cm.

with age as a result of wear or damage. The relatively high proportions of 84 month and 120 month old males with horns within 3 mm (2,6%) of the qualifying length supports this (Table 10.8).

In relative terms, duiker can therefore develop into trophy animals at an earlier age than bushbuck. These results also indicate that trophies of both species are likely to be prime animals competing for females. Since horn size is determined more by genetic than phenotypic factors (Spinage 1969d), overexploitation of prime males could result in a decline in trophy quality (as well as other favoured attributes) in subsequent years. (Bergerud (1971c) suspected intensive hunter selection for large antlers to be responsible for the decline in caribou trophies in areas of Newfoundland, where environmental factors may play a major role in determining antler growth and size, see above). In conclusion, "non-natural" mortality must impose its own selective pressure (see Geist 1971b; Mitchell et al. 1977) and until this kind of influence has been considered adequately, it is probably much safer to utilize both sexes in the same proportions that occur in natural, unexploited populations. If this is not acceptable to hunters, then they should be discouraged from continually harvesting prime males. This can best be achieved by imposing an increased tariff on any trophy animal that is shot, which is a common practice in many hunting areas. If the trophy tariff is double that of a smaller male, this would still provide hunting at extremely reasonable rates, and well below many of those charged by private organisations (which tend to include a daily rate and accommodation at substantially higher prices, see the 1984-1986 special hunting editions of Nyala News, numbers 59, 63 and 67; Ferrario 1985). Provided that hunters are informed of these proposed tariff increases for large males well in advance, I see no reason why these should not be accepted; claims that shot animals were not recognised as trophies in the field are unlikely if all those hunting at Weza have passed a recognised proficiency test. Because Forestry management staff will have little if any experience

in measuring trophies, any marginal heads should be charged at the lower rate. In any event all shot animals should be measured and their ages determined using the criteria detailed in Chapter Three if the impact of hunting is to be assessed (see below). If trophy animals continue to be selected in spite of these precautions, management may decide to reduce the number of males to be harvested, offer new areas of hunting or alter the hunting strategies permissible at Weza.

10.2.3.5 Recommended methods of monitoring the impact of hunting

Caughley (1977) describes two approaches to the problem of harvesting populations in a fluctuating environment. The first, a "mean strategy", ignores variability and the yield is estimated as if the population was stable in size, the "steady density" being obtained from the population size averaged over several years. Alternatively, a "tracking strategy" may be adopted where the trend of a population is followed and yields changed as the population changes.

Neither of these strategies can be implemented with complete success at Weza, since population sizes cannot be assessed with any degree of precision or accuracy. Furthermore, unless hunting is confined to a very small section of the proposed hunting area, it is unlikely that extensive pre- and post-hunting surveys of animal abundance, population structure and sex ratios will detect any significant changes in either population hunted at the proposed levels. Even if a greater proportion of bushbuck and duiker are harvested in future years, it is highly improbable that the effects of hunting can be identified and isolated from those of current timber management practices (particularly since both activities may influence distribution as well as performance). The potential biases associated with timber management activities may be reduced, but not eliminated (the concept of a control area is impractical at Weza), by extensive sampling, but in any event trends could be assessed most profitably by a simple but

standardised count index rather by any attempt to estimate absolute numbers (Chapter Nine). Attempts to monitor the impact of hunting directly by conducting counts prior to and after hunting are therefore probably futile. Instead, counts should be conducted each winter over fairly extensive areas to obtain some index of abundance which can be used for comparative purposes in estimating population trends in future years. The impact of hunting should be monitored using less direct means.

All animals shot at Weza should be made available for post-mortem examinations. In spite of these recommendations (which were made in 1983 and included a comprehensive list of reasons why specific biological samples should be collected and analysed), Forestry staff have merely recorded the mass and body dimensions of each harvested animal. Lower jaws should be retained for age determination purposes, but if the animal is a trophy then an impression of the left mandible would suffice. Physiological condition could be assessed from kidney fat indices and percentage dry mass values of the marrow from the metatarsus. Females should be examined for the presence of an embryo or foetus, and lactational status should also be recorded. Finally, a sample of the rumen contents should be taken for diet assessment purposes. The removal of these samples will not affect the condition of the skin or carcass in any way, and every hunter should be informed prior to hunting that such samples will be taken from his animal(s). This material, together with morphometric data, should be used to assess age structure, growth, diet, reproduction and physiological condition, and the results of these parameters should be compared to existing data and to data obtained in future hunts. Sample sizes will clearly depend on hunting success and whether sex- and/or age-selective harvesting occurs.

During this initial level of utilization it is recommended that considerable attention be given to monitoring the logistics of sport hunting on State land. This should include evaluations of hunting effort, identification of the major factors influencing this, levels

of control and supervision of hunting and hunting-management interactions. These efforts should then minimise any areas of potential conflict, and help to ensure that both parties are completely satisfied with the feasibility and instigation of such an amenity. Hunter effort should not be simply measured in terms of the time required to harvest each animal because although the effort expended by hunters will increase as numbers decline, other factors will also affect yields. It is anticipated that hunting effort will inevitably increase with time since both species (which by nature are timid and wary) will become more secretive and cautious in response to the additional disturbance caused by hunting activities (see above). Hunters should therefore furnish details of all antelope observed in the field, irrespective of whether these were shot, missed or regarded as unsuitable specimens. Other methods of assessing hunting effort have been detailed in Roseberry et al. (1969), Holsworth (1973) and Caughley (1977). It is recommended that any questionnaire used to evaluate effort should be specific in its objectives and prepared and scrutinised thoroughly to avoid or minimise ambiguities.

10.3 FUTURE RESEARCH

This study suffered from several limitations in the quality and quantity of data collection and in subsequent analyses. The most notable limitations involved age determination procedures, the evaluation of mortality rates, duiker habitat selection patterns and the impact of management practices on this species at Weza, and estimates of animal abundance. A thorough analysis of the population dynamics of both antelope species was not possible due to the broad age classes resulting from the restrictive methods of estimating age. Since distinct cementum annuli were not evident in either species, the only means of improving the age determination criteria developed in this study would be to examine the teeth of animals recaptured over known intervals, or by marking a number of neonates and examining tooth wear in subsequent years when representatives of this

marked sample were sacrificed (or when fresh carcasses were recovered). Either method would require a considerable amount of time, effort and expense and cannot be justified at a time when financial resources are lacking. Similarly, assessments of juvenile mortality could be achieved by monitoring the fate of marked neonates, but the effort in searching for infants and the costs involved in determining the causes and spatial and temporal distributions of natural mortalities are not warranted in the present economic climate. However, every attempt should be made to routinely collect the skulls from all carcasses found in the field; the intensive management of timber plantations provides an ideal opportunity to systematically search specific compartments each year and local management's reluctance to do this should not be accepted in future years. It is highly unlikely that any additional research will provide an accurate, reliable and practical method of determining antelope numbers in intensively managed plantations and consequently future attempts to monitor these species should be based the recommendations detailed in Chapter Nine.

The paucity of data on several aspects of the ecology of duiker at Weza was largely due to problems associated with radio tracking; transmitters developed in this study were totally unsuitable. Much smaller, reliable transmitters that are commercially obtainable should be fitted to duiker as soon as funds are available. Many of the conclusions regarding habitat selection and the effects of timber management on this species are necessarily conjectural, and a more thorough understanding of the habitat requirements of duiker are required if proposed habitat modifications and future management are to be successful. These aspects should therefore receive priority. Radio tracking would also facilitate estimates of natural mortality and/or dispersion, particularly if some duiker were monitored in localised areas prior to and during specific activities such as felling, thinning or extensive cleaning. Radio tracking programmes should also be continued with bushbuck; areas of interest should include assessments of the movements and performance of this species in indigenous forests, while bushbuck and

duiker equipped with reliable transmitters would be invaluable in determining the effects (particularly disturbance) of hunting activities.

It is highly probable that the findings of this study will be very relevant to other similar plantations in the Natal midlands. However it would be injudicious to extrapolate all the results from this study to other regions without first conducting similar surveys for comparative purposes. Since many of the problems associated with monitoring antelope in plantation areas have now been identified and, wherever possible adapted accordingly, comparative studies in other timbered areas would require considerably less expense and time to complete than in this study. If interest in other areas is confined to their hunting potential, this could best be assessed by obtaining indices of abundance from extensive nocturnal surveys conducted during winter in conjunction with a knowledge of the proportions and availability of key habitats.

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APPENDIX A.

COMMON INDIGENOUS AND EXOTIC TREES IN WEZA STATE FOREST

TABLE A.1 Common trees of the indigenous forests, Weza.
(Nomenclature follows Coates Palgrave (1977)* and de Winter, Vahrmeijer and von Breitenbach (1978)**).

Species	Common Name
<u>Allophylus dregeanus</u>	Simple leaved allophylus
<u>Apodytes dimidiata</u>	White pear
<u>Bersama tysoniana</u>	Common bersama
<u>Calodendrum capense</u>	Cape chestnut
<u>Canthium inerme</u>	Turkey-berry
<u>Casearia gladiiformis</u>	Swordleaf
<u>Celtis africana</u>	White stinkwood
<u>Combretum kraussii</u>	Forest bushwillow
<u>Cryptocarya latifolia</u>	Broad-leaved laurel
<u>Cryptocarya myrtifolia</u>	Camphor laurel
<u>Cryptocarya woodii</u>	Cape laurel
<u>Cunonia capensis</u>	Red alder
<u>Curtisia dendata</u>	Assegai tree
<u>Cussonia spicata</u>	Cabbage tree
<u>Dais cotinifolia</u>	Pompon tree
<u>Dovyalis zeyheri</u>	Wild apricot
<u>Ekebergia capensis</u>	Cape ash
<u>Fagara davyi</u>	Knobwood
<u>Ficus capensis</u>	Cape fig
<u>Ficus craterostoma</u>	Rare forest fig
<u>Garcinia gerrardii</u>	Forest garcinia
<u>Halleria lucida</u>	Tree fuchsia
<u>Harpephyllum caffrum</u>	Wild plum
<u>Heteromorpha arborescens</u>	Parsley tree
<u>Ilex mitis</u>	African holly
<u>Kiggelaria africana</u>	Wild peach
<u>Leucosidea sericea</u>	Oldwood
<u>Linociera foveolata</u>	Fine-leaved ironwood
<u>Maytenus acuminata</u>	Silky bark
<u>Maytenus heterophylla</u>	Common spikethorn
<u>Maytenus peduncularis</u>	Blackwood maytenus
<u>Nuxia floribunda</u>	Forest elder
<u>Ochna holstii</u>	Red ironwood
<u>Ocotea bullata</u>	Stinkwood
<u>Olea capensis</u>	Ironwood
<u>Olea woodiana</u>	Forest olive
<u>Olinia radiata</u>	Natal hard pear
<u>Oricia bachmannii</u>	Twin-berry tree
<u>Pittosporum viridiflorum</u>	Cheesewood
<u>Pleurostyliia capensis</u>	Coffee pear
<u>Podocarpus falcatus</u>	Outeniqua yellowwood
<u>Podocarpus henkelii</u>	Henkel's yellowwood

TABLE A.1 continued.

Species	Common Name
<u>Podocarpus latifolius</u>	Real yellowwood
<u>Protea caffra</u>	Common sugarbush
<u>Protea roupelliae</u>	Silver sugarbush
<u>Prunus africana</u>	Red stinkwood
<u>Ptaeroxylon obliquum</u>	Sneezewood
<u>Rapanea melanophloeos</u>	Cape beech
<u>Rhamnus prinoides</u>	Dogwood
<u>Rhus chirindensis</u>	Redcurrant
<u>Rothmannia capensis</u>	Common rothmannia
<u>Rothmannia globosa</u>	Small-flowered rothmannia
<u>Schefflera unbellifera</u>	Bastard cabbage tree
<u>Scolopia flanaganii</u>	Small-leaved thorn pear
<u>Scolopia mundii</u>	Red pear
<u>Scolopia zeyheri</u>	Thorn pear
<u>Seemannaralia gerrardii</u>	Wild maple
<u>Syzygium cordatum</u>	Waterberry
<u>Syzygium gerrardii</u>	Forest waterberry
<u>Trichilia dregeana</u>	Forest Natal mahogany
<u>Trichilia emetica</u>	Natal mahogany
<u>Trichocladus ellipticus</u>	White witch-hazel
<u>Trimeria grandifolia</u>	Wild mulberry
<u>Vepris undulata</u>	White ironwood
<u>Warburgia salutaris</u>	Pepperbark tree
<u>Xymalos monospora</u>	Lemonwood

* Coates Palgrave, K. (1977) Trees of Southern Africa. Cape Town: Struik.

** de Winter, B., Vahrmeijer, J. & von Breitenbach, F. (1978) The National List of Trees. 2nd edition. Pretoria: van Schaik.

TABLE A.2 Some of the exotic trees occurring at Weza.
(Nomenclature follows Poynton (1971)*)

Species	Common Name
<u>Abies religiosa</u>	Sacred fir
<u>Acacia mearnsii</u>	Black wattle
<u>A. melanoxylon</u>	Blackwood
<u>Acer buergerianum</u>	Chinese maple
<u>A. negundo</u>	Ash-leaved maple
<u>Catalpa speciosa</u>	Cigar tree
<u>Cedrus deodara</u>	Deodar
<u>Chamaecyparis lawsoniana</u>	Lawson's cypress
<u>Cinnamomum camphora</u>	Camphora tree
<u>Cryptomeria japonica</u>	Japanese cedar
<u>Cupressus lusitanica</u>	Mexican cypress
<u>C. torulosa</u>	Himalayan cypress
<u>Eucalyptus diversicolor</u>	Karri gum
<u>E. elata</u>	River peppermint gum
<u>E. fastigata</u>	Cut-tail
<u>E. grandis</u>	Saligna gum
<u>E. oreades</u>	Altior gum
<u>E. paniculata</u>	Grey ironbark
<u>Fraxinus excelsior</u>	European ash
<u>Ginkgo biloba</u>	Maiden hair tree
<u>Grevillea robusta</u>	Silky oak
<u>Ligustrum lucidum</u>	Chinese privet
<u>Liquidambar styraciflua</u>	Liquidambar
<u>Liriodendron tulipifera</u>	Tulip tree
<u>Pinus ayacahuite</u>	Mexican white pine
<u>P. elliottii</u>	Slash pine
<u>P. engelmannii</u>	Engelmann's pine
<u>P. kesiya</u>	Khasi pine
<u>P. leiophylla</u>	Smooth-leaved pine
<u>P. michoacana</u>	Michoacan pine
<u>P. montezumae</u>	Montezuma pine
<u>P. oocarpa</u>	Ocote pine
<u>P. patula</u>	Patula pine
<u>P. pinaster</u>	Cluster pine
<u>P. pseudostrobus</u>	Pseudostrobus pine
<u>P. radiata</u>	Monterey pine
<u>P. roxburghii</u>	Chir pine
<u>P. taeda</u>	Loblolly pine
<u>Plantanus acerifolia</u>	London plane
<u>Populus deltoides</u>	Match poplar
<u>Quercus alba</u>	White oak
<u>Q. prinus</u>	Swamp chestnut oak
<u>Q. robur</u>	English oak
<u>Sequoia sempervirens</u>	Californian redwood
<u>Ulmus parvifolia</u>	Chinese elm

* Poynton, R.J. (1971) Characteristics and uses of trees and shrubs obtainable from the Forest Department. Bulletin No.39. Pretoria: The Government Printer.

APPENDIX B
SEASONAL VARIATIONS IN THE CONDITION OF BUSHBUCK AT WEZA

TABLE B.1 Seasonal variations in the KFI values of adult male bushbuck.

Season (n) Mean $\pm$ S.E.	DJF (16) 15,64 $\pm$ 2,24	JJA (12) 9,84 $\pm$ 0,79	ALL (66) 11,31 $\pm$ 0,73
MAM (14) 12,01 $\pm$ 1,33	n.s.	n.s.	n.s.
SON (24) 8,75 $\pm$ 0,60	t=3,52 p<0,001	n.s.	t=2,02 p<0,05
ALL (66) 11,31 $\pm$ 0,73	t=2,35 p<0,05	n.s.	

TABLE B.2 Seasonal variations in the % DM humerus values of adult male bushbuck.

Season (n) Mean $\pm$ S.E.	DJF (14) 31,61 $\pm$ 2,73	JJA (7) 40,39 $\pm$ 7,12	ALL (57) 30,80 $\pm$ 1,45
MAM (15) 33,77 $\pm$ 2,33	n.s.	n.s.	n.s.
SON (21) 24,94 $\pm$ 1,18	t=2,53 p<0,02	t=3,47 p<0,002	t=2,34 p<0,05
ALL (57) 30,80 $\pm$ 1,45	n.s.	t=2,01 p<0,05	

TABLE B.3 Seasonal variations in the % DM radius values of adult male bushbuck.

Season (n) Mean $\pm$ S.E.	DJF (15) 71,42 $\pm$ 8,03	JJA (8) 82,81 $\pm$ 5,80	ALL (61) 63,93 $\pm$ 4,07
MAM (16) 76,26 $\pm$ 5,87	n.s.	n.s.	n.s.
SON (22) 42,99 $\pm$ 6,77	t=2,69 p<0,02	t=3,36 p<0,01	t=2,65 p<0,01
ALL (61) 63,93 $\pm$ 4,07	n.s.	n.s.	

TABLE B.4 Seasonal variation in the % DM metacarpus values of adult male bushbuck.

Season (n) Mean $\pm$ S.E.	DJF (15) 73,75 $\pm$ 8,17	JJA (8) 84,93 $\pm$ 4,61	ALL (61) 65,77 $\pm$ 4,00
MAM (16) 73,32 $\pm$ 5,83	n.s.	n.s.	n.s.
SON (22) 47,88 $\pm$ 7,09	t=2,37 p<0,02	t=3,04 p<0,01	t=2,27 p<0,05
ALL (61) 65,77 $\pm$ 4,00	n.s.	n.s.	

TABLE B.5 Seasonal variations in the KFI values of adult female bushbuck.

Season (n) Mean $\pm$ S.E.	DJF (6) 34,23 $\pm$ 14,18	JJA (12) 15,68 $\pm$ 4,38	ALL (60) 16,27 $\pm$ 2,44
MAM (12) 25,19 $\pm$ 7,21	n.s.	n.s.	n.s.
SON (30) 9,34 $\pm$ 1,27	t=3,779 p<0,001	n.s.	n.s.
ALL (60) 16,27 $\pm$ 2,44	t=2,039 p<0,05	n.s.	

TABLE B.6 Seasonal variations in the % DM humerus values of adult female bushbuck.

Season (n) Mean $\pm$ S.E.	DJF (6) 32,47 $\pm$ 2,55	JJA (7) 50,30 $\pm$ 5,06	ALL (51) 37,23 $\pm$ 1,72
MAM (13) 43,51 $\pm$ 2,63	t=2,586 p<0,02	n.s.	n.s.
SON (25) 31,45 $\pm$ 2,03	n.s.	t=4,048 p<0,001	t=2,328 p<0,05
ALL (51) 37,23 $\pm$ 1,72	n.s.	t=2,619 p<0,02	

TABLE B.7 Seasonal variations in the % DM radius values of adult female bushbuck.

Season (n) Mean $\pm$ S.E.	DJF (6) 83,33 $\pm$ 7,04	JJA (7) 86,21 $\pm$ 9,19	ALL (53) 64,95 $\pm$ 4,52
MAM (13) 84,01 $\pm$ 3,57	n.s.	n.s.	t=2,041 p<0,05
SON (27) 46,17 $\pm$ 6,52	t=2,591 p<0,02	t=2,924 p<0,01	t=2,391 p<0,02
ALL (53) 64,95 $\pm$ 4,52	n.s.	n.s.	

TABLE B.8 Seasonal variations in the % DM metacarpus values of adult female bushbuck.

Season (n) Mean $\pm$ S.E.	DJF (6) 86,67 $\pm$ 2,84	JJA (8) 95,91 $\pm$ 1,44	ALL (54) 67,89 $\pm$ 4,34
MAM (13) 86,19 $\pm$ 2,78	n.s.	t=2,594 p<0,02	t=2,036 p<0,05
SON (27) 46,85 $\pm$ 6,29	t=2,933 p<0,01	t=4,189 p<0,001	t=2,777 p<0,01
ALL (54) 67,89 $\pm$ 4,34	n.s.	t=2,467 p<0,02	

TABLE B.9 Seasonal comparisons of mean body mass values for adult male bushbuck.

Season (n) Mean $\pm$ S.E.	DJF (16) 61,66 $\pm$ 1,52	JJA (12) 60,25 $\pm$ 1,93	ALL (67) 58,59 $\pm$ 0,92
MAM (15) 60,52 $\pm$ 2,21	n.s.	n.s.	n.s.
SON (24) 54,51 $\pm$ 1,37	t=3,434 p<0,02	t=2,418 p<0,05	t=2,337 p<0,05
ALL (67) 58,59 $\pm$ 0,92	n.s.	n.s.	

APPENDIX C
PLANT SPECIES CONSUMED BY BUSHBUCK AND DUIKER

TABLE C.1 Plant species browsed by bushbuck and duiker in the field but not recorded in rumen samples.

SPECIES	SPECIES
<u>Agrimonia odorata</u>	<u>Allophylus dregeanus</u>
<u>Amaranthus</u> sp.	<u>Argyrolobium tomentosum</u>
<u>Aristea</u> sp.	<u>Begonia sutherlandii</u>
<u>Behnia reticulata</u>	<u>Buddleja auriculata</u>
<u>Buddleja salviifolia</u>	<u>Caesalpinia decapetala</u>
<u>Canthium ciliatum</u>	<u>Carissa bispinosa</u>
<u>Cassia mimosoides</u>	<u>Cassia plumosa</u>
<u>Chlorophytum comosum</u>	<u>Ciclospermum leptophyllum</u>
<u>Cineraria deltoidea</u>	<u>Cleome monophylla</u>
<u>Clutia pulchella</u>	<u>Combretum krausii</u>
<u>Commelina benghalensis</u>	<u>Crassocephalum crepidioides</u>
<u>Cyphostemma natalitium</u>	<u>Dovyalis rhamnoides</u>
<u>Droguetia urticaefolia</u>	<u>Galium</u> sp.
<u>Helichrysum splendens</u>	<u>Hibiscus trionum</u>
<u>Hypochoeris radiata</u>	<u>Hypoestes aristata</u>
<u>Hypoestes verticillaris</u>	<u>Isoglossa cooperi</u>
<u>Kedrostis hirtella</u>	<u>Kerria japonica</u>
<u>Maytenus heterophylla</u>	<u>Maytenus nemorosa</u>
<u>Mohria caffrorum</u>	<u>Nidorella auriculata</u>
<u>Oenothera villosa</u>	<u>Oplismenus hirtellus</u>
<u>Panicum aequinerve</u>	<u>Pinpinella</u> sp.
<u>Plantago lanceolata</u>	<u>Plectranthus</u> sp.
<u>Polygonum lapathifolium</u>	<u>Protasparagus africanus</u>
<u>Protasparagus virgatus</u>	<u>Pseudognaphalium luteo-album</u>
<u>Rhaphanus raphanistrum</u>	<u>Rhoicissus tridentata</u>
<u>Richardia brasiliensis</u>	<u>Rumex angiocarpus</u>
<u>Sonchus gigus</u>	<u>Trichocladus ellipticus</u>
<u>Verbena bonariensis</u>	<u>Verbena venosa</u>
<u>Vepris undulata</u>	<u>Zanthoxylum davyi</u>

TABLE C.2 Annual and monthly diet of duiker in Weza State Forest between September 1980 and July 1984 as determined by rumen content analysis. Values are expressed as :

(a) percent composition (aggregate volume) and

(b) frequency indices.

Species (Common name)	Over- all	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Fungi	(a) 28,26 (b) 0,71	22,37 1,00	1,93 0,44	33,16 1,00	44,21 0,89	25,72 0,89	60,41 0,89	22,61 0,67	9,92 0,42	4,46 0,60	14,59 0,63	10,68 0,36	16,60 0,91
<u>Solanum mauritianum</u> (Bugweed)	14,99 0,40	17,49 0,33	8,96 0,44	16,46 0,54	1,37 0,22	5,84 0,44	21,49 0,56	34,62 0,83	47,33 0,83	27,60 0,62	2,46 0,21	0,21 0,09	2,06 0,18
<u>Rubus cunifolia</u> (Bramble)	13,02 0,82	32,88 1,00	20,04 1,00	13,68 0,92	5,29 0,67	5,02 0,89	1,37 0,78	3,39 0,67	0,25 0,33	34,38 0,80	34,44 0,83	61,61 1,00	30,66 1,00
<u>Quercus robur</u> (English oak)	8,38 0,06				23,98 0,22	24,67 0,22		0,82 0,17	13,99 0,17				
<u>Crataegus pubescens</u> (Mexican hawthorn)	5,26 0,03				17,15 0,11					6,31 0,40	23,83 0,04		
Unidentified	4,35 0,95	2,57 1,00	15,26 1,00	3,55 0,92	0,56 1,00	4,74 1,00	2,57 1,00	11,63 1,00	4,15 0,83	2,91 0,80	2,80 0,92	5,00 1,00	4,12 1,00
<u>Acacia nearnsii/A.dealbata</u> (Black/silver wattles)	2,61 0,65	2,21 0,33	4,07 0,89	4,54 0,69	0,22 0,44	2,67 0,67	0,51 0,78	3,23 0,83	3,67 0,75	0,48 0,40	0,71 0,54	10,52 0,64	5,23 0,82
<u>Acalypha schinzii</u>	2,05 0,13	2,89 0,17		5,19 0,23	0,07 0,11						0,09 0,04	1,25 0,36	15,10 0,54
<u>Acalypha punctata</u>	1,83 0,18	11,66 0,17	0,10 0,11	0,41 0,23	1,03 0,11				0,94 0,08		0,95 0,21	1,46 0,27	11,79 0,64
<u>Acacia melanoxylon</u> (Blackwood)	1,81 0,48	1,11 0,83	0,45 0,67	1,74 0,46	0,39 0,33	5,01 0,56	3,08 0,89	0,25 0,67	0,85 0,42	0,59 0,40	0,93 0,29	0,16 0,27	6,48 0,45
<u>Solanum aculeastrum</u> (Poison-apple)	1,48 0,15		6,48 0,33	2,90 0,31	1,59 0,33	0,02 0,44	1,68 0,22	1,39 0,17	0,08 0,08		tr.* 0,04		
<u>Solanum nigrum</u>	1,47 0,10		0,56 0,33	0,12 0,15	1,11 0,22	13,15 0,33	0,92 0,11						0,09 0,09
<u>Physalis peruviana</u>	1,28 0,11	tr. 0,17	0,05 0,11	1,77 0,15		1,75 0,56	0,05 0,22	12,51 0,33	tr. 0,08				
<u>Acalypha ecklonii</u>	1,22 0,06		2,98 0,22	6,48 0,23		0,36 0,11				1,19 0,20			
<u>Pinus spp. (green)</u> (Pines)	1,15 0,40	0,06 0,50	tr. 0,22	0,43 0,38	0,88 0,33	0,14 0,56	0,25 0,67	5,47 0,67	1,33 0,67	11,35 0,80	2,37 0,33		0,24 0,18
<u>Taraxacum officinale</u> (Dandelion)	1,04 0,13	0,20 0,33	1,71 0,33		0,06 0,11	4,07 0,11	0,27 0,11	0,72 0,17			5,22 0,13	0,78 0,18	1,20 0,18

TABLE C.2 continued.

Species (Common name)	Over- all	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
<u>Ficus carica</u> (Fig)	1,00 0,01		14,42 0,11										
<u>Pellaea viridis</u>	0,99 0,61	0,44 0,87	2,26 0,89	2,92 0,62	0,42 0,56	0,49 0,67	0,12 0,67	1,40 0,67	0,09 0,42	0,18 0,60	1,50 0,75	1,15 0,55	0,03 0,27
<u>Pentania prunelloides</u>	0,87 0,14	0,80 0,17	1,39 0,11	3,15 0,38	0,49 0,11		0,06 0,22			0,24 0,20			2,19 0,54
<u>Podocarpus henkelii</u> (Henkel's yellowwood)	0,66 0,01								6,07 0,08				
<u>Galopina circaeoides</u>	0,60 0,24	0,96 0,83	0,24 0,22	0,05 0,08	0,21 0,22	3,17 0,56	0,08 0,22	1,08 0,50	0,04 0,17		0,03 0,04	0,63 0,45	1,78 0,18
<u>Solanum tuberosum</u> (Potato)	0,59 0,01		8,55 0,11										
<u>Prunus persica</u> (Peach)	0,55 0,05		4,64 0,11			0,24 0,22			1,84 0,08		0,07 0,04	0,31 0,09	
<u>Pinus spp. (brown)</u> (Pines)	0,52 0,46	0,16 0,50	tr. 0,11	0,91 0,69	0,04 0,44	0,16 0,44	2,93 0,78	0,06 0,50	0,01 0,33	0,07 0,20	0,07 0,63	tr. 0,09	0,80 0,45
<u>Phytolacca heptandra</u> (Inkberry)	0,47 0,05			0,39 0,15	0,10 0,22		3,86 0,11	0,01 0,17					
<u>Citrus aurantium</u> (Orange)	0,39 0,02								3,59 0,17				
<u>Cupressus lusitanica</u> (Cypress)	0,30 0,06	0,08 0,17		0,18 0,15	0,26 0,11				0,03 0,08		2,85 0,04		0,02 0,09
Grasses	0,29 0,60	0,86 0,67	0,06 0,89	0,21 0,85	0,01 0,56	1,08 0,44	0,03 0,56	0,01 0,67	0,13 0,58	2,14 0,60	0,64 0,42	1,04 0,54	0,20 0,64
<u>Duchesnia indica</u>	0,25 0,07		1,49 0,22		0,03 0,11	0,08 0,11		0,57 0,17	0,85 0,08		0,10 0,13		
<u>Ligustrum sp.</u> (Privet)	0,21 0,09	0,10 0,17	0,07 0,11			0,02 0,11	0,09 0,22		1,31 0,17		0,07 0,04	0,52 0,09	0,42 0,18
<u>Halleria lucida</u> (Tree-fuchsia)	0,19 0,11	0,08 0,33	1,61 0,22			0,37 0,22	0,05 0,22	0,15 0,17	0,13 0,17		0,21 0,08	0,05 0,09	
<u>Populus deltoides</u> (Poplar)	0,18 0,03					1,02 0,11					1,21 0,08	0,26 0,09	
<u>Melia azedarach</u> (Syringa)	0,17 0,01										2,28 0,04		

TABLE C.2 continued

Species (Common name)	Over- all	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
<u>Trimeria grandifolia</u>	0,03 0,01				0,15 0,11								
<u>Rhus carnolusa</u>	0,02 0,04			0,05 0,08		tr. 0,11	0,15 0,33						
<u>Eucalyptus</u> spp. (Gums)	0,02 0,02			0,03 0,08					0,09 0,08				
<u>Senecio</u> sp.	0,01 0,01		0,07 0,11										
<u>Cirsium vulgare</u>	0,01 0,01										0,09 0,04		
<u>Pteridium aquilinum</u> (Bracken fern)	0,01								0,02 0,17		0,02 0,04		
<u>Scilla nervosa</u>	0,01 0,01												0,09 0,09
<u>Dierama</u> sp.	0,01 0,02												0,09 0,18
<u>Conyza canadensis</u>	0,01 0,02		0,02 0,11	0,02 0,08									
<u>Bidens biternata</u> (Blackjack)	tr. 0,02					tr. 0,11		0,07 0,17					0,02 0,09
<u>Gnidia puchella</u>	tr. 0,01						0,02 0,11						
<u>Protoasparagus devenishii</u>	tr. 0,01										0,02 0,04		

*tr. - indicates trace (< 0,01%)

TABLE C.3 Annual and monthly diet of bushbuck in Weza State Forest between September 1980 and July 1984 as determined by rumen content analysis. Values are expressed as :

(a) percent composition (aggregate volume) and

(b) frequency indices.

Species (Common name)	Over- all	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Unidentified	60,87 1,00	78,25 1,00	71,14 1,00	51,15 1,00	68,10 1,00	75,31 1,00	42,86 1,00	63,54 1,00	44,35 1,00	48,86 1,00	41,06 1,00	76,83 1,00	79,29 1,00
<u>Acacia melanoxylon</u> (Blackwood)	7,30 0,60	0,97 0,33	0,80 0,54	13,56 0,75	17,68 1,00	5,88 0,69	9,49 0,90	2,57 0,63	22,15 0,85	2,24 0,58	2,60 0,41	0,75 0,46	2,01 0,50
<u>Rubus cunifolia</u> (Bramble)	6,45 0,74	7,48 1,00	3,47 0,77	1,32 0,63	2,17 0,88	1,41 0,75	0,71 0,60	1,12 0,75	0,77 0,38	6,65 0,58	29,02 0,97	10,92 0,69	10,67 0,79
<u>Pellaea viridis</u>	3,75 0,92	5,26 1,00	13,92 1,00	7,16 0,88	4,16 0,88	1,34 0,88	1,82 0,90	2,48 0,88	1,15 0,92	1,52 0,95	3,75 0,91	1,97 0,92	2,67 1,00
<u>Eucalyptus spp.</u> (Gums)	3,31 0,08			0,13 0,13					17,02 0,38	21,53 0,05	4,48 0,18		
Grasses	2,94 0,72	0,42 0,67	0,49 0,62	0,15 0,88	0,39 0,75	1,06 0,75	0,51 0,80	8,34 1,00	3,60 0,77	13,26 0,84	6,38 0,65	0,44 0,62	0,21 0,57
<u>Solanum aculeastrum</u> (Poison-apple)	2,72 0,18		0,47 0,31	0,24 0,38	0,52 0,25	3,24 0,50	22,42 0,60	1,23 0,38			0,28 0,03		0,01 0,07
<u>Acacia mearnsii/A.dealbata</u> (Black/silver wattles)	1,72 0,47	0,21 0,67	3,27 0,54	0,46 0,50	0,73 0,63	5,86 0,63	2,16 0,60	1,46 0,88	0,29 0,46	0,61 0,63	0,20 0,32	tr.* 0,08	0,65 0,21
<u>Quercus robur</u> (English oak)	1,37 0,02			7,87 0,13		0,01 0,06		0,01 0,13					
<u>Clematis brachiata</u>	1,35 0,03	4,71 0,33		12,12 0,25		0,89 0,06							0,33 0,07
<u>Phytolacca heptandra</u> (Inkberry)	1,26 0,03					0,22 0,13	13,78 0,20			0,10 0,05			
Fungi	0,90 0,05			0,17 0,25					3,52 0,08	2,22 0,11	4,36 0,09		
<u>Solanum mauritianum</u> (Bugweed)	0,86 0,14	0,62 0,67	0,23 0,23	0,15 0,13		0,41 0,13	1,80 0,20	2,44 0,63	5,35 0,31	1,00 0,11		0,46 0,15	
<u>Populus deltoides</u> (Poplar)	0,70 0,04	1,80 0,33	4,15 0,15	3,40 0,13					0,22 0,08			0,79 0,15	
<u>Halleria lucida</u> (Tree-fuchsia)	0,65 0,14		0,41 0,15	0,51 0,25	1,36 0,38	1,41 0,25	1,36 0,30	0,11 0,25	0,78 0,31		0,03 0,03	0,44 0,08	tr. 0,07
<u>Acalypha punctata</u>	0,61 0,08					0,34 0,13					2,09 0,03	0,88 0,15	3,00 0,57

TABLE C.3 continued

Species (Common name)	Over- all	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
<u>Pinus</u> spp. (brown) (Pines)	0,35 0,70	0,28 1,00	0,41 0,69	0,26 1,00	0,05 0,38	0,36 0,69	0,18 0,70	0,60 0,63	0,29 0,69	0,32 0,63	0,69 0,76	0,44 0,54	0,36 0,86
<u>Pinus</u> spp. (green) (Pines)	0,34 0,11		tr. 0,15		tr. 0,13	tr. 0,13		0,40 0,38	0,02 0,08	tr. 0,05	2,81 0,12	tr. 0,15	tr. 0,14
<u>Pentanisia prunelloides</u>	0,28 0,03		0,13 0,08			1,67 0,13						0,04 0,08	0,12 0,07
<u>Solanum nigrum</u>	0,27 0,04				1,80 0,13	0,42 0,31							
<u>Citrus limon</u> (Lemon)	0,26 0,01											5,81 0,08	
<u>Cotoneaster pannosa</u> (Cotoneaster)	0,23 0,01					0,06 0,06		3,27 0,13					
<u>Ipomoea nil</u>	0,22 0,01										1,92 0,03		
<u>Stephania abyssinica</u>	0,19 0,01						2,09 0,10						
<u>Bidens biternata</u> (Blackjack)	0,19 0,06				1,59 0,13	0,05 0,25	tr. 0,10	tr. 0,25				0,13 0,08	
<u>Physalis peruviana</u>	0,12 0,03				0,07 0,25		0,72 0,10	0,76 0,25					
<u>Drougetia urticaefolia</u>	0,12 0,01									1,44 0,05			
<u>Cirsium vulgare</u>	0,12 0,01							1,72 0,13					
<u>Duchesnia indica</u>	0,10 0,01			1,11 0,13									
<u>Melia azedarach</u> (Syringa)	0,08 0,01				0,69 0,13								
<u>Lilium regale</u>	0,06 0,01				0,55 0,13								
<u>Rumex sagittatus</u>	0,05 0,01												0,49 0,14
<u>Galopina circaeoides</u>	0,05 0,03		0,65 0,08								0,02 0,03	0,09 0,15	

TABLE C.3 continued

Species (Common name)	Over- all	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
<u>Moraea</u> sp.	0,04 0,02								0,42 0,08	0,05 0,05	0,09 0,03		
<u>Cupressus lusitanica</u> (Cypress)	0,03 0,04		0,13 0,08		0,07 0,13			0,06 0,38		0,11 0,05			tr. 0,07
Bryophytes	0,03 0,04		0,26 0,15		0,07 0,13						0,03 0,09		
<u>Leucosidea sericea</u> (Oldwood)	0,02 0,01		0,03 0,08					0,29 0,13					
<u>Acalypha schinzii</u>	0,02 0,03										0,02 0,03		0,16 0,21
<u>Cryptomeria japonica</u> (Japanese cedar)	0,01 0,01							0,09 0,13			0,03 0,03		
<u>Taraxacum officinale</u> (Dandelion)	0,01 0,01			0,09 0,13									
<u>Protoasparagus devenishii</u>	0,01 0,04					tr. 0,06	0,11 0,20		tr. 0,08	tr. 0,05	tr. 0,03		
<u>Phaseolus vulgaris</u> (Common bean)	0,01 0,02								0,06 0,08		0,09 0,06		
<u>Trimeria grandifolia</u>	0,01 0,01					0,04 0,06							
<u>Andrachne ovalis</u>	0,01 0,01			0,16 0,13									
<u>Calpurnia aurea</u> (Wild laburnum)	0,01 0,01									0,10 0,05			
<u>Momordica foetida</u>	tr. 0,01							0,03 0,13					
<u>Gnidia puchella</u>	tr. 0,01		0,03 0,08										
<u>Pteridium aquilinum</u> (Bracken fern)	tr. 0,07			tr. 0,13	0,02 0,13	tr. 0,25	tr. 0,10		tr. 0,08			0,02 0,15	0,02 0,07

*tr. - indicates trace (< 0,01%)

APPENDIX D

CAPTURE, MARKING & RADIO TRACKING

D.1. INTRODUCTION

The ability to recognise individual animals is a prerequisite to the monitoring of the social and spatial organisation exhibited by that species. Furthermore, recognition of specific individuals may facilitate studies concerning growth and development (e.g. Allen-Rowlandson 1980), the determination of mortality rates (Chapter Four), aspects of reproduction (e.g. age at first parturition, calving intervals etc.; see Chapter Five), assessments of habitat utilization and preference (Chapter Seven), and estimates of population numbers (e.g. the Petersen estimate; see Chapter Nine). Recognition of individual *Tragelaphids* based on natural markings has been accomplished by Jacobsen (1974), Leuthold (1974, 1979), Waser (1975a, 1975b), Allsopp (1978) and Owen-Smith (1984). Such an approach was impractical at Weza due to the largely nocturnal activities of this species, the dense nature of much of the vegetation, and because few animals were habituated to vehicles or humans and so consequently usually moved off as soon as they were encountered. Such an approach was also totally unsuitable for duiker as these antelope possess no distinguishing characteristics other than markings caused by injuries (such as broken horns, torn ears etc). This problem was therefore solved in part by applying artificial marks to animals in the form of conspicuously coloured and specifically coded collars, when only the neck of the animal needed to be observed to ensure recognition. Such marked animals were rarely seen during the day however, and could not be detected in dense vegetation. Radio tracking was therefore employed as an additional aid, since this technique obviates the problems of differential visibility and greatly facilitates the monitoring of animals in more inaccessible areas.

Both these methods of marking individual animals necessitated capture of the subjects, and numerous techniques

for ungulate capture have been described (Pienaar 1973a, 1973b; Harthoorn 1976). Several of these had to be extensively adapted to suit the conditions at Weza, and cognizance of the value that marked animals could have to the success of this project led to considerable attention being given to these aims; the costs in effort and finance may not be warranted in other studies or areas.

D.1.1 Previous Studies

Odendaal (1977) fitted five radio transmitters (designed and built by the CSIR, Pretoria) on bushbuck in the southern Cape, to facilitate studies on habitat preferences and spatial organisation (Odendaal and Bigalke 1979a, 1979b). These animals had been caught in nets which were situated in or around patches of indigenous forest.

Wilson (1967) employed drug immobilization techniques to remove unwanted captive or semi-captive duiker from households in Zimbabwe. The immobilizing drug principally used was etorphine hydrochloride (from 0,1 mg to 0,4 mg per animal), although varying amounts of chlorpromazine hydrochloride were also used. Wilson (1967) succeeded in capturing 34 duiker using this technique, of which two animals died.

D.2 METHODS

D.2.1 Capture

Earliest attempts to capture animals involved the use of drop nets and box traps (e.g. Hawkins et al. 1967). Wooden frames approximately 3m x 3m were covered with nylon netting and suspended by means of ropes and pulleys over selected game trails. These drop nets were activated by a trip wire and the box traps by a tilting platform (floor); the trigger mechanisms for both these traps resembled those described by Taber and Cowan (1969). Neither of these methods proved

successful, and because the drop nets had to be constantly attended to whenever activated, these were abandoned in favour of drive nets which were used in April and September 1981 (e.g. Silvy et al. 1975; Beasom et al. 1980; Smith 1980). Game nets (100-150 mm mesh size) were strung 1,5-2,5 m above the ground on stakes, vegetation or light wire clips attached to trees. The lower portion of the nets were arranged so that their base draped over the ground forming an apron (Pienaar 1973b). A funnel effect was achieved by placing "wings" of opaque plastic sheeting at right angles to each end of the net. Animals were driven towards the net by approximately 30 inexperienced beaters, and in the September operation six leashed beagles lent by a local hunt club were also used. (A similar approach was adopted by Bramley (1966) cited in Zwickel (1969) to capture roe deer). Up to six experienced handlers were concealed close to the net so that entangled animals could be quickly restrained. Insufficient numbers of handlers resulted in several animals escaping through collapsed sections of the net, but the inclusion of more, inexperienced personnel led to animals either being roughly treated (resulting in the paralysis of one adult female bushbuck) or inadequately restrained, which put other handlers at considerable risk. This method was successful only in indigenous forests, (five bushbuck in four days in April; three bushbuck in four days during September), presumably because of the greater cover afforded in such areas (so that animals did not leave the vicinity while nets and plastic were being erected). Further limitations of this method included the fact that netting is not selective with respect to sex or age class (an important consideration when fitting collars, particularly radio collars, of predetermined size), the operations required considerable manpower and were therefore expensive, while the hiring of experienced staff and equipment depended entirely on the capture schedule and commitments of the Natal Parks Board. As a result of these restrictions an alternative form of netting was devised for duiker that involved a maximum of three personnel. A localised food resource (approximately 1,0 ha of Mexican hawthorns) was completely surrounded by nets that were hung on available vegetation or old fences or suspended from

tripods made from gum samplings, again with an apron on the ground. During the day several sections of the net were hooked up along distinct paths thereby permitting free access in and out of the Mexican hawthorn stand. At night these sections of nets were dropped and the sealed area was then systematically searched on foot; any animals encountered were flushed into the nets. Prior to resetting the enclosure was also surveyed by spotlights to ensure that no animals had been missed. The nets were again inspected early the following morning before being raised for the remainder of the day. One bushbuck and twelve duiker were caught in this manner between August and November 1981. Although this method did not require extensive labour, the nets had to be checked at least twice daily to ensure that undisturbed animals had not become entangled in the dropped sections of the net. This procedure proved to be too time consuming and instead cannon-netting (e.g. Hawkins et al. 1968; Twigg 1975) was considered. Small plots, approximately 0,3-0,5 ha in size were planted with vegetables and fodder crops in open grassland areas. Unfortunately, legislation prevented my use of detonators (classified as explosives) and despite repeated efforts, suitably qualified personnel could not be found to operate this equipment. These planted areas did however, attract substantial numbers of antelope and proved to be of considerable value when the last and most successful method of capture, namely drug immobilization, was employed.

Possibly the greatest benefit offered by drug immobilization is that it allows selection of specific animals in or adjacent to areas and habitats of interest to the researcher. The major problem associated with this technique involves locating the immobilized animal, particularly in habitats with a closed canopy where the use of a helicopter is impractical. Problems of detection are further compounded when the subjects are largely nocturnal. Thus, before drug immobilization could be used as a successful capture method at Weza, some means of detecting immobilized bushbuck and duiker at night had to be devised. This problem was solved by the use of beagles which had been trained for hunting purposes on neighbouring farms. (Merriam

(1962) and Hill (1966) both cited in Zwickel (1969) also found dogs to be extremely useful in trailing drugged animals). In order to prevent injury either to the immobilized animal or to the hounds prior to induction, the beagles were leashed when tracking and removed from the scene once the immobilized animal was found. Several hounds were used during the course of this study but those that were the keenest and most independent hunters were generally best suited for this work. Initially, darted antelope were tracked by a pair of hounds controlled by two handlers, but with experience one dog was found to be adequate. I trained my own beagle by allowing it to follow older, experienced dogs on the scent of darted antelope for two months, and from May 1983 onwards (when the beagle was five months old) this dog was used exclusively until capture operations were terminated in July 1984. With experience it was found that detection of the darted antelope depended on when the beagle was offered the scent. Bushbuck in open areas tended to run for cover as soon as they were darted, and unless the precise location where the antelope entered dense vegetation could be observed, it was advisable to commence tracking as soon as possible. Immediate tracking also yielded best results when several animals were observed in the same area. However, when bushbuck were darted in thick vegetation they rarely ran for more than 50-100 m unless chased by the dog prior to induction, so in these instances a time interval of 5-10 minutes between darting and introducing the beagle to the scent usually ensured detection of the animal in close proximity to the vehicle and equipment. Duiker invariably ran off after being darted and the hound was employed as soon as visual contact with the darted animal was lost.

Darting equipment used to test the feasibility of this method in September 1981 was lent by the Natal Parks Board and consisted of a carbon dioxide powered "Cap-Chur" (Palmer) gun and automatic projectile syringes (darts) of 3 ml capacity fitted with barbed needles 2,8 cm long. Thereafter a powder-charged "Capchur" rifle, considered to be of greater utility, and 2-3 ml darts with 1,8-2,8 cm needles were used throughout the study. The rifle was fitted with a telescopic

sight suitable for use at night (the sighting mechanism consisted of a light emitting diode) and had two specially constructed adaptors to reduce the velocity of the dart. The short-range adaptor used with a 1,25 grain blank (0,22 calibre) had an effective range of 5-15 m while the long-range adaptor in conjunction with 2,0 grain blanks had a range of 30-50 m. Animals at intermediate distances were darted using a combination of the short-range adaptor and 2,0 grain blanks or the long-range adaptor and 1,25 grain cartridges. The trajectory of darts propelled by local blanks was highly variable and imported ammunition proved to be much more consistent. With the exception of one animal darted by a Natal Parks Board official, only one marksman was used during this study (for safety reasons and to minimise dart losses). On all but two occasions animals were darted at night, with the aid of spotlights, from the back of an open truck, or more rarely, on foot. Whenever possible animals were hit in the hindquarters but when the rear of the animal was hidden a dart was aimed at the shoulder region. Animals were rarely darted over distances exceeding 50 m since it was extremely difficult to ascertain if the target had been hit at this range at night. Thin bands of reflective tape were however stuck around the tail section of each dart to facilitate detection.

The immobilizing agents selected for bushbuck and duiker capture were etorphine hydrochloride ("M99", Reckitt), xylazine hydrochloride ("Rompun", Bayer) and azaperone (Janssen). Detailed pharmacological descriptions of these drugs have been given by Harthoorn (1973, 1976). Etorphine was used at a concentration of 1 mg per ml of buffered solvent, xylazine at 50 mg or 100 mg per ml of solvent and azaperone at 100 mg per ml. Syringes were filled with additional buffered solvent where necessary. Antidotes administered were nalorphine hydrochloride ("Lethidrone") at 10-20 mg per ml and diprenorphine hydrochloride ("M5050", Reckitt) at 4 mg per ml. These were given either intramuscularly or intravenously into the recurrent tarsal vein, or more commonly, into a convenient ear vein. Dart wounds were treated with a commercial wound aerosol and

"Terramycin" (Pfizer) and animals suffering from any cuts or lesions were given intramuscular injections (approximately 2 ml) of long-acting penicillin ("Compropen").

Once the darted animal was found by the beagle and handler, he either directed the remaining capture team to the animal by calls or, if nearby, left an illuminated torch next to the immobilized animal and brought the beagle back to the vehicle. Two-way radios were used in an attempt to speed up the arrival of the capture team but due to problems in describing precise locations at night, these were of little value. When the animal had travelled several hundred metres before collapsing, all the equipment was carried by vehicle to the nearest road or track, and then taken on foot. Occasionally immobilized duiker and female bushbuck were carried by hand to a more convenient site before being processed. Inaccessible animals were therefore usually immobilized for longer periods than readily accessible ones, although this period was also reduced as members of the capture team became more familiar with the intensive study areas. As soon as an immobilized animal was encountered it was placed in sternal recumbency to prevent bloating or inhalation of rumen contents.

Field data were recorded on standardized forms during all capture programmes. The following were noted: drug dosage, time darted, time found, antidote dosage, time antidote administered and time the animal recovered (i.e. standing), standard body measurements, age assessment (from tooth replacement or wear patterns), condition and external parasite loads (both assessed subjectively), visible reproductive parameters (i.e. mammary gland status and the presence of any large foetus), initial position when first observed, release site, distance travelled by animal, details of capture equipment and range when darted, climatic conditions, group size and composition, and collar details. Time intervals were recorded to the nearest 0,5 minute.

D.2.2 Marking

All released bushbuck and duiker were fitted with conspicuous, individually identifiable collars made from two or three ply machine belting. Collar widths ranged from 6 cm (duiker and some female bushbuck) to 9 cm (female and male bushbuck). Male bushbuck collars were between 55 cm and 65 cm long, while lengths used for female bushbuck and duiker averaged 40 cm and 35 cm respectively. Collar construction follows Allen-Rowlandson (1980) and Brooks (1981) in that "Sterkolite" (a tough polyvinyl plastic material reinforced with nylon thread) was secured to the belting by contact adhesive and pop rivets. Symbols were cut out from another contrasting layer of "Sterkolite" which was then placed on top; this provided the general colour of the collar while the symbol colours were provided by the exposed underneath layer of "Sterkolite". Potential confusion of collars in the field was reduced by using only a limited variety of letters and numbers (see Allen-Rowlandson 1980) and by making extensive use of clearly identifiable, large symbols such as horizontal or vertical stripes etc. (carefully considered colour combinations further reduced any ambiguity). Additional symbols were made from reflective adhesive tape ("Scotchlite") which was also used by Ealey and Dunnet (1956) and McIlroy (1976). These reflective symbols proved to be extremely effective at night but peeled away from the "Sterkolite" in time. This problem was solved by sticking the tape to thin (1 mm) sheets of aluminium and then cutting the required symbol from these which in turn were fastened to the collar by rivets. Five colours of reflective tape were commercially available and carefully considered symbol designs (records were maintained of all details of collars fitted to animals in the field) and colour combinations again reduced similarities.

Collars were fitted to animals by means of nuts and bolts or pop rivets. Numbered steel ear tags ("Ketchum" tamperproof cattle tags) were fastened on all captured animals. Although of no aid to field identification, ear tags were used as a precautionary measure in case collars

deteriorated beyond recognition during subsequent capture programmes or, indeed as happened, if collars were purposely removed from animals that had been illegally hunted.

Except for the inclusion of the transmitter package and antenna, radio collars were constructed in an identical manner. Individual-specific markings facilitated the identification of the subject when visual contact was required or when animals were observed at times other than when radio tracked. In addition, these markings permitted identification of animals required for recapture purposes once transmitters had ceased to function.

D.2.3 Radio Tracking

The first 14 transmitters used in this study were built by or under the guidance of the Department of Electrical Engineering, University of Natal. These were slightly modified versions of transmitters designed by R. Martin (pers. comm.). Each transmitter emitted a pulsed signal in the 73 MHz band and was powered by two 9 volt manganese alkaline batteries connected in parallel (with a rated capacity of 1000 milliamp hours) yielding an estimated field life of approximately 200 days. All of these transmitters had a rather restricted range and of the 13 recovered, six had ceased transmitting due to moisture in the circuitry or resistor failures. Consultations with a private concern (Ron Tomlin & Co.(Pty.)Ltd.) led to the development of a further modified and smaller transmitter (5cm long, 2 cm wide and 1,5 cm tall). Two of these prototypes were tested in the field and were found to have a much improved range. All of the subsequent 101 transmitters used in this study were of this latter design and were constructed by the author. A straight whip antenna proved to be impractical for either bushbuck or duiker and instead the antenna was curved around the collar and protected between the belting and "Sterkolite". Transmitter antenna length was determined using Amlaner's (1980) formula and was either one eighth or one sixteenth of a wavelength for bushbuck and duiker respectively. This

latter length resulted in a marked reduction in range but was unavoidable due to the small neck circumference in this species. (A girth harness incorporating a transmitting antenna of one eighth wavelength was designed for use on duiker but was not readily accepted by these animals and was therefore abandoned). In the absence of any sophisticated equipment at the field station, all transmitters were tuned by hand and tested with the receiving equipment before encapsulation. Because the circuit was of high impedance, low leakage potting compounds were used with polyurethane foam proving to be the most suitable. Excess foam was trimmed from the transmitter when dry and the transmitter was then sealed either in silicon rubber or placed in a specimen tube sealed with silicon rubber. Retuning was occasionally necessary before the application of a generous protective coating of either fibre glass resin or dental acrylic. In order to reduce the mass of the transmitter package, some transmitters were sealed in tubes made from P.V.C. conduit, and although sealed with adhesive putty, moisture penetrated all of these causing short circuits or component failure and this practice was discontinued. Batteries were also sealed in resin and initially were housed separately from the transmitter to facilitate battery replacement. It was extremely difficult to protect such a system from moisture however, and all subsequent transmitters were sealed together with the power supply. Potential disconnection of wires through movement of the batteries was prevented by binding these in resin, or more usually in much lighter polyurethane foam. Collars containing radio transmitters were made of the same materials as conventional collars. The pre-sealed transmitter and batteries were mounted between two layers of belting (one being the actual curved surface of the collar), which were secured at either end by pop rivets. These two layers effectively clamped the transmitter package; resin or dental acrylic was then poured into this mould as a protective filler and entirely enclosed the package and batteries. Machine screws at least 15 mm long protruding into the mould prior to filling ensured adequate anchorage of the package.

Although the current drain of the modified transmitters was not determined, it certainly exceeded that of the earlier models and the two 9 volt (Mn 1604) batteries never provided a field life in excess of 150 days. To overcome this problem, 1,5 v manganese alkaline batteries with a rated capacity of 1800 to 5000 mAh (depending on size) were connected in series. Limited supplies of imported lithium batteries were also used in series but surprisingly had a lower performance than commercially available manganese alkaline models. The mass of the entire radio collar varied according to size, battery type and number etc.

The receivers and earphones used in this study were manufactured by W.R.S. Electronics in Zimbabwe (Model NP 62). Each of these provided 128 channels in 2,5 KHz spacing from 73,400 MHz to 73,720 MHz. Transmitters were a minimum of 5 KHz apart (usually a 10 KHz separation) to ensure that confusion from signal overlap did not occur. An important feature of this model of receiver was variable front end attenuation which permitted accurate direction sensing at ranges from a few metres to several kilometres. In addition, this facility was used as a tuning indicator when peaking the transmitter at the field station where other instrumentation was not available. The two receiving antennas (built by the Department of Electrical Engineering at the University of Natal) were horizontally polarised three element Yagis with the driven element consisting of a folded dipole. These half wavelength antennas (length of the reflector was 205 cm) were mounted on specially constructed rotating stands. Bearings were read by means of a pointer attached to the rotating mast and a fixed compass rose (a 360 degree protractor) at the base of the stand, and were usually taken using the null-average method or occasionally by the loudest signal method (Springer 1979). When bearings were recorded from and with reference to known topographical or geographical points, this method obviated the use of a compass which was considered to be unreliable if used in close proximity to a vehicle or other structures that would locally influence the magnetic field. Although the antenna stands were portable, these were usually kept at two base stations approximately

1150 m.a.s.l. and a third collapsible and detachable stand was built for vehicle use. The two base tracking stations were approximately 2 km apart and situated so that the majority of simultaneous bearings in the intensive study area during the first year of operation intersected at approximately 90 degrees. Furthermore, the majority of animals were tracked at distances within 2 km. Both these practices improve the accuracy of the system (Heezen and Tester 1967; Tester 1971; Springer 1979).

Bearings were taken simultaneously either by two-way radio communication or pre-arranged schedules whenever assistance was available, but when all the bearings were taken by one operator, a time lapse not exceeding 30 minutes occurred between the taking of two consecutive bearings for any individual animal. Since neither bushbuck or duiker ranged over large distances or moved at a rapid rate (see Chapter Eight), this unavoidable delay was considered to be of minor importance (also see Tester et al. 1964; Macdonald and Amlaner 1980). All bearings used in this study were recorded by operators thoroughly experienced with the equipment and who had managed to locate and retrieve transmitters purposely hidden in the field. As the number of animals fitted with radio collars increased, it became more practical to obtain simultaneous bearings from one fixed station and from one of several sites that were easily accessible to a vehicle. Choice of site for individual animal bearings depended on a number of factors including signal strength, intersection angles etc. The strength of the signal and therefore to a certain extent the proximity of the subject, could be rapidly determined by use of a quarter wavelength omnidirectional whip antenna mounted on the vehicle. This obviated the need to erect and dismantle the stand and unwieldy Yagi antenna until such times when a bearing was required. The whip antenna also facilitated the general detection of "lost" animals where signals were inaudible at the most strategically placed tracking sites, and was also employed to check if a transmitter that had not been heard for some time was still functional if the animal was observed during other research activities.

Unusual locations of radio collared animals determined by triangulation were investigated on foot. The conventional receiving aerials were usually too cumbersome for this purpose. Instead, use was made of more portable equipment consisting of either a tuned loop antenna with a diametrically mounted telescopic aerial or a collapsible dipole antenna which was based on a design by Parish (1980) but modified for use at 73 MHz using Amlaner's (1980) formula. Similarly, this equipment was used to locate animals when pairs of simultaneous bearings indicated immobility for several days and therefore the possible demise of the subject.

All bearings were plotted by protractor on Forestry maps (1:12 000 scale) with a superimposed grid at 1 cm (120 m) intervals. Each map was numbered and the longitudinal axis of the grid was marked alphabetically and the latitudinal grid numerically. Since animal locations determined by radio triangulation are rarely discrete points (Heezen and Tester 1967; Springer 1979), each grid square was further divided into four equal quadrants which were denoted by lower case letters (a,b,c and d). Each radio determined position was therefore detailed by reference to the number of the map, the grid square and one of 60 m x 60 m quadrants. Where two vegetation types occurred within any specified quadrant, the one occupying the greatest area of the quadrant was listed as the habitat being used by the subject at that particular time.

D.3 RESULTS AND DISCUSSION

D.3.1 Capture

A total of 74 individual bushbuck (40 males and 34 females) and 38 duiker (21 males and 17 females) were captured either by nets or drug immobilization, and radio transmitters were fitted to 77% and 21% of these animals respectively (Table D.1). Bushbuck were captured on 139 separate occasions; each animal was caught an average of 1,9

TABLE D.1 A summary of bushbuck and duiker capture and marking details at Weza between April 1981 and July 1984.

Capture and marking details	Bush-buck	Duiker	Total
No. of animals caught in nets	9	12	21
No. of animals immobilized	65	26	91
Total no. of animals captured	74	38	112
No. of times caught in nets	9	12	21
No. of times immobilized	130	31	161
Total no. of times captured	139	43	182
No. of animals fitted with transmitter	57	8	65
No. of times transmitter fitted	109	8	117

times (range = 1 to 7) and all recaptures were by drug immobilization, thus demonstrating that the technique was repeatable. Due to problems associated with transmitters and reduced resighting rates (see below), duiker were captured/recaptured less frequently (on 43 occasions) at an average of 1,1 times per animal (range 1 to 3 times).

Netting accounted for 13,8% and 31,6% of the total number of bushbuck and duiker caught respectively, but only 6,5% and 27,9% of the total number of times bushbuck and duiker were captured (see Table D.1). One animal (an adult female bushbuck) had to be destroyed after a zealous but inexperienced handler had broken its back. This death represents a mortality rate of 4,8% using nets.

Drug immobilization resulted in the capture of 65 bushbuck on 130 occasions (Table D.1) between September 1981

and July 1984. Details of drug combinations used are listed in Tables D.2 and D.3. Bushbuck were successfully immobilized with the contents of a single dart on 121 occasions; the analgesic-neuroleptic combination of etorphine and xylazine hydrochlorides was most commonly used. Initially males were immobilized with a combination of 1 mg "M99" and 50 mg "Rompun" while 0,75 mg "M99" and 50 mg "Rompun" were adequate for female bushbuck. Since there were no published accounts of recommended dosages for bushbuck, these amounts were derived (by approximate mass ratios) from dosages used to immobilize the congeneric kudu (Allen-Rowlandson 1980). However, different doses for males and females meant that loaded darts intended for males had to have some distinguishing mark or be kept separate from those for females. This practice also necessitated the filling of at least two darts (more if duiker were required, see below) on every darting occasion, without any guarantee that even one of these would be used. Finally, the time spent in inserting the appropriate dart in the gun once a suitable animal had been observed often negated any element of surprise the marksman might have had, while the noise associated with this action frequently caused the target to flee out of range. To overcome these difficulties darts with a standardised analgesic dose were used. Since 0,75 mg "M99" proved to be inadequate for the immobilization of adult males (see Table D.3; two other males darted with 0,75 mg "M99" and 50-100 mg "Rompun" showed signs of ataxia but never collapsed and could not be redarted), all bushbuck irrespective of sex and age darted after March 1982 (n=114) received 1,0 mg of "M99" and, most frequently, 50 mg of "Rompun" with no evidence of overdosing. This dose was only reduced when it was necessary to redart an animal to induce immobilization (Table D.3). Although a dart with this standardised dose was inserted into the gun at the onset of a catching exercise, for safety reasons the adaptor and appropriate blank cartridge were loaded only when an animal was observed within range of the marksman.

Induction times could not be accurately determined since animals were frequently out of view when they became

TABLE D.2 Single doses of 121 free ranging bushbuck immobilized with combinations of Etorphine Hydrochloride (M99), Xylazine Hydrochloride (Rompun) and Azaperone.

Sex	No. of Bushbuck	M99 (mg)	Rompun (mg)	Azaperone (mg)
Males (n=69)	2	1,0	20	0
	4	1,0	40	0
	55	1,0	50	0
	2	1,0	100	0
	2	1,0	0	50
	2	1,0	0	100
	2	1,5	75	0
Females (n=52)	3	0,75	50	0
	1	0,75	0	50
	1	1,0	20	0
	2	1,0	40	0
	44	1,0	50	0
	1	1,0	0	50

TABLE D.3 Double doses of nine bushbuck immobilized with combinations of Etorphine Hydrochloride (M99), Xylazine Hydrochloride (Rompun) and Azaperone

Sex	Contents (mg) of 1st dart			Contents (mg) of 2nd dart			Time interval between administering 1st & 2nd darts (mins)	Time interval between administering 2nd dart & immobilization	Reason for redarting *
	M99	Romp	Azap	M99	Romp	Azap			
F	1,00	0	100	1,00	0	100	47	4	1
	1,00	50	0	0,50	50	0	33	15	1
M	0,75	0	50	0,75	0	50	18	12	2
	1,00	50	0	0,75	50	0	98	6	3
	1,00	50	0	1,00	50	0	90	4	1
	1,00	50	0	1,00	50	0	109	7	1
	1,00	50	0	1,00	50	0	65	7	1
	1,00	50	0	1,00	50	0	61	3	1
	1,00	50	0	1,00	50	0	59	15	1

* - 1 = Partial dose; 1st dart bounced off animal
 2 = Initial dose inadequate
 3 = Animal recovering from initial dose when found by dogs

immobilized. Instead, the time interval between time of darting and the time the animal was found was noted for 125 darted bushbuck and averaged 17,98 minutes ($\pm$ 20,65 (S.D.), range = 3 - 115) minutes. The mean time for darting to recovery was 53,78 ($\pm$ 25,76 (S.D.), range = 21 - 130) minutes, while the difference between these two periods, 35,80 ($\pm$ 16,89 (S.D.), range = 14 - 76) minutes, indicated "handling" time which included the transportation of marking equipment to the recumbent animal, processing it and the recovery time. The mean recovery time (i.e. the interval between administration of the antidote and when the animal managed to stand) of animals given intravenous antidotes was almost half that of those given antidotes intramuscularly, ($\bar{x}$ = 3,25 $\pm$ 1,92 mins, n = 75 and $\bar{x}$ = 6,23 $\pm$ 2,39 mins, n = 39 respectively). Intravenous injection was preferred whenever possible in this study once it was established that equipment could be retrieved and personnel could retire to a safe yet observable distance during recovery time. Intravenous injection would also be advisable where natural predators are common.

A total of 26 duiker were successfully captured on 31 occasions (each with the contents of a single dart) using similar drug combinations to those administered to bushbuck. Initially Wilson's (1967) suggested dosage of 0,4 mg "M99" was used together with 20 mg "Rompun" but this was found to be totally inadequate for both males and females. Only one of four duiker darted with this combination was captured, somewhat fortuitously, after it had fallen into a river and even though ataxic, this animal had to be manually restrained during the entire marking process. Female bushbuck doses of 0,75 mg "M99" and 50-75 mg "Rompun" or 50 mg azaperone were given to five duiker and all were immobilized successfully (Table D.4). However, for reasons of convenience detailed above, this dose was subsequently increased to 1,0 mg M99 and varying quantities of "Rompun" or azaperone (see Table D.4) without any deleterious effects to any of the darted duiker irrespective of sex and age. As with female bushbuck, it should be stressed that doses lower than 1,0 mg or even 0,75 mg M99 may be adequate for the immobilization of this

TABLE D.4 Single doses of 31 free ranging duiker immobilized with combinations of Etorphine Hydrochloride (M99), Xylazine Hydrochloride (Rompun) and Azaperone.

Sex	No. of Duiker	M99 (mg)	Rompun (mg)	Azaperone (mg)
Males (n=18)	1	0,75	75	0
	1	0,75	0	50
	5	1,0	0	50
	2	1,0	0	100
	1	1,0	20	0
	8	1,0	50	0
Females (n=13)	1	0,4*	20	0
	2	0,75	50	0
	1	0,75	0	50
	3	1,0	0	50
	2	1,0	0	100
	4	1,0	50	0

* - 0,4 mg M99 considered inadequate for adult male or female duiker.

species; the objective of this aspect of the study was simply to find an efficient, safe and reliable form of capture rather than the determination of threshold values for immobilization. The fact that Wilson's (1967) animals were tame or semicaptive might account at least in part for the contrasting results using 0,4 mg M99. Although Wilson (1967) reported that females reacted much more satisfactorily to M99 than males, there were no obvious differences between the sexes in the efficacy of the drug combinations and dosages used in this study.

Once darted, duiker were usually found sooner than bushbuck ($\bar{x} = 11,71 \pm 6,04$ mins (S.D.), range = 3 - 32 mins, $n = 28$) but these time differences were not significant ($t = 1,587$; d.f. = 151), and were probably due to the immediate searching for this smaller antelope. Similarly, the average time to find, mark and release darted duiker was of shorter

duration than for bushbuck ($\bar{x} = 46,90 \pm 17,01$ mins (S.D.), range = 27 - 89 mins) but again not significantly so ($t = 1,347$; d.f. = 151).

It also became increasingly more difficult to dart animals that had been captured on previous occasions as these individuals became more wary and increased their flight distances when illuminated by spotlights. Opinions regarding what constituted a reasonable darting opportunity therefore altered during the course of the study, particularly since the potential loss of darts and/or drugs was partially offset by the costs involved in repeatedly searching for these individuals. Dart losses were however, reduced by placing one pole at the position where the dart was fired and another where the target had been, and continuing the search for the dart during daylight hours. Using this technique, only 17,9% of all darts used were lost (Table D.5).

The overall proportion of darted animals found by beagles was 78,0%. Hounds used prior to May 1983 had a success rate of 73,3% but this increased to 83,3% when a young beagle specifically trained to follow darted animals was used exclusively from May 1983 onwards (Table D.5). Additional factors aggravated the problems of detection (Table D.5) and it is highly probable that one or several of these influenced every occasion when animals were not retrieved after May 1983. Darts bouncing off the target was a common cause of capture failure and also necessitated the redarting of seven animals (Table D.3). It was not always possible to avoid glancing shots, while bounce-offs (and damaged darts/needles) may also have resulted from excessive velocity caused by poorly judged distances (see Woodford et al. 1972; Drager et al. 1976). Because of their smaller size, greater care was required in darting duiker and these were usually hit at significantly shorter distances than bushbuck. The long range adaptor was therefore rarely used on this species, particularly since few animals were required for recapture. This additional care in dart placement and a generally reduced dart velocity was probably responsible for the fact that bounce-offs were not witnessed, nor did any

TABLE D.5 Darting details during the drug immobilization of 130 bushbuck and 31 duiker in Weza State Forest.

Details of Darts Fired	
No. of shots fired	290
No. of hits	218
% of hits	75,2%
No. of misses	72
% of misses	24,8%
No. of darts recovered from hit animals	182
No. of darts recovered from misses	56
% of darts recovered	81,4%
No. of darts not recovered from hit animals	36
No. of darts not recovered from misses	16
% of darts lost	17,9%
DETAILS OF HIT ANIMALS & DETECTION BY HOUNDS	
No. of hit animals detected by beagles	170
No. of hit animals not detected by beagles	48
% detected by beagles	78,0%
No. of hit animals detected prior to May 1983	85
No. of hit animals not detected prior to May 1983	31
% detected prior to May 1983	73,3%
No. of hit animals detected from May 1983	85
No. of hit animals not detected from May 1983	17
% detected from May 1983	83,3%
POSSIBLE REASONS FOR HIT ANIMALS NOT DETECTED	
Dart bounced off	9
Dart penetrated - poor placement	7
Dart/needle broken	5
Two or more animals in a group	5
Initial dose insufficient	5
Individual animal resistance	2
Unknown causes (e.g. animal possibly not hit)	15
Overall success rate (no. of animals immobilized and detected/no. of shots fired)	58,6%
No. of shots for each successful immobilization	1,7

duiker require the contents of a second dart to induce immobilization (Table D.3). The subsequent recovery of darts from bushbuck initially darted several hours or days previously demonstrated that poor dart placement also accounted for several of these recorded failures (Table D.5). Ineffective absorption resulted from darts hitting the rumen region, while needles protruding from the tail, above the hock or from skin on the silhouette of the animal indicated that little or none of the drugs had been injected into the bushbuck concerned. Five darts that had hit the target but failed to immobilize bushbuck were recovered in a damaged state, the most common cause of damage being the needle breaking at the base. Failure to recover darted bushbuck also occurred at the onset of this study when inadequate doses were used, and also occasionally when the darted animal was in close proximity to other conspecifics. This latter problem was frequently solved however by returning to the original site after an unsuccessful search and allowing the dog to recommence tracking. Alternatively, two hounds could be used, with the handlers encouraging each dog to follow separate scents when these were encountered; in such instances independent hunting dogs are preferable to those experienced in pack hunting. One female bushbuck proved to be notoriously difficult to immobilize even with adult male doses (e.g. 1 mg M99 and 100 mg azaperone). She was darted on four separate occasions but captured only on two of these, when manual restraint was also necessary. At both times of capture the ineffective darts were also recovered and had detonated on impact into muscle. None of the needles had been blocked, and because there was no obvious cause of failure, it is assumed that this animal exhibited a greater resistance to the immobilizing agents than did other bushbuck. Reasons for the remaining failures are largely conjectural (Table D.5). Although several of these failures may have resulted from the beagle's inability to track animals over difficult terrain or where scents were confusing (e.g. over sections of burnt grassland) the possibility that failures were also due to a) detonator failure (e.g. see Gasaway et al. 1978; Allen-Rowlandson 1980), b) other dart malfunctions (e.g. blocked needles, plunger penetrated by

detonator, exploded darts (see Woodford et al. 1972; Drager et al. 1976) particularly since darts although carefully examined on recovery were recycled and used repeatedly), c) subcutaneous injection or injection into fat, and d) inaccurate assessments of when an animal was hit etc. cannot be eliminated.

Nine deaths (eight bushbuck and one duiker) were directly attributable to capture by immobilization. Of these, five animals received skeletal injuries due to poor marksmanship and/or excessive dart velocities (resulting from worn and therefore inadequate tail flights) and had to be destroyed (also see Valkenberg et al. 1983). Two other animals died before the antidote could be administered, and the remaining two died within two days of capture (Table D.6). These losses represent a mortality rate during immobilization of 5,6% and 5,5% for the entire capture operation.

Given the conditions of capture at Weza, these fatalities must be considered as acceptable, particularly since the majority of animals were caught in winter or early spring when they were in poor physiological condition (Chapter Four). The relatively low mortality rate is undoubtedly due in part to the wide safety margin (or effective margin; Harthoorn 1976) of etorphine hydrochloride. Darting at night is obviously more difficult than during the day, particularly since ranges are difficult to assess at night; incorrectly estimated ranges undoubtedly resulted in misses and in some instances poor dart placements which necessitated the humane destruction of the subject. Several of these deaths might also have been avoided if it had not been necessary to recapture many individuals; several of these were not seen for several months and thus when encountered were darted at ranges or conditions that would not have been considered under normal circumstances.

Finally, drug immobilization techniques were preferable to and more successful than netting at Weza for several reasons. Firstly, netting proved to be extremely costly,

TABLE D.6 Bushbuck and duiker deaths directly attributable to capture by immobilization techniques (All animals received 1 mg M99 and 50 mg Rompun).

Sex	Age (months)	Dart Site	Details
F	4,5	Neck	Duiker mistakenly identified as adult - range overestimated and animal struck in neck causing immediate paralysis; destroyed.
M	72	Right leg	Right femur broken by dart; bushbuck destroyed.
M	96	Right leg	Right tibia broken by dart; bushbuck destroyed.
F	72	Lumbar region	Bushbuck hit in spine causing immediate paralysis; destroyed.
F	132	Pelvis	Bushbuck hit in dorsal region of pelvis causing immediate paralysis; destroyed
F	72	Right flank	Bushbuck became immobilized while crossing deep section of river and drowned before found by handler and beagle.
M	96	Left flank	Ataxic bushbuck fell down 10 m cliff into shallow river - rescued and recovered with no obvious signs of internal or external injuries; found drowned 500 m away 2 days later.
M	156	Right shoulder	Emaciated bushbuck unattended for 65 mins. prior to detection, repeated coughing during excessive recovery time (13 mins) animal died following day. Speckled liver and copious fluid in thoracic cavity indicative of passive congestion.
F	72	Right flank	Bushbuck in good condition, ran for 50 m and was immobilized within 5 mins, no obvious injuries but died 15 mins after darting (no antidote administered). Cause of death not revealed by post mortem analysis.

largely because of the manpower required (approximate costs in 1982 for each bushbuck caught were R250,00 using equipment lent by Natal Parks Board). Darting exercises were also expensive (unfortunately no details other than drug and dart losses were recorded) with the author and at least one, usually two assistants spending over 250 nights (approximately 6 hours per night and excluding nights when no shots were fired) in capture operations. However, offset against these costs would be the data simultaneously recorded concerning the localities and activities of marked and unmarked animals which made a significant contribution to the studies of habitat utilization and selection, movements, home range evaluation, social organisation and population estimation. Such information was obviously not available during the highly disruptive netting programmes. Secondly, capture by darting permitted a much greater degree of selectivity in terms of both area and individuals, the latter being particularly important when wishing to fit radio collars of predetermined size. Lastly, numerous animals had to be recaptured to recover faulty transmitters and replace these with functional ones. Due to the largely haphazard and opportunistic nature of netting, the only feasible way of achieving this was by drug immobilization. This study has demonstrated that capture by darting is repeatable, admittedly with substantially increased effort and costs.

D.3.2 Marking and Radio Tracking

None of the animals marked in this study lost their collars and all the collars remained clearly identifiable throughout field work. Reflective symbols adhered directly to "Sterkolite" occasionally lasted for more than one year, but when stuck to the aluminium sheeting and then fastened to the collar, usually remained intact for periods exceeding two years, particularly if the symbols (often strips) were fastened across rather than along the longitudinal axis of the collar. One tag was lost from the ear of an adult male bushbuck; both ears of this animal were badly torn, presumably as a result of fighting.

A total of 109 transmitters were used at different times on 57 individual bushbuck, but none of the eight duiker similarly marked had their transmitters replaced (Table D.1). The mass of individual radio collars never exceeded 3% of the average adult live mass for either species, and were therefore well within the limits recommended by Brander and Cochran (1969). Although bushbuck fitted with radio collars showed no overt differences in their behaviour compared to unmarked animals, one duiker showed an initial reaction to a collar weighing 400 g. Fortunately this animal was manually restrained several minutes after release and the offending collar was removed and replaced with a visual collar. It was extremely difficult to construct duiker collars under 300 g however, without some sacrifice to the duration of the power supply (which at best was only 7 months, see below), or adequate protection to both transmitter and batteries. A further complication concerned the circumference of the subjects neck, which limited the length of the transmitting antenna to one-sixteenth wavelength. (Attempts to increase this to one-eighth wavelength by coiling the aerial within the collar provided no obvious improvement.) This short length of antenna resulted in a very restricted tracking range (usually not exceeding 500 m) and consequently much time in travelling and searching for these animals was required. As a result of these constraints, together with the fact that marked duiker were seen much less frequently than marked bushbuck (and therefore provided fewer recapture opportunities), data from this species were extremely fragmentary, and all efforts to replace transmitters and continue radio tracking duiker were abandoned in December 1982.

The effective tracking time (field life) of both bushbuck and duiker transmitters was difficult to assess for a number of reasons. Firstly, although transmitters were fitted to animals as soon as possible after they had been constructed, inevitable delays (e.g. due to the weather, the supply of immobilizing drugs, and the opportunities to immobilize a suitable target) occurred between collar

construction and fitting. Since transmitters used in this study were rarely equipped with any kind of switch to conserve power until the collar was fitted, this led to a waste of active or effective transmitter life. Secondly, due to the rather short transmitter life experienced at the onset of the tracking programme, 12 animals were recaptured, when they provided a suitable opportunity, while their collars were still functional. These recaptures were therefore a precautionary measure in an attempt to ensure continuity. Collars transmitting perfectly were also recovered from 18 animals that had died of natural or other causes. All of these transmitters were connected to new power supplies and, if necessary, retuned before being refitted, usually to other animals. Thus the effective time of these transmitters must be regarded as minimal. Similarly, transmitters were recovered from 16 bushbuck that were not working satisfactorily at the time of recapture. The average voltage of the batteries recovered from these transmitters indicated that their poor performance was rarely if ever due to exhausted power (see below). Finally, nine transmitters were still functional at the termination of the field work, and again the field life of these should be regarded as minimal values.

With these considerations in mind, the mean field life expectancy of bushbuck transmitters was at least 111 days (Table D.7). The performance of transmitters obviously improved during the course of the project since the mean effective duration of 81 recovered collars (the majority of which were fitted earlier in the study) was 96 days compared to the 156 days of the 28 collars remaining in the field (Table D.7). This same trend was apparent for both functional and non-functional transmitters (also see a provisional account of initial transmitter performance at Weza in Potgieter 1984). The maximum transmitting time recorded for any collar was 727+ days. This however, does not reflect effective time as the transmitter continued to function after field work was terminated; the animal was killed by dogs in July 1985 at which time the transmitter was still producing a strong signal. The maximum effective time

TABLE D.7 Estimated duration (days) of 109 radio transmitters fitted to bushbuck at Weza.

Transmitters		Transmitting Satisfactorily	Transmitting Unsatisfactorily	Not Transmitting	Total
Recovered	n	30	16	35	81
	$\bar{x}$	125,0	58,8	89,3	96,5
	S.D.	136,6	48,6	75,9	101,3
Still in field	n	9	-	19	28
	$\bar{x}$	254,3	-	114,6	155,9
	S.D.	124,5	-	76,7	111,7
Total	n	39	16	54	109
	$\bar{x}$	152,2	58,8	98,2	111,4
	S.D.	142,9	48,6	76,4	106,7

recorded in this study was 493 days and again, this is a minimal value as the transmitter was still operating at the end of October 1984 when field work was completed.

The mean ($\pm$ S.D.) voltage of recovered batteries was 7,3 v ($\pm$ 1,2 v), 8,4 v ($\pm$ 0,7 v) and 4,1 v ($\pm$ 3,1 v) for collars that were functional, not transmitting satisfactorily and of established termination respectively. The lowest voltage recorded from a functional transmitter was 5,7 v, while power supplies of nonfunctional transmitters varied according to the cause of failure (Table D.8), and in many instances were probably much lower at the time of recovery than when transmitters initially failed, unless the circuits has been interrupted for some reason. Cause of failure was not always easy to establish at the field station due to a lack of sophisticated equipment and expertise. Recovered transmitters not emitting a signal were connected to a fresh power supply and retuned if necessary; if no signal could be detected each of the 27 components were painstakingly

TABLE D.8 Causes of transmitter failure, transmitting time and voltages of batteries recovered from bushbuck fitted with radio collars.

Cause of Failure	n	Transmitting time ($\bar{x} \pm SD$)	Voltage of recovered batteries ($\bar{x} \pm SD$)
Power supply exhausted	13	134,4 $\pm$ 56,9	3,7 $\pm$ 1,7
Component malfunction	10	92,0 $\pm$ 94,8	4,8 $\pm$ 4,0
Ingress of moisture	9	48,7 $\pm$ 40,8	2,6 $\pm$ 3,3
Incorrect tuning	2	8,5	5,1
Loose terminal	1	0,0	9,0
Total	35	89,3 $\pm$ 75,9	4,1 $\pm$ 3,1

removed, one at a time, and replaced with a new counterpart, until a pulsed signal was audible. Suggested causes of failure are listed in Table D.8 although it should be noted that in the particular instance of component failure, this may on occasion have been due to a poor electrical connection or invisible penetration of moisture etc. The most common cause of failure was due to an exhausted power supply; such transmitters performed satisfactorily when connected to a new source of batteries. Transmitting time was greater in these instances than with any other cause of failure. Failures attributed to component malfunction still provided a field life almost twice that of transmitters that failed due to penetration by moisture, which most commonly occurred within two months of fitting. Ingress of moisture most frequently occurred in transmitters that had less protection (in order to maximise on power and yet remain within 3% of adult body mass). The other cause of failure, namely incorrect tuning and loose connections, were undoubtedly due to inexperience during the construction of these models. Similarly, reasons

why some transmitters did not perform well in the field may also be partially attributed to inexperience (particularly with tuning), although other factors were also responsible. These included experimentation with whip antennas, the supply of crystals from three different sources and with possible varying resonances (making it impossible to standardise tuning procedures) and intermittent signals.

Results from duiker transmitters were much more disappointing. Of the six transmitters recovered, five had ceased to function due to exhausted batteries (mean voltage $\pm$ S.D. = $2,6 \pm 1,3$ v) and had yielded an effective life of 31,0 ($\pm 70,4$) days. The sixth transmitter had produced a continuous signal within 24 hours of placement on the subject and this obviously accounted for the depleted voltage of 0,2 v when the collar was recovered. The remaining two collars fitted to duiker were never recovered but had effective transmitting times of 156 days and 212 days.

The fact that any radio tracking system is influenced by several sources of error (Heezen and Tester 1967; Tester 1971; Macdonald and Amlaner 1980) is appreciated. Error arcs usually did not exceed 3 degrees when transmitters were hidden in the field by an independent observer and subsequently tracked by operators thoroughly familiar with the equipment (no locational data were recorded from animals until the author was satisfied with the tracking ability of the various assistants employed in this study). However, for reasons detailed below, the accuracy of tracking radio equipped animals could rarely be evaluated. Errors were nevertheless reduced by following the recommendations of Heezen and Tester (1967), and during the majority of the study by utilizing a mobile receiving station (guided by the operator at one of the base stations through two-way radio communication). Consequently one of the two simultaneous bearings was usually recorded at close proximity (300-500 m) to the subject to maximise accuracy (see Heezen and Tester 1967; Tester 1971; Irwin and Peek 1983) without causing a disturbing influence.

The precision of the technique similarly could rarely be assessed, although the carcasses or collars of 18 animals fitted with transmitters were recovered by tracking. Static signals indicative of immobility were subsequently investigated using portable equipment and collars and/or animals were detected in several unusual locations. These included one collar (cut from the animal) at the bottom of a perennial stream, a drowned animal, a bushbuck hidden under a pile of brush and leaves, two snared animals, a collar thrown into a quarry (the butchered carcass was later identified by the ear tag) and a collar collected by a forest guard and stored in an iron shack. Several other authors have used this technique to home in on their live subjects in order to overcome problems of accuracy associated with these system, movement and topographical errors (e.g. Cumming 1971, 1975; Macdonald 1978; Kenward 1980). However, exclusive use of this technique was impractical at Weza due to the following reasons:

- a) the number of animals involved;
- b) the inability of the operator to travel silently on foot in many of the vegetation types, particularly in timbered areas;
- c) the density of the vegetation which frequently reduced the range of visibility to less than 15 m;
- d) the antipredator behaviour of both bushbuck and duiker (individuals might freeze until flushed, move slowly and silently out of range or simply run off) and;
- e) the largely nocturnal activities of these two species.

Even when it was possible to home in and observe an animal, it was often exceedingly difficult to determine the precise location on a map (particularly in habitats with closed canopies) while the influence of the observer on the recorded position of the subject at the time of sighting

could rarely be evaluated. Consequently, the method was used only to verify (by visual contact) or reject unusual positions determined from triangulation or to establish whether the animal had died; in all other instances triangulation was considered to be the most reliable method for the conditions at Weza despite the potential errors and biases associated with this technique (see Heezen and Tester 1967; Tester 1971; Springer 1979; Amlaner 1980; Macdonald and Amlaner 1980; Morris 1980).

There can be little doubt that radio tracking data provided a significant contribution to this study, even though the methods employed in data collection and transcription were much less sophisticated (due to financial and manpower constraints) than others that have been devised and utilized recently (e.g. Deat et al. 1980; Kolz et al. 1980; Kroll and Johnson 1980; Macdonald and Amlaner 1980; Mauget 1980; Mech 1980). While radio tracking proved to be an invaluable and productive tool at Weza, it would however, be grossly misleading to imply that the operation was highly successful or trouble-free, even if the major problems associated with performance, namely signal strength and life span are excluded. Lance and Watson (1980) have listed several constraints on the user of radio tracking equipment and all of these apply to my experiences at Weza, namely;

- i) the cost and availability of equipment
- ii) breakages and other malfunctions
- iii) the difficulties of effecting repairs or replacements in a field station
- iv) possible adverse effects on the subjects
- v) restrictions in size and weight (and hence performance) of radio collars in order to minimise (iv), and
- vi) the ways in which the decision to use radio tracking can affect the logistics of fieldwork.

Unquestionably, more time and effort was spent on the construction, fitting and replacing of radio transmitters and the subsequent monitoring of radio equipped animals than any other aspect of this study, yet such efforts are not necessarily reflected in terms of the quantity and quality of the results obtained. In hindsight, it may well have been more profitable, both in time and financial terms to purchase more sophisticated and proven transmitters from a commercial source. Admittedly the initial cost of such equipment would have been high (and indeed appeared prohibitively so when these factors were initially considered; the costs of components used to construct transmitters at Weza was approximately R35,00 per unit) but the use of commercially available transmitters may have obviated the need to recover and replace so many faulty transmitters, and hence the necessity of recapture. This could have led to substantial savings in both time and effort, and although a financial breakdown of the costs involved in transmitter construction and replacement and recapture are not available at present, it is highly probable that these costs negated any saving initially proposed by personal construction when the need for radio tracking equipment was first realised.

Breakages and other malfunctions may be minimized to a certain extent by careful handling, but are likely to be experienced in any radio tracking study (e.g. Sargeant 1980). Interruptions in data collection may be avoided by having spare, backup receiving equipment but such investments require additional funds which were not available in this study. Of greater concern was the problems of effecting repairs in the field. Transmitters were repaired largely by trial and error and hence were time consuming (again particularly so if the effort involved in recapture and subsequent replacement is included) while repairs to receiving antennas etc. were relatively easy to perform. The major problem experienced in this study, and frequently causing frustrating but unavoidable delays in data collection, concerned failures in both receivers. These occurred on average every three months and were never

attributable to rough handling; the most frequent causes of failure were associated with the integrated circuits used in frequency synthesis, other component malfunctions and attenuation problems which made direction finding virtually impossible. All of these repairs were very kindly carried out by a private concern (Ron Tomlin & Co.(Pty.) Ltd.); without this interest, goodwill and prompt service the radio tracking aspects of this study would have run into severe difficulties.

Adverse effects on animals equipped with transmitters were minimized by limiting the size and mass of the radio collars. The original transmitters used at Weza were slight modifications of those designed by Martin (pers. comm.) which were intended for use on elephants, where the length of the transmitting antenna and the mass of the power supply is unlikely to be determined by constraints on the size of the subject. Experience has shown that a transmitter operating on a lower voltage (and therefore of lower mass) would be preferable for use on bushbuck and duiker, but again the costs involved in experimentation and development necessary for such a modification were beyond the budget of this study. In addition, the problems of restricted transmitter aerial length could have been solved by using a system at higher frequency (i.e. shorter wavelength, e.g. 150 MHz), but this was impractical at Weza because it would have necessitated a completely new design of transmitter and the procurement of additional receivers. While a system of higher frequency may have resulted in an improved tracking range, this might have led to greater distortion of signals by reflection or refraction however (e.g. Anderson 1971; Tester 1971; Macdonald and Amlaner 1980; Sargeant 1980).

Finally, there is no doubt that radio tracking, and all the activities associated with it, was occasionally carried out at the expense of other aspects of field work. Accidents, predation and transmitter failures all necessitated additional time being spent on replacing transmitters, while every effort was made to check unusual or nonsensical localities. Costs in time and effort may have

been reduced by additional manpower or automated equipment, but either of these would have involved a substantial increase in financial costs which were not available. In addition to the obvious problems associated with the topography and dense vegetation at Weza (see also Tester 1971; Amlaner 1980; Macdonald and Amlaner 1980; Sargeant 1980) difficulties were also experienced when tracking was carried out on windy days, during electrical storms (because of atmospheric noise) and when power lines and telephone wires were nearby, particularly in I.S.A.2, as these caused interference and a marked reduction in range. Furthermore, conditions for tracking in forested areas are far from ideal, as uniform stands of conifers appear to polarize the signal (Macdonald and Amlaner 1980) while horizontally polarized receiving antennas (as used in this study) are less effective in thick forest than vertically polarized ones (Amlaner 1980). However, at the risk of inferring circular reasoning, it is largely because of the problems of topography and the state of the vegetation (together with the fact that both bushbuck and duiker were largely nocturnal and generally elusive) that radio tracking was deemed necessary at the start of this study. It should also be noted that some of these problems were partially offset by the extensive network of roads within the intensive study areas (see Fig. 2.7), thus making most regions relatively accessible.

In conclusion, these detailed discussions concerning the problems experienced with capture and radio tracking should not diminish the value that both techniques provided to the study, but should hopefully dispel any notion that capture by immobilization and data collection by radio tracking is easily accomplished. As Woodford *et al.* (1972) point out, reports concerning the drug immobilization of wild animals all too frequently gloss over, or ignore, the difficulties that are encountered, and the same is certainly true for numerous studies on radio tracking. While radio tracking can provide answers to biological questions which are otherwise unassailable, it should not be undertaken lightly since it is expensive, time-consuming and often frustrating (Macdonald and Amlaner 1980) and should never be considered merely on

the basis of the convenience such a technique may offer (Lance and Watson 1980). While many of the problems associated with radio tracking may be overcome with enough persistence, ingenuity, funding and/or hard work (Mech 1980) experiences gained from this study indicate that such problems are exacerbated when transmitters are personally constructed. Admittedly transmitter performance improved during the study and was probably best just prior to the termination of field work; it would have been much more beneficial if this improved performance had been achieved much earlier. Consequently, much of the funds used in this study were unavoidably spent on the development of a suitable radio tracking system and in providing the constructor with sufficient amateur knowledge and experience. Such a system is not recommended for use in other studies of a similar nature, but if used, at least the researcher should be able to calculate a more realistic budget (both in time and financial terms) than could be achieved in this study.

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