Blue duiker *Philantomba monticola* densities in the Tsitsikamma National Park and probable factors limiting these populations

N. HANEKOM and V. WILSON

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Numbers of blue duikers recorded on 157 and 28 variable width transect counts, done over a two year period in the Tsitsikamma Coastal National Park (TCNP) and Tsitsikamma Forest National Park (TFNP) respectively, did not differ significantly ($P > 0,10$) with seasons (summer v. winter). Population density estimates from transects were similar to those from game drives (0,18 v. 0,19 duikers/ha (TCNP) and 0,13 v. 0,17 duikers/ha (TFNP); $P > 0,10$), higher than from faecal pellet counts ($P < 0,10$) and at least three times lower than estimates from the Kenneth Stainbank Nature Reserve and Umdoni Park in Natal. Factors contributing to the low population densities in the Tsitsikamma national parks were investigated. Twenty-seven and seven percent of leopard (25) and caracal (12) scats respectively analyzed contained blue duiker remains, but predator numbers appear to be low. Forest characteristics were investigated, and results from this and other studies suggest that undergrowth cover does not markedly influence blue duiker densities in the southern Cape forests. Field and stomach analysis indicate that blue duikers feed primarily on freshly fallen leaves and fruit, and are selective foragers. In the Tsitsikamma national parks (TNPs) the frequency of occurrence of trees known to be palatable to duikers are low, while less than 45 percent of the dominant tree species fruit fully annually. This apparent scarcity of food, the low numbers of antelope species and individuals in these forests and results from duiker research in Zaire, suggest that habitat rather than predation is limiting duiker numbers in the Tsitsikamma national parks.

N. Hanekom. Tsitsikamma National Park, P.O. Storms River, 6308 Republic of South Africa;
V. Wilson. Chipangali Wildlife Trust, P.O. Box 1057, Bulawayo, Zimbabwe.

Introduction

Blue duikers, *Philantomba monticola* (Thunberg, 1789), are rare in South Africa (Smithers 1986) and confined to forests and thickets, primarily in the coastal strip extending from the Umfolozi River system in Natal to George in the southern Cape (Smithers 1983; Wilson 1987). They are recorded from only two South African national parks, Zuurberg and Tsitsikamma, but are found in several nature reserves in Natal (Bourquin *et al.* 1971; Bowland 1990a) and unprotected areas throughout their distribution (Bowland *pers. comm.*).

In the southern Cape numbers of blue duikers apparently decreased in the late 1940s and early 1950s and remained depressed throughout the 1950s and 1960s, but have subsequently increased in the Tsitsikamma Coastal National Park (TCNP) (Crawford & Robinson 1984). This decrease in duiker numbers and the slow recovery of the populations were

respectively attributed to an increased abundance of caracal (*Felis caracal* Schreber, 1776) in the forests during (the drought of) the late 1940s (Thesen *in litt.* 1952 in Skead 1980; Liversidge 1966) and subsequent hunting by dogs and poachers (Liversidge 1966; Crawford & Robinson 1984). This study compares blue duiker densities in the Tsitsikamma Coastal and Forest National Parks (TNPs) with those from other regions (Von Gadow 1978; Koster & Hart 1988; Bowland 1990a) and discusses the probable effect of predation and habitat on the populations of the southern Cape. It complements the work of Crawford (1984) and Bowland (1990a, 1990b) on blue duiker in the TCNP and Natal respectively and forms part of a Pan-African decade of duiker research (Wilson 1987).

Study area

The terrestrial section (ca. 70 km x 0,8 km) of the Tsitsikamma Coastal National Park

Fig. 1. Maps of : (A) southern Africa, (B & C) the Storms River region of the Tsitsikamma Coastal National Park (TCNP) and the Tsitsikamma Forest National Park (TFNP) respectively, showing transect paths, game drive areas and trail used by Crawford (1984). KSNR = Kenneth Stainbank Nature Reserve.

Fig. 2. Mean numbers of blue duikers seen per transects along the entire Blue Duiker Trail during winter (April - September) and summer (October - March) periods between June 1986 to August 1988.

(TCNP) lies on a steeply sloping (0-180 m high) coastal escarpment, while the small (478 ha) Tsitsikamma Forest National Park (TFNP), which was deproclaimed and ceded to Department of Environment Affairs in 1989, is on the lower slopes of the Tsitsikamma Mountain Range (ca. 240 - 550 m above sea level), some 7 km inland from Storms River Mouth (Figure 1). The climate in both areas is mild, with mean annual minimum and maximum temperatures approximating 8 °C and 24 °C respectively, while rainfall (1 000-1 200 mm) is evenly distributed throughout the year. The vegetation is mainly dry high (Afro-montane) forest, dry scrub forest and mountain fynbos in the TCNP (Hanekom *et al.* 1989), and medium moist to moist Afro-montane forest in the TFNP (Geldenhuys 1981). These forests are part of the southern Cape or Knysna (Afro-montane) forest complex, a belt of isolated forest patches along the coastal plateau and lower slopes of the Outeniqua and Tsitsikamma mountains (Von Breitenbach 1974; Hanekom *et al.* 1989).

Methods

Variable width transects:

For census purposes blue duikers in the study area may be regarded as active throughout the day (Craw-

ford 1984) and all counts in this study were done between 14:30 and 18:30. The 4.2-km Blue Duiker Trail, through forest and scrub forest in the TCNP (Figure 1B), was walked approximately once a week between June 1986 and August 1988 ($n=157$), while 28 transects were done along a 3.2 km path through forest in the TFNP (Figure 1C). Blue duikers seen along the trails were recorded, and animal to transect path distances were determined for the last 54 and 15 sightings in the TCNP and TFNP respectively. Population densities were estimated applying the equation used by Bowland (1990a), namely:

$$D = \frac{Y}{2L}W, \quad \text{where}$$

D = density per ha,

Y = total number of animals seen along transect path,

L = length of transect path and

W = mean animal to sampling path distance (Collinson 1985).

Drive counts:

To determine the range of visibility within the forests and suitable spacing intervals between beaters on game drives, maximum distances at which a (30 cm x 40 cm) brown sighting board was readily visible, were assessed in June 1988 and January 1989. Measurements were taken at 100 m intervals along the transect paths.

Three game "drives" were done in area A-B-C-D (in TCNP) and four in area G-H-I-J (in TFNP, Figure 1) between June and August 1988. Observers were spaced approximately 10 m apart and kept (as far as possible) abreast of each other as they moved quietly through the forest. Blue duikers in the study areas were accustomed to pedestrian traffic and could nor-

Fig. 3. Frequency distributions of animal-to-sampling path distances recorded along the Blue Duiker Trail and in the TFNP.

mally be approached to within 5-15 metres. This, together with the fact that they usually emit a shrill whistle when flushed (Crawford 1985), facilitated the counting process. Blue duikers are reluctant to leave their territories, they usually double back or hide on reaching territory boundaries (Bowland 1990b). Observers recorded numbers of duikers seen, the direction in which they moved and segment (north, middle or south) of the study areas where sightings were made. Two or three observers stationed on paths C - D and I - J (Figure 1) recorded any animals fleeing the areas. Five and seven consecutive drives were needed to cover the study areas of the TCNP and TFNP respectively. By plotting the locality of each sighting and the direction in which the animals were moving, replicate records of the same individual were identified and the total number of duikers seen determined.

Both study sites lie length ways along steeply sloping escarpments and it was necessary to compensate for this when determining the area covered on each drive. Therefore, estimates of the vertical area (mean height x mean breadth) of the study region were added to the (surface area) planimeter readings (m^2) from 1:10 000 orthophotographs.

Faecal pellet counts:

During these game drives the three most experienced beaters also recorded numbers of faecal pellet piles. It was assumed that: (i) the effective strip width for pellet counts was exactly 1,5 m, (ii) faecal piles, which had not yet turned "mouldy" or started disintegrating were less than 25,5 days old (Von Gadow 1978) and (iii) the defecation rate of blue duikers was 2,5 piles per day (Von Gadow *op cit.*). Duiker densities were then calculated using the equation:

$$D = \frac{Y}{X}Z, \text{ where:}$$

D = density per ha,

Y = number of faecal piles per ha,

X = defecation rate per 24 h and

Z = Decay rate in days (Koster & Hart 1988).

Blue duiker densities recorded from various southern Cape forests were compared with those of bushbuck, the other major antelope species in the above forests. To equate these values, bushbuck densities were multiplied by the ratio of the metabolic rate of bushbuck divided by that of blue duiker [adult masses = 35 kg and 4,2 kg respectively (Smithers 1983)], as determined by the mass (M) metabolism (R) equation: $R \text{ (kcal/h)} = (0,676 M^{0,75})$ (Schmidt-Nielsen 1985):

In March 1990 a fresh (c. one hour old) road-kill was found about 0,5 km from the TCNP study site. The duiker carcass was measured and the abdominal organs removed. The liver was frozen and sent to the Regional Veterinary Laboratory in Stellenbosch for trace element analyses using atomic spectrometry. The stomach contents were washed in a 1,0 mm mesh sieve and sorted. Ingested items were compared with intact leaf and fruit specimens collected from the forest, and where possible items were identified to species level using herbarium samples and referring to Von Breitenbach (1974). The various fractions were then oven dried at 80 °C for 48 h, weighed to the nearest 0,01 g and expressed as a percentage of the total sample.

The duiker had apparently been feeding in the area, as freshly ingested food items were abundant in the forest bordering the road-kill site. Freshly fallen leaves and fruit were quantitatively collected from 100 (0,25 m^2) quadrats randomly placed along the forest floor. Food items were identified, sorted and

Table 1

Maximum distance at which sighting board was still readily visible in the forest ($\bar{x} \pm SE$) and values for variable width transects, game drives and faecal pellet counts done in the Tsitsikamma national parks

	TCNP	TFNP
Sighting- Board:		
Trail segments (Fig.1)	0 - 25	26 - 42
Max. dist. (winter)	6,2 + 0,5 m	6,6 + 0,5 m
Max. dist. (summer)	6,0 + 0,5 m	6,4 + 0,6 m
Line Transects:		
Trail segments	0 - 25	26 - 42
Length of trail (L) [‡]	2 300 m	1 600 m
Duiker/transect (Y)	0,55 + 0,07	0,62 + 0,07
Strip width (W)	12,3 m	10,9 m
Duiker/ha (Dx10000)	0,10 + 0,01	0,18 + 0,02
Game Drives:		
Forest region (Fig. 1)	A-B-C-D	G-H-I-J
Area covered (ha)	-	36,8
Duiker/drive	-	7,00 + 0,58
Bushbuck/drive	-	0,67 + 0,67
Duiker/ha	-	0,19 + 0,01
Bushbuck/ha	-	0,02 + 0,01
Faecal Pellet Counts:		
Faecal pellets/ha (Y)	-	7,41 + 2,79
Defaecation / day (X) ^{‡‡}	-	2,5
Age of pellets (Z) ^{‡‡}	-	< 25,5
Duiker/ha (D)	-	0,12 + 0,04

[‡] through forest

^{‡‡} values derived from Von Gadow (1978).

treated as described above. These values were then compared with those from the stomach analysis.

The stem densities and dominant species in the shrub (1-2 m) and tree (>2,5 m) strata (Bowland 1990a) of the forests were determined along three equally spaced north-south transects through study sites A-B-C-D and G-H-I-J (Figure 1), using the point-centre quarter method (Mueller-Dombois & Ellenberg 1974). Measurements were taken at 20 m intervals along transect lines. Plants were identified using Von Breitenbach (1974) and the Saasveld herbarium, while stem diameter at breast height (DBH) was determined for each tree.

Leopard and caracal scats, which are fairly large with a segmented appearance (Walker 1981), were collected whenever encountered in the TNPs or adjoining areas. There was no clear way of differentiating between the scats of small leopard and that of large caracal. Therefore, all scats having maximum diameter > 20 mm were regarded as leopard, while those < 20 mm as caracal (Norton *et al.* 1986). Scat samples were analyzed in the manner described by Grobler &

Wilson (1972), with prey items being identified from fragments of hooves, nails, bones, teeth, hairs or feathers found in the faeces. The percentage occurrence and relative frequency of each prey item were determined.

Results

Maximum distances, at which the 30 cm x 40 cm sighting board was readily visible in the forest bordering the Blue Duiker Trail, were similar in both summer and winter (paired *t*-test=1,05; *df*=77; *P*>0,10, Table 1). Therefore, seasonal variations in visibility were unlikely to influence transect counts.

The mean numbers of blue duikers recorded per transect along the Blue Duiker Trail (segments 0 - 42) during the summer (October to March) and winter (April to September) periods between June 1986 and August 1988

Table 2
Density estimates of blue duiker from Tsitsikamma (Table 1), Knysna (Von Gadow 1978), Zaire (Koster & Hart 1988) and Natal (Bowland 1990a)

Study site	Density estimates		
	Transect counts	Game drives	Pellet counts
Southern Cape			
Tsitsikamma			
TCNP	0,18	0,19	0,12
TFNP	0,13	0,14	0,07
Knysna			
Woodville	-	-	0,09 [‡]
Biervlei	-	-	0,17 [‡]
Gouna	-	-	0,28 [‡]
Diepwalle	-	-	0,55 [‡]
Zaire			
Maji Mbili	-	0,11	0,08
Kapituri	-	0,14	0,13
Natal			
Umdoni Park	3,20	-	-
KSNR-C ^{‡‡}	1,51	1,4	2,38
KSNR-A	1,1	-	-
KSNR-B	0,9	-	-

[‡] Von Gadow's (1978) equation, which separated fresh from old faecal piles, is incorrect and density estimates were recalculated using the combined values for fresh (2 days) and old faeces (3 - 25,5 days), assuming that these faecal groups were found in a ratio of 1: 11,75, as was recorded at Diepwalle (Von Gadow 1978).

^{‡‡} KSNR = Kenneth Stainbank Nature Reserve - area C.

varied from 0,89 to 1,35 (Figure 2). However, these variations were not significant (anova = 0,81; $df = 4 \text{ \& } 152$; $P > 0,10$, Snedecor 1965), and fluctuations were taken to be chance variations with no biological meanings.

Most blue duikers were sighted in open forest glades, their normal foraging areas (Bowland 1990a), and the animal-to-sampling line distances suggested duikers kept a "safe" distance (ca. 5 m) from transect path used, especially the busy Blue Duiker Trail (Figure 3). This means that some animals may have

Table 3
Normal and metabolically standardized (relative to blue duiker) population density estimates for bushbuck and blue duiker in various southern Cape forests. Normal estimates for TNPs, Goudveld (bushbuck) and adjoining Gouna (bushbuck and duiker) Afromontane forests were taken from Table 1, Seydack (1983), Odendaal et al. (1980) and Von Gadow (1978 in Table 2) respectively, while the ratio of the metabolic rate of bushbuck to that of duiker = 4,9 : 1

Density	(Goudveld)	Gouna	TFNP	TCNP
	Bushbuck	Bush- : Duiker buck	Bush- : Duiker buck	Bush- : Duiker buck
Normal (animals/ha)	(0,06)	0,05 : 0,28	0,03 : 0,14	0,02 : 0,19
Standardized (duiker equivalents/ha)	(0,29)	0,25 : 0,28	0,15 : 0,17	0,10 : 0,19

Table 4
Stomach contents of blue duiker compared to the composition of freshly fallen leaves collected from forest floor

		Duiker (TCNP)			
		Stomach content			Forest
		Estimated numbers	Dry mass (%)	% of identified leaves	Leaf litter mass (%)
Fruit:					
<i>Dietes iridioides</i>	(G)	22	28,5 [‡]	-	6,0(G)
<i>Canthium mundianum</i>	(T)	125	13,3 [‡]	-	0,2
Fungi	(G)	2	0,7	-	0,0
Dicotylendinous leaves:					
Unidentified	(T)	580	50,3	-	-
Identified	(T)	84	7,4	-	-
Identified dicotylendinous leaves:					
<i>Canthium obovatum</i>	(T)	-	5,1	68,0 [‡]	3,7
<i>Canthium mundianum</i>	(T)	-	0,8	10,7 [‡]	1,1
<i>Cassine papillosa</i>	(T)	-	0,4	5,3 [‡]	2,7
<i>Apodytes dimidiata</i>	(T)	-	0,4	5,3 [‡]	1,7
<i>Olea capensis macrocarpa</i>	(T)	-	0,4	5,3	9,8
<i>Olinia ventosa</i>	(T)	-	0,3	4,0	9,3
<i>Ocotea bullata</i>	(T)	-	0,0	0,0	0,7
<i>Maytenus peduncularis</i>	(T)	-	0,0	0,0	0,0
<i>Nuxia floribunda</i>	(T)	-	0,0	0,0	1,1
<i>Diospyros whyteana</i>	(T)	-	0,1	1,3	0,6
<i>Pterocelastrus tricuspidatus</i>	(T)	-	0,0	0,0	18,5 [‡]
<i>Gonioma kamassi</i>	(T)	-	0,0	0,0	9,3 [‡]
<i>Curtisia dentata</i>	(T)	-	< 0,1	0,5	9,8 [‡]
<i>Trichocladus crinitus</i>	(S)	-	0,0	0,0	6,4 [‡]
<i>Rapanea melanophloeos</i>	(T)	-	0,0	0,0	9,6 [‡]
<i>Podocarpus latifolius</i>	(T)	-	0,0	0,0	1,7
<i>Podocarpus falcatus</i>	(T)	-	0,0	0,0	0,6
<i>Cassine eucleiformis</i>	(T)	-	0,0	0,0	1,2

(T) = tree, height > 2,5 m

(S) = shrub, height = 1,0 - 2,5 m

(G) = ground flora, height <0,5 m

(A) = abundant

[‡] = marked differences between stomach content and forest litter.

moved out of the observer's range of visibility before being detected, resulting in an underestimation of duiker numbers (Bowland 1990a). Despite this, density estimates from transect counts were similar to those from game drives (Table 1; Mann-Whitney *U*-test, $z = 0,44$ & $0,35$; $df=158$ & 29 ; $P > 0,10$ for TCNP & TFNP respectively; Siegel 1956).

The first game drive count in the TFNP, where beaters were unfamiliar with the con-

ditions, was much lower than subsequent drive counts (namely, 2 v. 5, 7, 9 duikers), as well as the largest group of duikers recorded on a transect. This count was therefore assumed to be inaccurate and excluded from the density calculations in Table 1. In the TCNP replicate drive counts corresponded well with both each other ($SE = 0,58$) and estimates from transect counts (Table 1).

Counts of faecal pellet piles, although less accurately done than drive- or transect

Table 5

Structural characteristics and species composition of forests in the study areas of the TCPs relative to those in Umdoni Park and sections A - C of Kenneth Stainbank Nature Reserve (KSNR) (Bowland 1990a). Key: DBH = diameter at breast height, † species recorded in duiker stomach

Characteristics:

	TCNP	TFNP	Umdoni	KSNR-C	KSNR-A	KSNR-B
Trees (> 2,5 m high)						
Numbers measured	280	272	133	300	136	300
Size frequency (%)						
DBH > 15 cm (A)	27,8	24,3	9,8	4,3	5,9	2,7
DBH < 15 cm	72,2	75,8	90,2	95,7	94,1	97,3
Basal areas (cm ²)ha ⁻¹	285	408	226	128	133	82
Stem densities						
Trees (ha ⁻¹)	2 066	2 892	1765	2941	1993	2572
Shrubs (ha ⁻¹)	3 629	5 724	1784	2731	2451	1933
Trees /shrubs (B)	1,75	1,98	1,01	0,93	1,23	0,75
[% trees >15 cm]/ [trees / shrubs] or (A/B)	15,9	12,3	9,7	4,9	4,8	3,6
Number of species (n = 90)						
Trees	23	19	28	27	28	21
Shrubs	7	5	17	22	17	16
Duiker densities	0,19	0,17	3,2	1,6	1,1	0,9

Composition:

	TCNP	TFNP	Umdoni	KSNR-C	KSNR-A	KSNR-B
Dominant trees (>2,5m high)						
<i>Trichocladus crinitus</i>	23,2	40,1	-	-	-	-
<i>Olea capensis macrocarpa</i> †	7,1	6,6	-	-	-	-
<i>Cassine papillosa</i> †	6,4	1,8	-	3,3	-	-
<i>Gonioma kamassi</i>	6,1	3,7	-	-	-	-
<i>Pterocelastrus tricuspidatus</i>	5,4	1,5	-	-	-	-
<i>Podocarpus latifolius</i>	5,0	8,8	-	-	-	-
<i>Cassine peragua</i>	5,0	0,0	-	-	-	-
<i>Acokanthera oppositifolia</i>	4,3	0,0	-	-	-	-
<i>Maytenus peduncularis</i>	3,9	0,7	-	-	-	-
<i>Rapanea melanophloeos</i>	3,6	0,0	<3,0	-	-	-
<i>Burchellia bubalina</i>	1,8	4,8	-	-	-	-
<i>Ocotea bullata</i>	1,4	8,8	-	-	-	-
<i>Nuxia floribunda</i>	1,4	2,9	-	-	-	-
<i>Apodytes dimidiata</i> †	1,4	2,9	<3,0	-	-	-
<i>Diospyros whyteana</i> †	1,1	2,9	-	-	-	-
<i>Rothmannia capensis</i>	0,0	1,8	-	-	-	-
Palatable trees						
<i>Canthium obovatum</i> †	1,4	1,5	<3,0	-	<2,8	-
<i>Canthium mundianum</i> †	1,1	0,7	-	-	-	-
Dominant shrubs (1 - 2,5 m high)						
<i>Trichocladus crinitus</i>	60,0	85,7	-	-	-	-
<i>Carissa bispinosa</i>	15,4	0,0	-	-	-	-
<i>Ocotea bullata</i>	(1,1)	5,1	-	-	-	-

counts, did confirm that duiker densities were extremely low in the TNPs (Table 1).

ized relative to blue duiker, of bushbuck from these forests (Table 3).

Blue duiker density assessments from various southern Cape forests ranged from 0,09 to 0,55 duikers/ha (Table 2), and were comparable to those, "metabolically" standard-

In 95 percent of feeding observations ($n=19$) blue duikers foraged at ground level and often (78 % of the records) in areas where ground flora was scarce (cover < 10 %).

Table 6
Percentage occurrence and relative frequency of different prey items in 25 leopard and 12 caracal scats found in or bordering the TNPs

Prey	Leopard		Caracal	
	Occur. (%)	Rel.freq. (%)	Occur. (%)	Rel.freq. (%)
Birds	27	20	29	21
Rodents	15	11	43	32
Dassie (<i>Procavia capensis</i>)	15	11	14	11
Blue duiker (<i>Philantomba monticola</i>)	27	20	7	5
Bushpig (<i>Potamochoerus porcus</i>)	12	9	7	5
Bushbuck (<i>Tragelaphus scriptus</i>)	8	6	-	-
Baboon (<i>Papio ursinus</i>)	8	6	-	-
Porcupine (<i>Hystrix africaeaustralis</i>)	8	6	-	-
Caracal (<i>Felis caracal</i>)	4	3	-	-
Sheep	-	-	7	5
Insects	12	9	29	21

These duikers appeared to feed primarily on freshly fallen leaves and fruit, and were very selective in their foraging, sniffing at numerous food items, but eating only a few. This was supported by the stomach analysis, where leaves and fruit from trees (>2,5 m high) comprised about 71 percent (by mass) of the ingested food, and relative to food items collected from the forest floor, there appeared to be a strong selection for leaves of the trees *Canthium obovatum* and *C. mundianum*, as well as seed pods of the iris *Diets iridioides* (Table 4).

The forests of the TNPs differ from those studied by Bowland (1990a) in Natal, with densities of both large trees (height > 2,5 m; DBH > 15 cm) and shrubs (1-2 m high) being greater in the TNPs (Table 5). Furthermore, few tree species are common to both forest groups, and the tree (> 2,5 m high) and shrub (1-2,5 m high) strata in the TNPs are dominated by the apparently unpalatable *Trichocladus crinitus*, while palatable trees *Canthium obovatum* and *C. mundianum* and the iris *Diets iridioides* are uncommon (Tables 4 & 5).

Blue duiker remains were respectively recorded in 27 and 7 percent of the leopard and caracal scats containing identifiable prey items (Table 6).

Discussion

All duiker species extensively studied have been found to be territorial (Jarman 1973; Bowland 1990a), and, contrary to Crawford's (1984) results, transect counts for the Blue Duiker Trail and study period showed no significant seasonal (summer v. winter) variation (anova = 0,81; $df = 4 \text{ \& } 152$; $P > 10$). Likewise, mean density estimates from transect counts done during August 1987, April 1988 and August 1988 in the Kenneth Stainbank Nature Reserve (KSNR) were similar [1,53, 1,55 and 1,44 blue duikers/ha respectively (Bowland 1990a)], suggesting that variable strip transects may be successfully employed during any season.

Blue duiker densities from the TNPs are similar to those determined from Von Gadow's (1978) and Koster & Harts' work (1988) in four southern Cape and two Zaïrese forests respectively (Table 2). However, except for one, all these values are at least three times lower than densities recorded in the Umdoni Park & KSNR (A - C) in Natal (Bowland 1990a, Table 2). Such discrepancies in population densities are presumably caused by factors such as predation, food or habitat or a combination of these three.

Likely predators of blue duikers in the TNPs are man, dogs, caracal and leopard

Table 7

The frequencies of occurrence of the ten dominant tree species in the KSNR C and KSNR B, feeding preference scores of blue duiker for freshly picked and fallen leaves of these trees (modified from Bowland 1990a), as well as the estimated availability of food and blue duiker densities

Tree Species	% Frequency Occurrence		Picked Leaves			Fallen Leaves		
	KSNR C	KSNR B	Feed Pref Score	Available Food KSNR C	Available Food KSNR B	Feed Pref Score	Available Food KSNR C	Available Food KSNR B
	A	B	C	A x C	B x C	D	A x D	B x D
<i>Protorhus longifolia</i>	34,3	9,8	0,55	18,9	5,4	0,37	12,7	3,6
<i>Milletia grandis</i>	10,1	22,9	0,17	1,7	3,9	0,21	2,1	4,8
<i>Strychnos henningsii</i>	6,9	-	0,37	2,6	-	0,07	0,5	-
<i>Drypetes arguta</i>	6,2	12,1	0,39	2,4	4,7	0,17	1,1	2,1
<i>Bequaertiodendron natalense</i>	6,0	6,6	0,23	1,4	1,5	0,22	1,3	1,5
<i>Brachylaena discolor</i>	5,3	-	0,49	2,6	-	0,14	0,7	-
<i>Croton sylvaticus</i>	3,9	8,5	0,0	0,0	0,0	0,0	0,0	0,0
<i>Vepris undulata</i>	3,3	3,4	0,11	0,4	0,4	0,25	0,8	0,9
<i>Cassine papillosa</i>	3,3	-	-	-	-	-	-	-
<i>Ekebergia capensis</i>	2,9	-	0,24	0,7	-	0,11	0,3	-
<i>Gardenia amoena</i>	-	3,9	0,41	-	1,6	0,42	-	1,6
<i>Xylothea kraussiana</i>	-	3,6	0,44	-	1,6	0,25	-	0,9
<i>Tabernaemontana elegans</i>	-	2,7	0,13	-	0,4	0,11	-	0,3
<i>Combretum molle</i>	-	1,7	0,37	-	0,6	0,18	-	0,3
Total Available Food				30,59	20,06		19,56	15,94
KSNR-C : KSNR-B ratio				1 : 0,66			1 : 0,81	
Duiker Density				1,6	0,9		1,6	0,9
KSNR-C : KSNR-B ratio				1 : 0,56			1 : 0,56	

(Liversidge 1966; Robinson 1976; Smithers 1983; Crawford & Robinson 1984). However, since the late 1970s the study areas have been regularly patrolled by park officials, and during this survey no signs of poachers, snares or dogs were seen. Furthermore, although blue duiker remains were recorded in 27 percent of the leopard scats analysed (Table 6), numbers of leopard in the TNPs appear low, because despite effective coverage during the two year study period, only 26 leopard scat piles were found. Therefore, factors other than predation are probably responsible for the low blue duiker densities in the Tsitsikamma national parks.

Blue duikers are territorial, obligate forest dwellers, and its forest habitat must provide both food and shelter throughout the year (Bowland 1990a). The tree stratum (> 2,5 m high) is the primary food source for blue duikers, while the shrub layer (1 - 2,5 m high)

is important in terms of cover (*pers. obs.*; Bowland 1990a). Above a certain threshold level of stem densities, Bowland (1990a) recorded a positive affiliation between blue duiker densities and the quotient from percentage occurrence of big trees (DBH > 15 cm) divided by the proportion of shrub to tree densities in the study sites (A / B in Table 5). The results of this study failed to conform with Bowland's (1990a) values, because despite the higher quotients recorded in the TNPs, duiker densities were lower than in Natal (Table 5). This discrepancy might be due the fact that the shrub and tree densities measurements failed to quantify the growth form of the plants, which would affect the plants ability to provide shelter or food for duikers. For example, the slender, erect stem and leafy branches of witch-hazel *Trichocladus crinitus*, which dominates the southern Cape forests (Table 5; Von Breitenbach 1974), provides scant cover for

duikers compared to a sprawling, multi-stemmed shrub, such as *Carissa bispinosa*.

The density of shrubs in the TFNP was 1,6 times greater than in the TCNP. Despite this, blue duiker density estimates from both transects and game drives in these two areas were similar (Mann-Whitney *U*-test, $z = 0.38$ & -0.44 ; $df = 182, 4$; $P > 0.10$); as were faecal pellet counts from forests (ca. 80 km west of TFNP) with abundant- and fairly abundant undergrowth cover (Von Gadow 1978). This suggested that shrub densities generally do not significantly influence the duiker densities in the southern Cape forests.

Small ruminants have high metabolic requirements relative to their stomach capacities (Schmidt-Nielsen 1985) and are under pressure to feed selectively (Milton 1979; McNaughton 1987). Bowland (1990a) recorded a positive correlation between feeding preferences of blue duikers and condensed tannin concentrations of freshly picked leaves. Although contrary to recorded trends in other "herbivores" [namely a preference for plants poor in condensed tannins (Oates *et al.* 1977; McKey *et al.* 1981; Cooper *et al.* 1988)], the results, together with field observations, indicate that blue duikers are very selective foragers.

Dicotyledonous leaves are the single most important dietary component of blue duikers in the Natal forests (Bowland 1990a), and constituted approximately 57 percent of the stomach contents analysed in this study (Table 4). Nevertheless, Bowland (1990a) recorded a strong, negative correlation ($r = 0.89$, $P > 0.05$) between fruit (a scarce, unreliable food source in dry coastal forests) and freshly fallen leaves (an abundant, year-round food source), suggesting a much greater preference for fruit. In the TNPs less than 45 percent of the dominant trees (frequency of occurrence > 1.7 % in Table 5) fruit successfully every year. For example, although *Pterocelastrus tricuspidatus*, *Cassine papillosa*, *C. peragua* and *Canthium obovatum* flower annually, they only develop full fruit crops every second or third year, while *Podocarpus latifolius*, *Rapanea*

melanophloeos, *Apodytes dimidiata*, *Olea capensis* subsp. *macrocarpa*, *Nuxia floribunda* and *Gonioma kamassi*, have flowering intervals of two or more years (Phillips 1926; Von Breitenbach 1974). Furthermore, the dominant "annually" fruiting species, *Trichocladus crinitus*, has small, encapsulated fruit (Von Breitenbach 1974), which are apparently seldom foraged on by birds or animals (*pers. obs.*). Therefore, fruit is a scarce, unreliable food source in the Tsitsikamma national parks.

The potential of freshly fallen leaves to serve as a prolific, year-round food source may also be limited, as the vegetation of the FNP is dominated by the apparently unpalatable *Trichocladus crinitus*, *Pterocelastrus tricuspidatus*, *Gonioma kamassi* and *Rapanea melanophloeos*, while palatable trees, *Canthium obovatum* and *C. mundianum*, are scarce (Table 4 & 5). Furthermore, the natural vegetation of the southern Cape is often deficient in copper (Joubert *et al.* 1969 in Odendaal 1983; Koen 1984), and the mean copper concentration determined from foliar analysis of three indigenous tree species from this region was 8 ppm (Koen 1988), lower than the minimum recommended for sheep on natural pastures in this region (Koen 1988). The liver copper concentration of 59 ppm determined from the blue duiker analysed was less than the means (137 ppm; range 29 - 533 ppm) from bushbuck in the Knysna forests (Odendaal 1983) and (84 ppm; range 18 - 208 ppm) from bontebok (*Damaliscus dorcas dorcas*) suffering from copper deficiencies (Zumpt & Heine 1978), but similar to sheep in winter from the nearby George area ($\bar{x} = 50$ ppm), where pastures are known to be deficient in copper (Odendaal 1983). Despite the low copper concentration in its liver, the blue duiker analysed showed no obvious symptoms of a copper deficiency (Maynard & Loosli 1969), being large (4.9 kg), with strong bones, glossy coat and lactating mammary glands. Nevertheless, the low mineral content and palatability of the vegetation in the southern Cape forests (Odendaal 1983; Koen 1984; Koen *et al.* 1988; Table 4), may increase the need of blue duikers to forage

selectively. McKey *et al.* (1978) postulated that as a consequence of similar feeding pressures, the monkey *Colobus satanas* in the Douala-Edea forest exists at a density roughly one-tenth the combined density of the two colobus species in the nutrient richer Kibale forest. It is, therefore, interesting to note that the densities of bushbuck in the nutrient poor southern Cape forests are approximately one-quarter those recorded from the savanna biome (Odendaal & Bigalke 1979; Seydack 1983; Van Daalen 1984), and that the blue duiker density in the KSNR (A) is approximately half that in the KSNR (C), where the estimated availability of palatable leaves was 1.3 times greater (Table 7). Hence diet quality may be regulating the population densities (Milton 1982; Crawley 1983; Watterman *et al.* 1988 in Bowland 1990a).

Bushbuck and blue duiker are the major antelope species in the Knysna forests (Von Breitenbach 1974; Robinson 1976; Seydack 1983), both feeding primarily on indigenous tree foliage (Odendaal 1983; Table 4). Therefore, if palatable foliage is limiting in the southern Cape forests, then these two species, of different sizes (ca. 35 kg v. 4.2 kg, Smithers 1983) and subject to different predation pressures (Table 6), could be expected to have low and comparable "metabolically" standardized, population densities. This is indeed the situation (Table 3), and the above, together with the fact that Koster & Hart (1988) determined no significant difference between the densities of blue duiker from two forests having markedly different histories of hunting and snaring ($t = 0.90$; $df = 13$ (drives); $t = 1.53$; $df = 28$ (pellet counts) $P > 0.05$), suggests that habitat rather than predation is the major factor controlling the population densities in the Tsitsikamma national parks.

Changes in habitat may also have been responsible for the decline in blue duiker abundance in the southern Cape during the late 1940s (Crawford & Robinson 1984). The annual rainfall values recorded at Bloukransbos in the Tsitsikamma for 1945, 1946 and 1949 were the lowest over the 90 year period 1890 - 1979 (Crawford & Robin-

son 1984), and the ensuing drought would have adversely affected the undergrowth cover, as well as leaf and fruit production in these forests. This in turn would have reduced the duikers' ability to escape predation, grow and raise offspring. The recovery of these populations was slow, but numbers have increased (Crawford & Robinson 1984). Transect counts (per kilometre) along the western sector of the Blue Duiker Trail (Table 1) are similar to those recorded by Crawford (1984; unpubl. data) along the eastern sector of the trail during 1980-2 ($t = 0.922$; $df = 515$; $P > 0.10$), suggesting that the population is near its upper asymptote and that further increases in population densities are unlikely.

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