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Using distance estimates in aerial censuses in northern Namibia

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ABSTRACT

Transect widths were previously disregarded as a serious source of bias in aerial censuses of large game in northern Namibia. The cumulative number of sightings per species was recorded at increasing distance away from the aircraft in recent aerial censuses in our region. Effective transect widths, as the distance away from the observer over which sightings accrue approximately linearly, were generally about half of the intended transect widths. Unless effective transect widths are determined, the spacing of flight lines in total aerial coverage censuses could bias population estimates severely. Effective transect widths may, however, be used for each species in a given census area counted by a random transect sample method.

INTRODUCTION

The visibility of an object is a function of its size and distance away from the observer (Norton-Griffiths 1978; Burnham & Anderson 1984; Burnham *et al.* 1985). Aerial censuses are usually designed to optimize the probability of counting all target individuals in a given area, although this design objective is seldom based on adequate data relevant to each census environment. The inability to detect all target animals over a specified transect width (counting strip width) is regarded as the most serious source of error and bias in aerial surveys (eg. Anderson & Posphala 1970; Caughley 1977; Norton-Griffiths 1978; Samuel & Pollock 1981; Burnham & Anderson 1984; Burnham *et al.* 1985). Transect widths used in aerial censuses in northern Namibia are, however, rarely based on any experimental work, and the question whether all animals occurring in a specified transect width are really detected, is seldom asked.

Previous aerial censuses in Namibia were based on census techniques developed in east Africa, with little or no effort spent to assess the suitability of techniques to local conditions. That transect widths were ignored as a serious source of bias was evident from the absence of any attempt to demarcate transect widths during census flights in the past (pers. obs., departmental census reports). The potential for undercounting or overcounting in such censuses can be considered severe. Population estimates derived from total area coverage aerial censuses, ie. a systematic coverage of an area with equally spaced flight lines, were, however, used without any correction factor or estimation of bias in management schemes for large game in Namibian parks.

Extensive experimental work has been done to reduce the bias in aerial surveys (Pennycuick & Western 1972; Caughley 1977; Norton-Griffiths 1978; Burnham & Anderson 1984; Burnham *et al.* 1985). Considerable experimentation is required to develop a sightability model or other bias-correcting technique to suit the Namibian censusing environment, as described in Caughley (1974); Caughley *et al.* (1976); Samuel & Pollock (1981); Gasaway *et al.* (1985); Bayliss & Giles (1985); Pollock & Kendall (1987); De Young *et al.* (1989); Johnson *et al.* (1989). While it may be possible to develop optimal census methods for each target species, the most urgent consideration at present is to optimize and standardize the multi-species aerial censuses used in northern Namibia.

A relatively easy and inexpensive method for detecting bias due to incorrect transect widths, is the analysis of the distribution of sightings over increasing distances away from the aircraft (Anderson & Posphala 1970; Burnham & Anderson 1984), as is commonly used in line-transect estimates of abundance (Burnham *et al.* 1980, 1985). The utility of this approach is outlined in this paper, regarding the detection of bias, determining effective transect widths and assessing individual performance of observers used in aerial counts of large game in northern Namibia.

MATERIALS AND METHODS

Counts of elephants (*Loxodonta africana*) as the largest and most visible target species in censuses of large game in northern Namibia were used to demonstrate the effect of increasing distance on the distribution of sightings. Streamers were attached to aircraft wing struts to represent distances of 0.5 km, 1.0 km, 1.5 km and 2.0 km away from the aircraft at 100 m altitude, following Norton-Griffiths (1978). A further category was used, namely greater than 2.0 km classed as 2.5 km. Distances from the transect line to all elephants seen were thus estimated in a series of elephant censuses in Etosha National Park (Etosha) (Lindeque 1988). The park was divided into two broad vegetation strata, namely woodland and scrubland based on the density and height of woody plants.

Estimates of the distance away from transect lines were obtained for all species counted in the 1987 total coverage aerial census of Etosha. Streamers were used to indicate distance intervals of 0.5 km, 1.0 km and 2.0 km to aid distance estimation. A part of this census was done by helicopter and streamers could not be used. Observers were asked instead to estimate the distance between transect lines and animal sightings as less or more than half the designated transect width. All distance data presented are estimates, as it was not possible to measure any distance from the aircraft accurately. Sightings directly underneath the aircraft were included in the first interval. The number of sightings at eg. 1.0 km represent sightings from the previous interval, eg. > 0.5 km up to 1.0 km.

The distances away from transect lines were estimated in multi-species sample aerial censuses of Etosha, the Kaokoveld, Khaudom Game Reserve (Khaudom), eastern Bushmanland and approximately 1800 km^2 of commercial farmland near Grootfontein in 1990, as described above. The distribution of sightings over increasing distance was used to define effective strip widths per species in each censusing area, as the distance over which the cumulative number of sightings did not show an inflection. Curves were evaluated by eye.

Transect width is the term used for the demarcated distance on both sides of the aircraft in which counting is done. Half-transect widths thus refer to the counting strip width on one side only. Effective transect widths are defined as twice the distance away from the aircraft over which sightings increase approximately linearly.

RESULTS

Single-species censuses

Neither the number of elephants nor the number of groups of elephants sighted over increasing distance from the transect line during elephant censuses in Etosha declined within the intended half-transect widths of 1.0 km and 2.0 km in the woodland and scrubland strata respectively (Fig. 1). A single experienced observer was used in this series of censuses and it seems that elephants can be accurately counted in comparatively wide transects in Etosha.

Multi-species censuses

During the 1987 multi-species aerial census of Etosha, most observers (including some of the most experienced and often-used participants in aerial censuses in Namibia) spotted significantly fewer groups in the further half of the transect width than in the nearer half (Fig. 2).

Elephant and Ostrich (*Struthio camelus*) were ranked most sightable while greater Kudu (*Tragelaphus strepsiceros*), and black rhino (*Diceros bicornis*) were ranked least sightable (Table 1). However, crude correction factors did not increase with decreasing sightability (Table 1).

Compared to Figure 1, the reduction in elephant sightings over the second half of the transect width (Table 1A) seems to indicate that observer bias was more severe during a multi-species, multiple observer census. The overall distribution of sightings in first and second halves of half-transect widths was similar in the helicopter and fixed-wing aircraft strata.

Determination of effective transect widths

In Figures 3-8 inflections and asymptotes indicate a decline in the rate of additional sightings at a given distance in a series of multi-species censuses in northern Namibia. The most severe misjudgement of intended transect width occurred in the census in the Kaokoveld (Figure 5) where despite the open terrain few sightings occurred beyond 1000 m, or half the intended transect width. Effective transect widths for nearly all species in all five census areas were half of the intended transect widths (Table 2), thus indicating that population sizes derived from these censuses would have been underestimated unless a correction procedure was used (eg. Lindeque & Lindeque 1997).

DISCUSSION

Estimates of the distance between aircraft and objects presented here cannot be used to provide additional data on animal density, in the sense of line-transect estimations of density (Burnham *et al.* 1985) or modified transect estimates (Caughley 1977; Collinson 1985). The

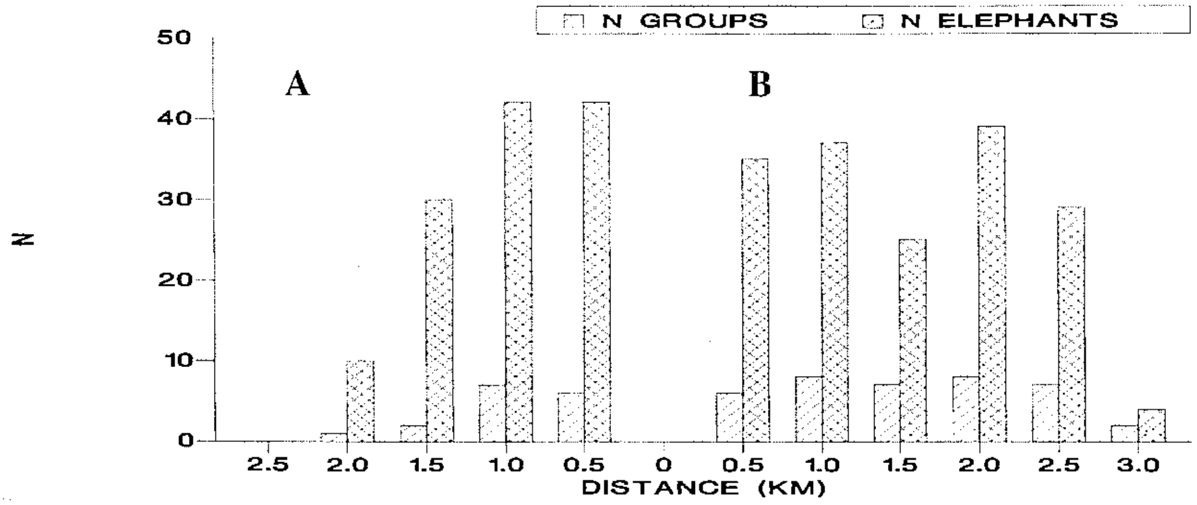

FIGURE 1: The number of groups and the number of elephants counted at increasing distance from the aircraft in the woodland (A) and shrubland (B) strata in Etosha National Park.

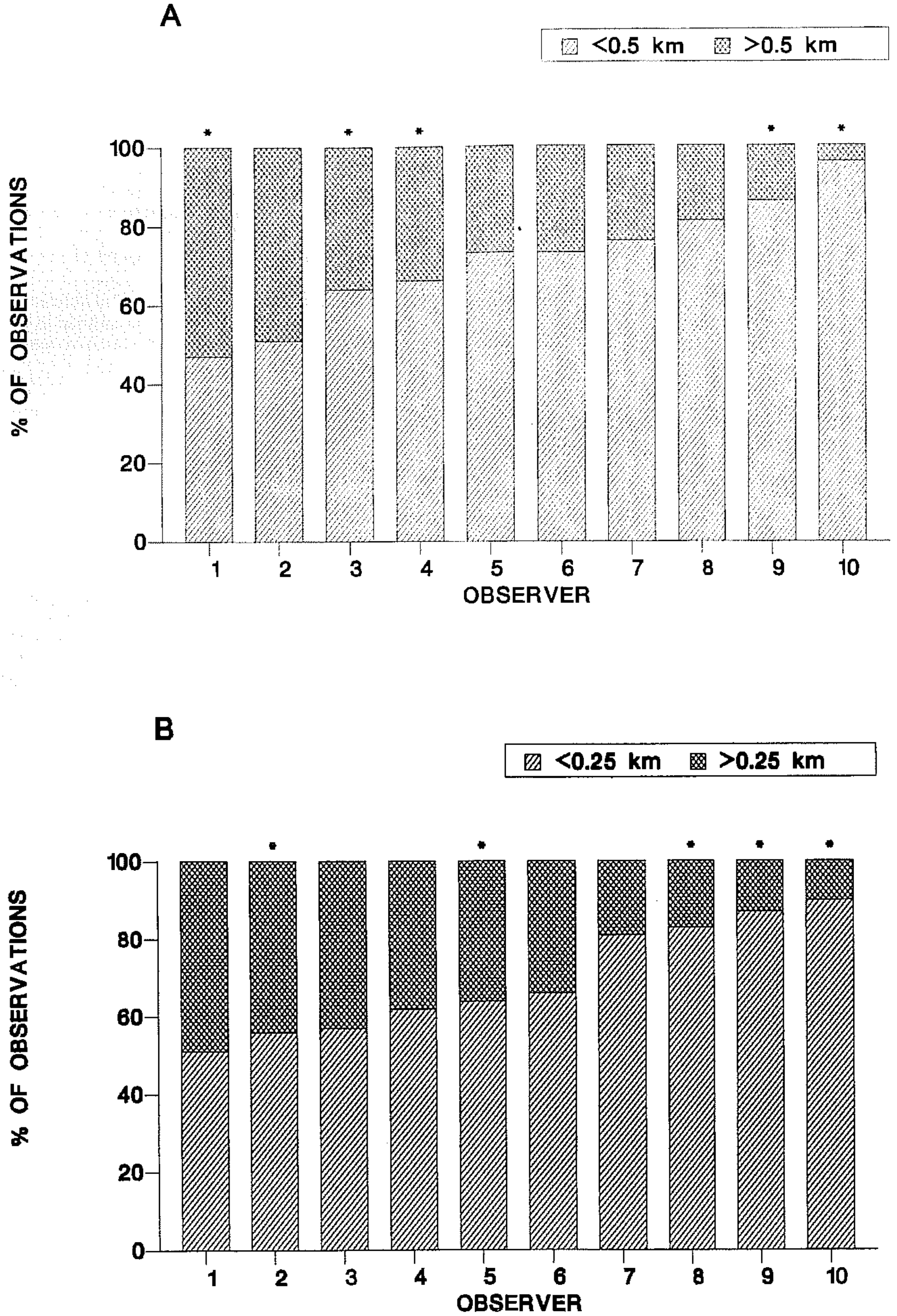

FIGURE 2: Schematic illustration of the differences in the number of groups of all species counted in the first and second halves of transect widths by ten observers in a fixed-wing aircraft (A) and ten observers in a helicopter (B) in the 1987 Etosha National Park census. (* denotes the most experienced census observers).

distance estimates presented here are regarded as too crude to allow any use other than an indication of suitable transect width in aerial censuses in Namibia. More accurate determination of the distances between observer and animals would allow either a correction of population estimates following Anderson & Posphala (1970) or entirely different treatment of data using more sophisticated methods (eg. Burnham *et al.* 1980).

TABLE 1: Number of groups and individuals ( ) of large game species counted in the first and second halves of the half-transect width by helicopter (A) and fixed-wing aircraft (B) in the 1987 aerial census of Etosha National Park. Species were subjectively ranked from most to least sightable.

A

Species[1]	Distance away from helicopter					
	< 0.25 km A		> 0.25km B		2A[2] (A+B)	
La	61	(500)	37	(332)	1.25	(1.20)
Sc	182	(512)	161	(401)	1.06	(1.12)
Ct	84	(1694)	44	(701)	1.31	(1.42)
Og	270	(1203)	146	(696)	1.30	(1.27)
Eb	209	(3001)	106	(989)	1.33	(1.50)
Ab	37	(307)	20	(150)	1.30	(1.34)
To	22	(163)	18	(83)	1.10	(1.33)
Am	186	(6208)	34	(847)	1.69	(1.76)
Gc	207	(605)	161	(345)	1.13	(1.27)
Ts	97	(486)	62	(373)	1.23	(1.13)
Db	42	(70)	19	(35)	1.34	(1.33)
Combined	1397	(14749)	808	(4952)	1.27	(1.50)

B

Species[1]	Distance away from fixed-wing aircraft					
	< 0.25 km A		> 0.25km B		2A[2] (A+B)	
La	36	(396)	38	(448)	0.97	(0.94)
Sc	102	(302)	77	(263)	1.69	(1.07)
Ct	15	(303)	17	(426)	0.94	(0.83)
Og	87	(212)	36	(101)	1.42	(1.36)
Eb	34	(703)	19	(227)	1.28	(1.51)
Ab	21	(87)	3	(24)	1.75	(1.57)
To	3	(26)	1	(6)	1.50	(1.63)
Am	76	(1498)	14	(330)	1.69	(1.64)
Gc	33	(79)	30	(81)	1.05	(0.99)
Ts	17	(79)	12	(58)	1.17	(1.15)
Db	20	(30)	7	(14)	1.48	(1.40)
Combined	444	(3715)	254	(1978)	1.27	(1.31)

[1] La = elephant (*Loxodonta africana*) Sc = ostrich (*Struthio camelus*), Ct= blue wildebeest (*Connochaetes taurinus*), Og= gemsbok (*Oryx gazella*), Eb= Burchell's zebra (*Equus burchelli*), Ab= red hartebeest (*Alcelaphus buselaphus*), To= eland (*Taurotragus oryx*), Am= springbok (*Antidorcas marsupialis*), Gc= giraffe (*Giraffa camelopardalis*), Ts= greater kudu (*Tragelaphus strepsiceros*), Db= black rhinoceros (*Diceros bicornis*).

[2] Crude correction factor to counter the apparent decrease in sightings over the second half of transect widths.

We have demonstrated that regardless of the census environment or technique followed, the rate of accumulation of sightings at increasing distance away from the observer, declines beyond a specific distance. This effect can be used to determine maximum transect widths which could be used to count a particular species or group of species in a given census area. More accurate determinations of the distance between objects and observers using accurate rangefinders are likely to reveal that effective transect widths should be even narrower than apparent from our data. From observations of observer behaviour during flights, it seems that fatigue and boredom lead to inadequate scanning of transect widths which require postural movements as well as differential eye focusing. These factors operate in addition to the expected decline in sightability over distance, which together result in biased population estimates.

We rarely have the resources to do single-species censuses in Namibia, and most censuses have to be optimized for a number of species. Optimal transect widths can be based on the overall distribution of sightings over distance, or the transect width indicated for the most important species among the target group. This constraint largely applies to total area coverage censuses, where the initial spacing of transects must be based on some knowledge of effective transect widths. If a standard transect width is chosen but not demarcated, some species may be undercounted, and others overcounted. The same group of animals recorded (but actually falling outside the transect width) on a transect would be seen by observers on the other side of the aircraft in the consecutive transect.

As long as the effective transect widths are determined for each species separately, the calculation of population estimates from random transect multi-species sample censuses is not affected, only the resulting sampling intensity. Transect widths are used in the calculation of population estimates from transect sample counts (Norton-Griffiths 1978) and the width used has a significant effect on population densities. There is no reason not to use individual transect widths for each species. There seems to be no better determination for locally effective strip widths available, other than those in Figures 3-8. We suggest that differential strip widths can be used to calculate population estimates from sample counts, where eg. giraffe (*Giraffa camelopardalis*) sightings in the Kaokoveld up to 600 m away from the aircraft are used, compared to elephant sightings up to 1000 m. The sampling intensity of such a sample census would thus be proportionately less for giraffe than elephants, as a smaller area was covered effectively. This approach would require an estimate of distance for every sighting in every census. The number of groups sighted in the relevant censuses were used throughout in this paper in favour of the number of individuals. With a large enough sample the latter could also be used, but could otherwise severely bias analyses of sightings over distance for species occurring at low density and/or with a clumped distribution.

Aerial censusing is the most important method for long-term monitoring of population trends in large game in

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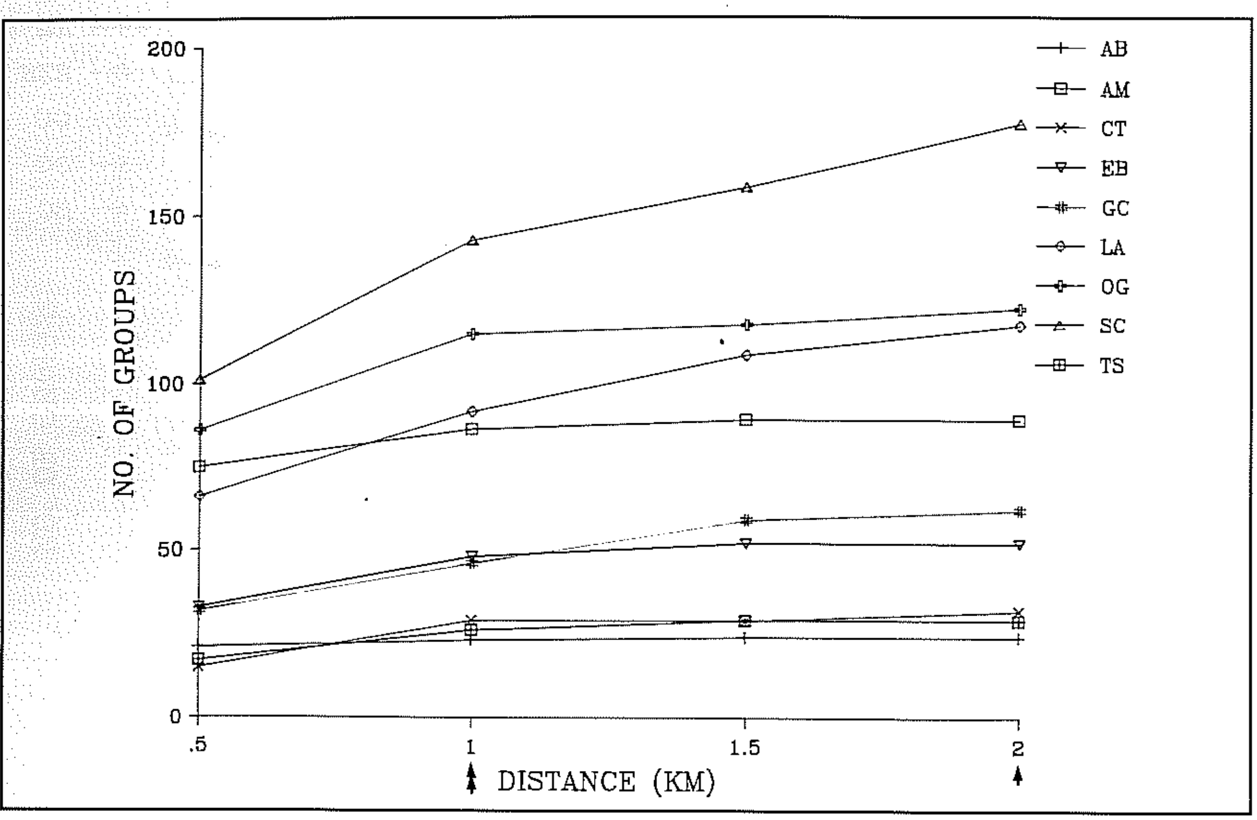

FIGURE 3: The cumulative distribution of sightings of groups of large game species at increasing distances away from transect lines in the September 1987 aerial census of Etosha National Park. (Arrow and double arrows denote intended aircraft half-transect width for the fixed-wing aircraft and helicopter respectively) (AB= red hartebeest, AM= springbok, CT= blue wildebeest, EB= Burchell's zebra, GC= giraffe, LA= elephant, OG= gemsbok, SC= ostrich, TS= kudu).

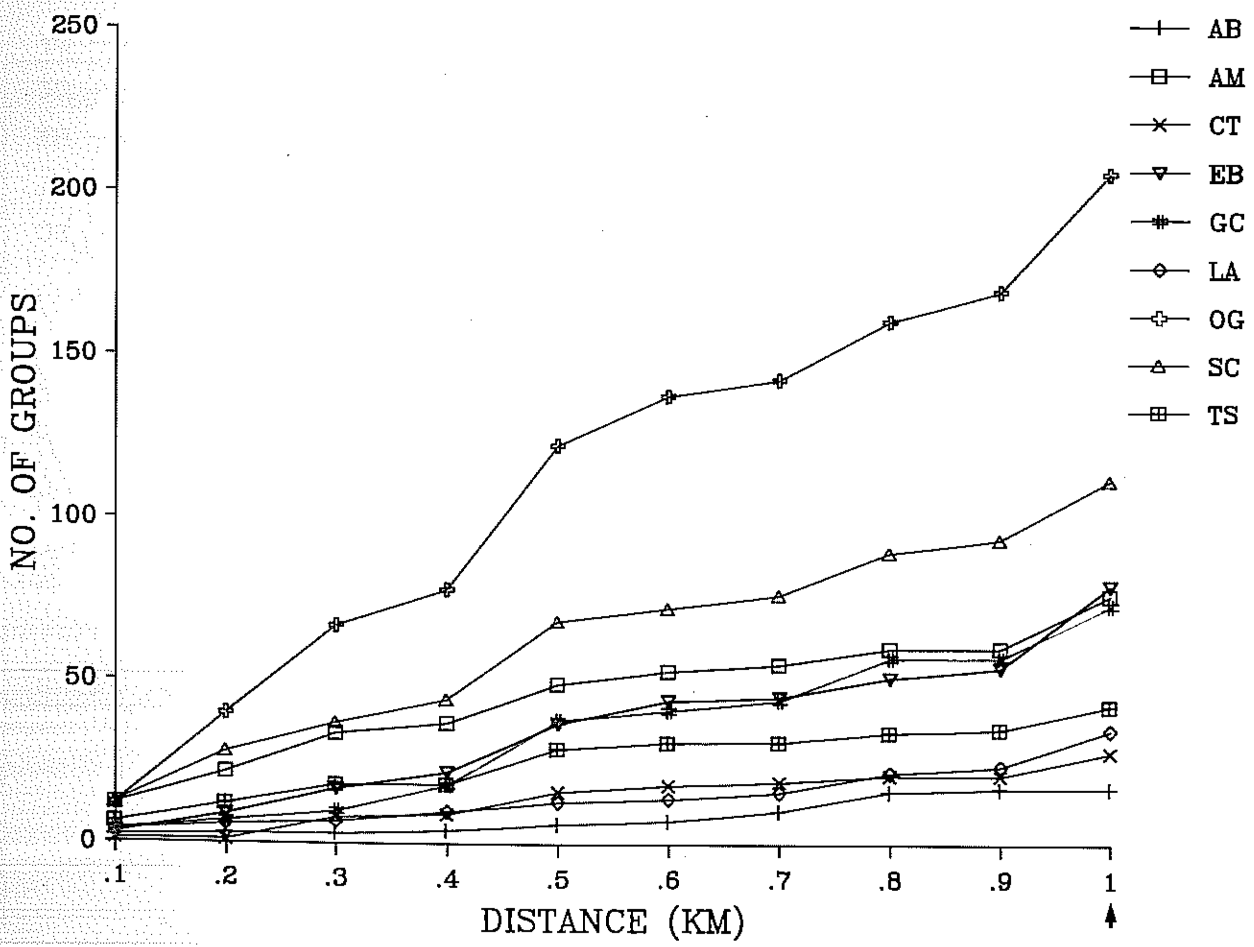

FIGURE 4: The cumulative distribution of sightings of groups of large game species at increasing distances away from transect lines in the August 1990 aerial census of Etosha National Park. (Arrow denotes intended half-transect width) (Species codes as in Figure 3).

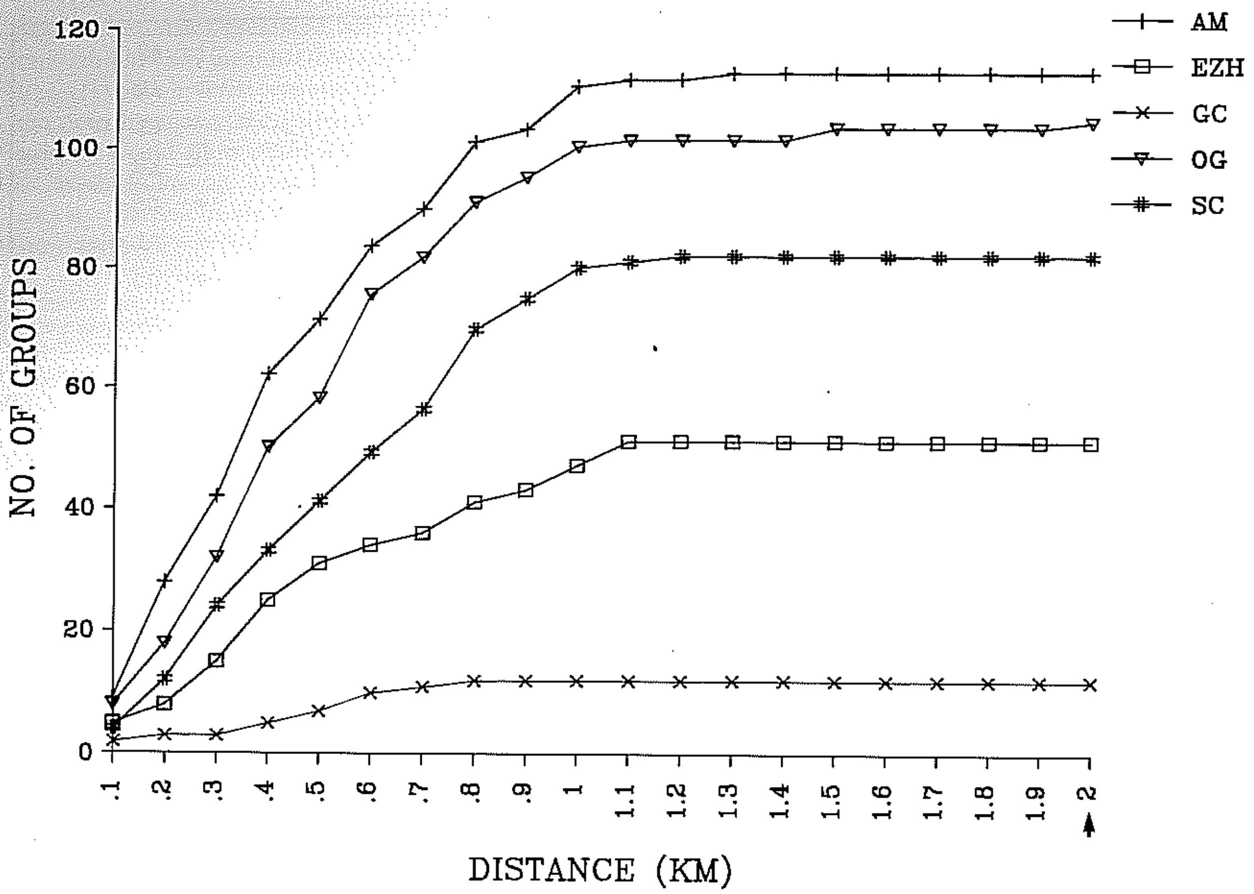

FIGURE 5: The cumulative distribution of sightings of groups of large game species at increasing distances away from transect lines in the May 1990 aerial census of the Kaokoveld (Skeleton Coast Park, Damaraland, western Kaokoland) (Arrow denotes intended half-transect width). (Species codes as in Figure 3, EZH= Hartmann's zebra).

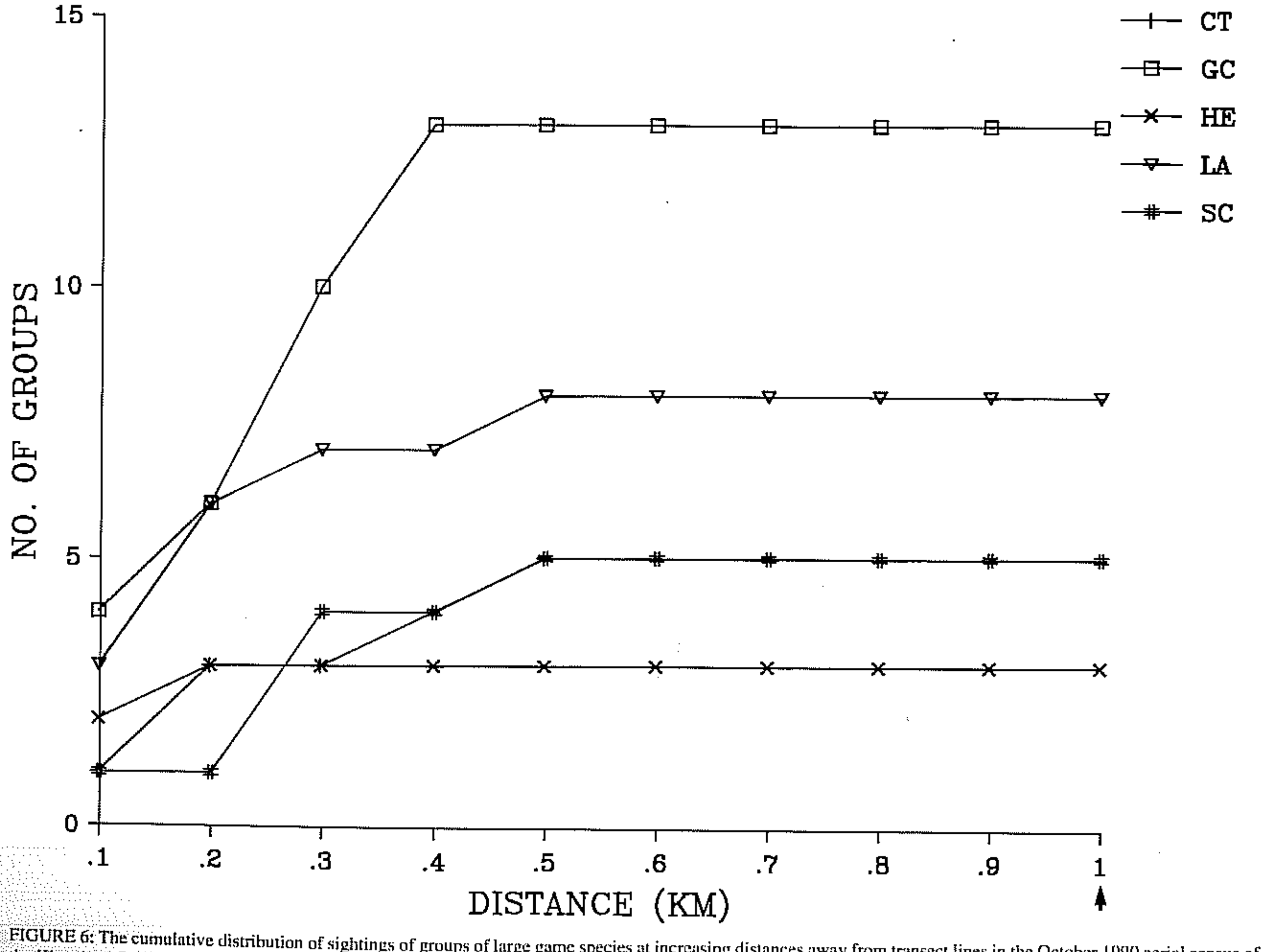

FIGURE 6: The cumulative distribution of sightings of groups of large game species at increasing distances away from transect lines in the October 1990 aerial census of the Khaudom Game Reserve (Arrow denotes intended half-transect width). (Species codes as in Figure 3, HE= roan antelope).

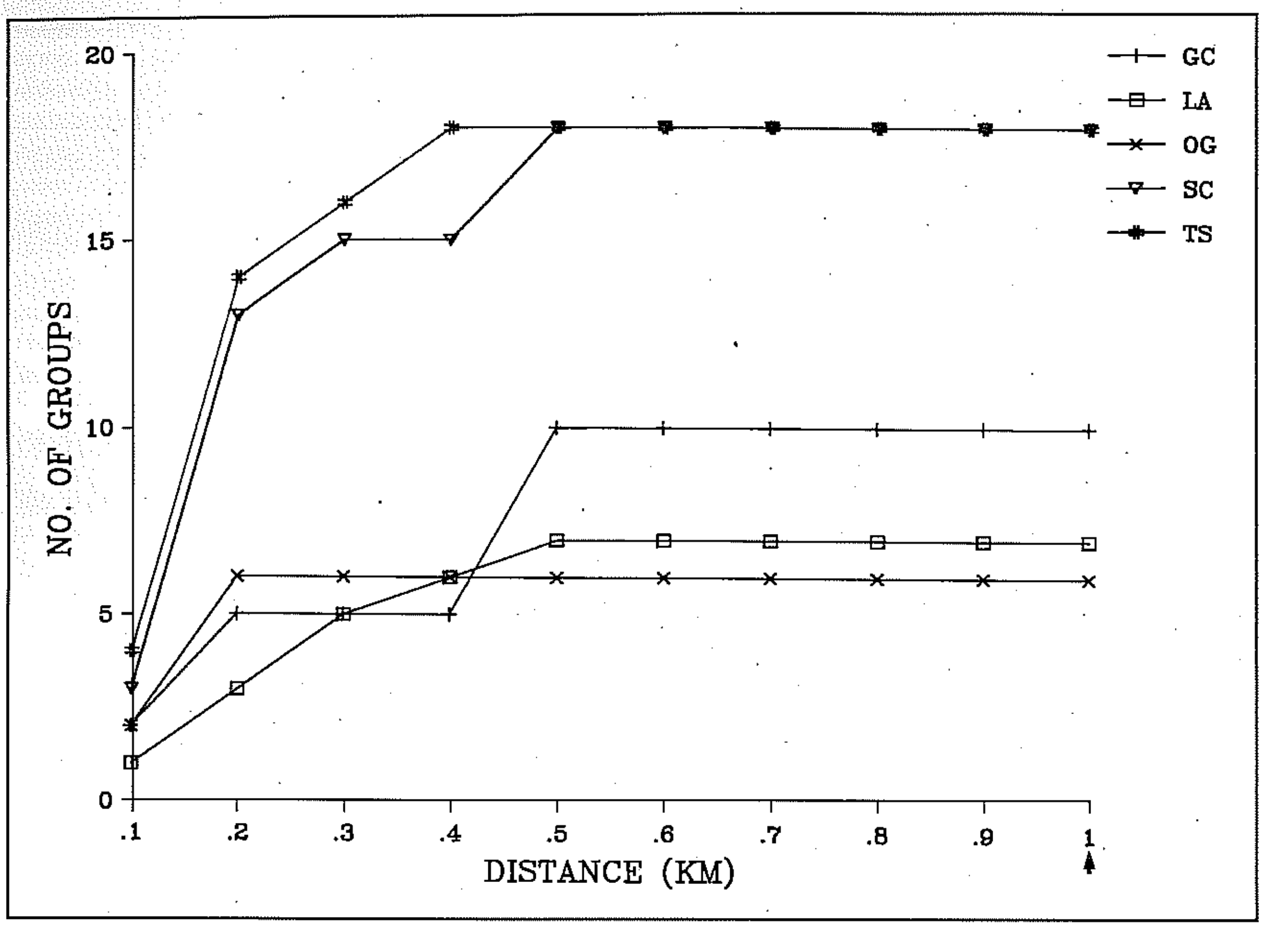

FIGURE 7: The cumulative distribution of sightings of groups of large game species at increasing distances away from transect lines in the October 1990 aerial census of eastern Bushmanland (Arrow denotes intended half-transect width). (Species codes as in Figure 3).

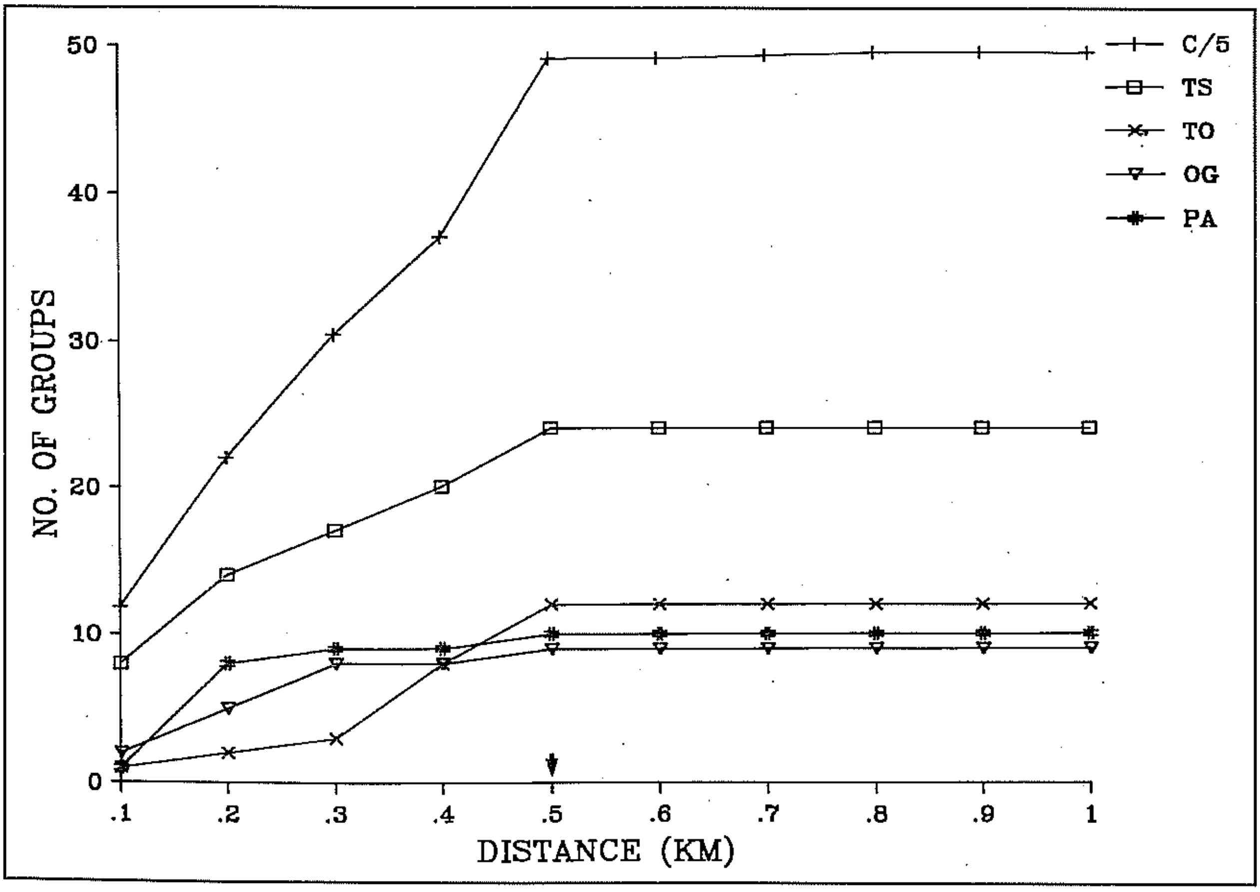

FIGURE 8: The cumulative distribution of sightings of groups of large game species at increasing distances away from transect lines in the November 1990 aerial census of approximately 1800 km² commercial farmland near Grootfontein (Arrow denotes intended half-transect width). (Species codes as in Figure 3, C= cattle, PA= warthog).

TABLE 2: Effective strip widths determined from the pattern of cumulative sightings over increasing distance from the aircraft for large game species counted in five census areas in northern Namibia.

SPECIES[1]	APPROX. LINEAR INCREASE IN SIGHTING (0-) IN km	EFFECTIVE STRIP WIDTHS IN km
ETOSHA		
La	1	2
Sc	0.5	1
Ct	0.5	1
Og	0.5	1
Eb	0.5	1
Ab	(1)[4]	(2)[4]
To[2]	(1-2)[4]	(1-2)[4]
Am	0.5	1
Gc	0.5	1
Ts	0.5	1
Db[2]	0.5	1
Amp[3,2]	(<0.5)[4]	(<0.5)[4]
Ezh[5,2]	0.5	1
KAOKOVELD		
La[2]	2	4
Sc	1	2
Og	1	2
Ezh	1.1	2.2
Gc	0.8	1.6
Am	1	2
KHAUDOM		
La	0.5	1
Sc	0.5	1
Ct	(0.3)[4]	1
Og[2]	0.5	1
He[6]	(0.2)[4]	1
Gc	0.4	1
EASTERN BUSHMANLAND		
La	0.5	1
Sc	0.5	1
Og	0.2	0.4
Gc	0.5	1
Ts	0.4	0.8
GROOTFONTEIN FARMS		
C	0.5	1
Og	0.3	0.6
To	0.5	1
Ts	0.5	1
Pa[7]	0.2	0.4

[1] As in Table 1

[2] Not illustrated in Figures 3-8

[3] Black-faced impala (*Aepyceros melampus petersi*)

[4] Sample sizes insufficient

[5] Hartmann's zebra (*Equus zebra hartmannae*)

[6] Roan antelope (*Hippotragus equinus*)

[7] Warthog (*Phacochoerus aethiopicus*)

northern Namibia. Despite this, censuses in the different census areas are characterized by a general lack of standardization and continuity. Bias has largely been ignored and population trends described from the previous census record are questionable. Escalating costs of aerial censuses have made a further change of method inevitable. Random transect sample counts have recently been done in census areas previously counted by total area coverage methods (Lindeque & Lindeque 1997) and with new emphasis on game on private land and adjacent to parks, the opportunity exists to develop a standard census method based on relevant sightability data for each census area.

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Aerial sample counts of large game in northern Namibia

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ABSTRACT

Simulated samples from total aerial censuses in Etosha National Park were used to assess inexpensive sample count methods designed for most large game species in northern Namibia. Random transect samples yielded population estimates with greater precision than systematic or weighted transect samples. Relatively low densities and extreme clumping in the distribution of populations within census zones resulted in imprecise sample count estimates. The precision of population estimates could be enhanced by using the number of groups sighted instead of the number of individuals per group, and after-the-event stratification. This combination of treatments has made a sample aerial design feasible for areas with highly aggregated game distributions but overall low game densities, but extensive stratification of aerial counts will be essential to further improve precision of population estimates of virtually all large game species.

INTRODUCTION

Total coverage of protected areas by aerial transects has thus far been the most important method used to monitor population trends of large game in northern Namibia. Several major sources of error and bias can occur in a total aerial census (Norton-Griffiths 1978) and total censuses are often not easy to repeat or standardize. The Namibian Ministry of Environment & Tourism has nevertheless accepted these limitations and has attempted to maintain its long-term schedule of censusing parks in this way. We have, however, finally reached the point where the cost of the census schedule is unaffordable. The need for better and more frequent censuses is ironically greater than ever before, as recent changes in conservation philosophy have emphasized the harvesting of game in or around parks to the benefit of rural communities. Better, more frequent, and more efficient monitoring of population trends, are required if interventive management of game populations is to be successfully applied on a sustainable basis. Alternative census methods therefore have to be developed, in order to find a compromise between our data requirements and financial resources.

A major censusing problem applicable to all conservation areas in northern Namibia is that game densities are lower and game distribution is more clumped than in those parts of Africa where the classic aerial census methods were developed (eg. Sinclair 1972, Norton-Griffiths 1973, Pennycuick *et al.* 1977). These methods do not necessarily yield adequate estimates of population size if applied to a different censusing environment. The process of refining and validating a census technique is problematical, particularly when the direction of development is towards a less intensive counting technique. Each method used to derive a population estimate has its own inherent sources of error, and can often not be used to validate an alternative method (Norton-Griffiths 1978). The accuracy of estimates derived from "total censuses" has never been assessed and these consequently have limited use in the validation of any new method, particularly as previous total censuses were usually not standardized. We are thus left with individual sample characteristics such as variance, as the only objective assessment of the validity of population estimates, derived from sample count methods.

The lack of funds to do total aerial censuses of several parks in 1990 forced us to use a sample count method, the development of which was based on sample simulations of previous total censuses. The aim of this paper is to evaluate the feasibility of aerial sample counting as a possible future standard census method for some parks in northern Namibia.

MATERIALS AND METHODS

No additional time or funds were available to do an experimental census, but the flight plans for total area coverage aerial censuses of elephants (*Loxodonta africana*) in Etosha National Park (hereafter referred to as Etosha), were modified to allow sample simulations. A sampling system was investigated by using a series of routine elephant censuses in Etosha. This was done by selecting a sample in various ways from a series of finite transects which had to be flown in any event. Two strata were defined, the eastern woodlands where transects were spaced 2 km apart (thus 2 km wide) from a randomly chosen starting point, and the western shrubland with transects at 4 km intervals. A maximum number of 186 transects was thereby established, represented as a double row of north-south transects in two broad vegetation strata.

The feasibility of a sample estimate is assessed by determining the appropriate sampling intensity (Norton-Griffiths 1978). Optimal sampling intensity yields the minimum variance of the estimate in terms of effort expended (time, cost) and is estimated by step-by-step increasing the sample size until additional sampling units do not increase the precision of the estimate (Jolly 1969; Norton-Griffiths 1978). Jolly's (1969) method 2 for unequal sized sampling units was used to calculate the population estimate (Y) and 95% confidence limits (CL) of Y (this means there is a 95% certainty that the true number of entities lies within the stated range) (where N = the number of sample units in the population; n = the number of sample units in the sample; Z = area of the census zone; z = area of any one sample unit; y = number of animals counted in that unit, and

R = ratio of animals counted to area searched $= \frac{y}{z}$

and the population total $Y = Z R$

and population variance $Var(Y) = \frac{N(N-n)}{n} s^2y - 2Rs_{zy} + R^2 s_z^2$

and population standard error $SE(Y) = \sqrt{} Var(Y)$

and 95% confidence limits (CL) of $Y = \pm t_{(n-1\ df)} SE(Y)$

Precision of the estimate Y is expressed as the 95% CL of Y as a percentage of Y and is used to indicate optimal sampling intensity. An alternative indication of optimum sampling intensity and intra-sampling variation is obtained by expressing the homogeneity between sampling units as the percentage similarity (PS) (Gauch 1982) where:

$$PS = \frac{200 \min A_j A_k}{A_j + A_k}$$

where 200 = denominator if samples are expressed as a percentage

A_j, A_k = abundance of animals in samples j and k.
min = minimum abundance of animals in either samples j or k (by implication, the number of animals in common in samples j and k).

A computer program was written where series of transect samples were chosen at increasing sampling intensities, according to a systematic, random and weighted random sampling system.

A combined fixed-wing and helicopter census done in September 1987 was used to determine sampling intensities for other large game in Etosha. The park was divided into a helicopter and fixed-wing aircraft stratum, corresponding to predetermined "high" and "low" game densities. Three series of north-south transects were flown, using roads and fences as boundaries. Sample counts were simulated for each species separately in the two strata, as described for the elephant simulations above.

Aerial transect sample counts were done in Etosha, Khaudom Game Reserve (hereafter referred to as Khaudom) and eastern Bushmanland, in August-September 1990. A sample intensity of 30% area coverage was used and transects were randomly allocated in the three series of north-south transects previously used in Etosha, and in similar units in Khaudom and eastern Bushmanland using features such as dry rivers and fences as boundaries. All transects were flown using a Maule four-seater fixed-wing aircraft, at an altitude of c. 100 m, speed of 100 km/h, and transect widths of 2 km. We could not stratify the census area into zones of homogeneous game densities prior to the census. High density zones were demarcated during census flights, where intensive flying was used to count game concentrations. Such areas were excluded from transect areas. The distance between aircraft and game observed was estimated for as many sightings as possible, using markers on the wing struts to indicate half-transect width for each side of the aircraft.

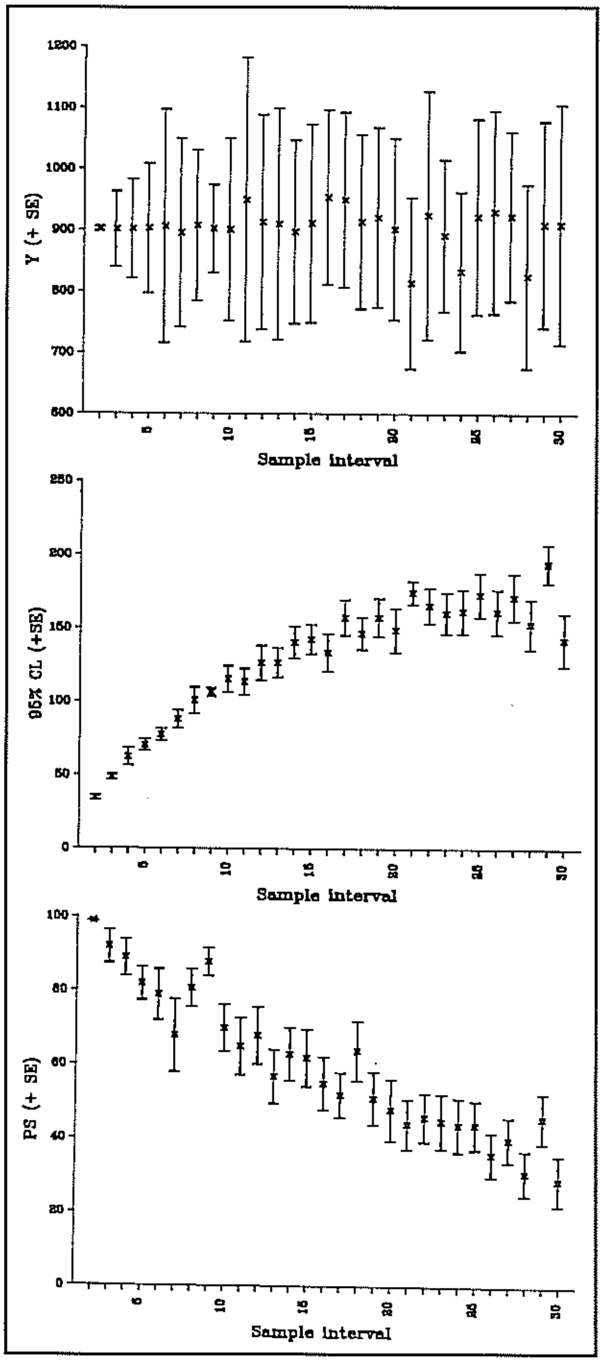

FIGURE 1: Mean (± SE) population estimates (Y), 95% confidence limits (CL) as a percentage of Y and the percentage similarity (PS) for simulated systematic transect sample counts of elephants in Etosha National Park. (Transects were not replaced in the sample, and the number of simulations are equivalent to the sample interval).

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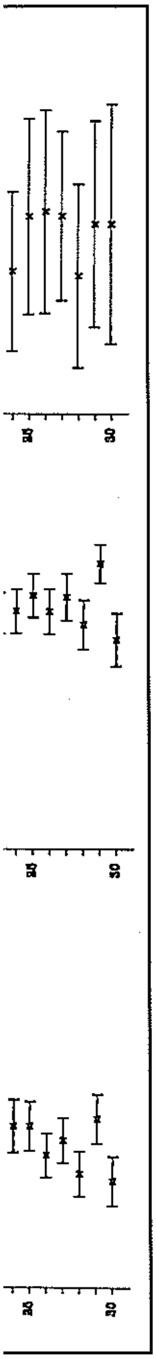

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Effective transect widths were determined as in Lindeque & Lindeque (1997), and population estimates calculated as above. A separate set of estimates was calculated for each census area excluding transects with zero counts and using the number of groups instead of actual totals observed. Population estimates in the latter instance were produced using mean group sizes for species per area. Final estimates were produced by adding the total per species observed in non-transect zones to sample estimates (Norton-Griffiths 1978).

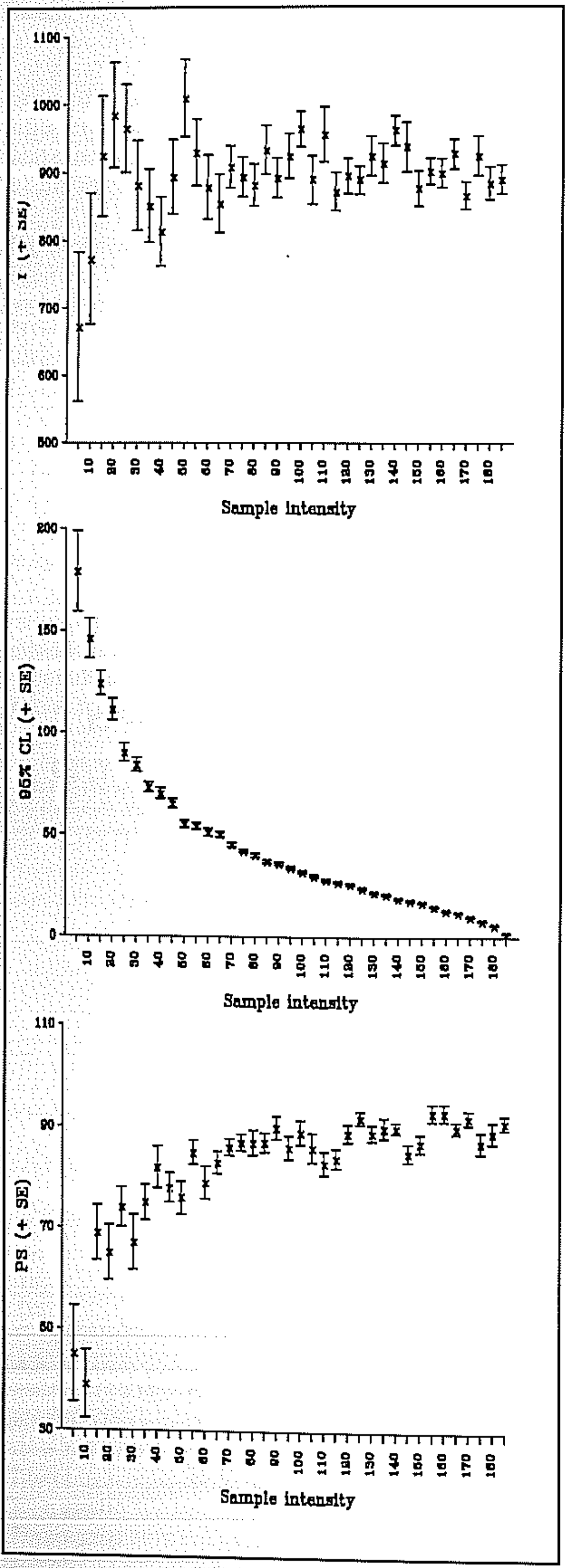

FIGURE 2: Mean (± SE) population estimates (Y), 95% confidence limits (CL) as a percentage of Y and the percentage similarity (PS) for 20 simulated random transect sample counts of elephants in Etosha National Park.

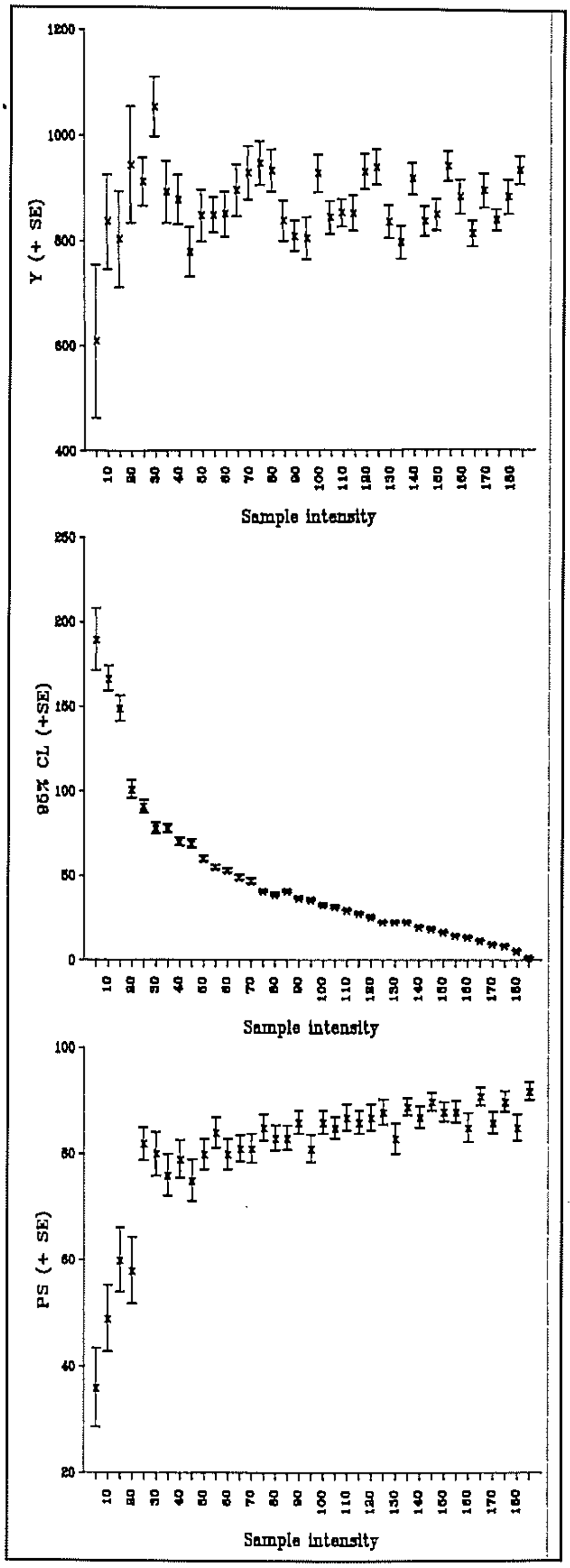

FIGURE 3: Mean (± SE) population estimates (Y), 95% confidence limits (CL) as a percentage of Y and the percentage similarity (PS) for 20 simulated weighted random transect sample counts of elephants in Etosha National Park.

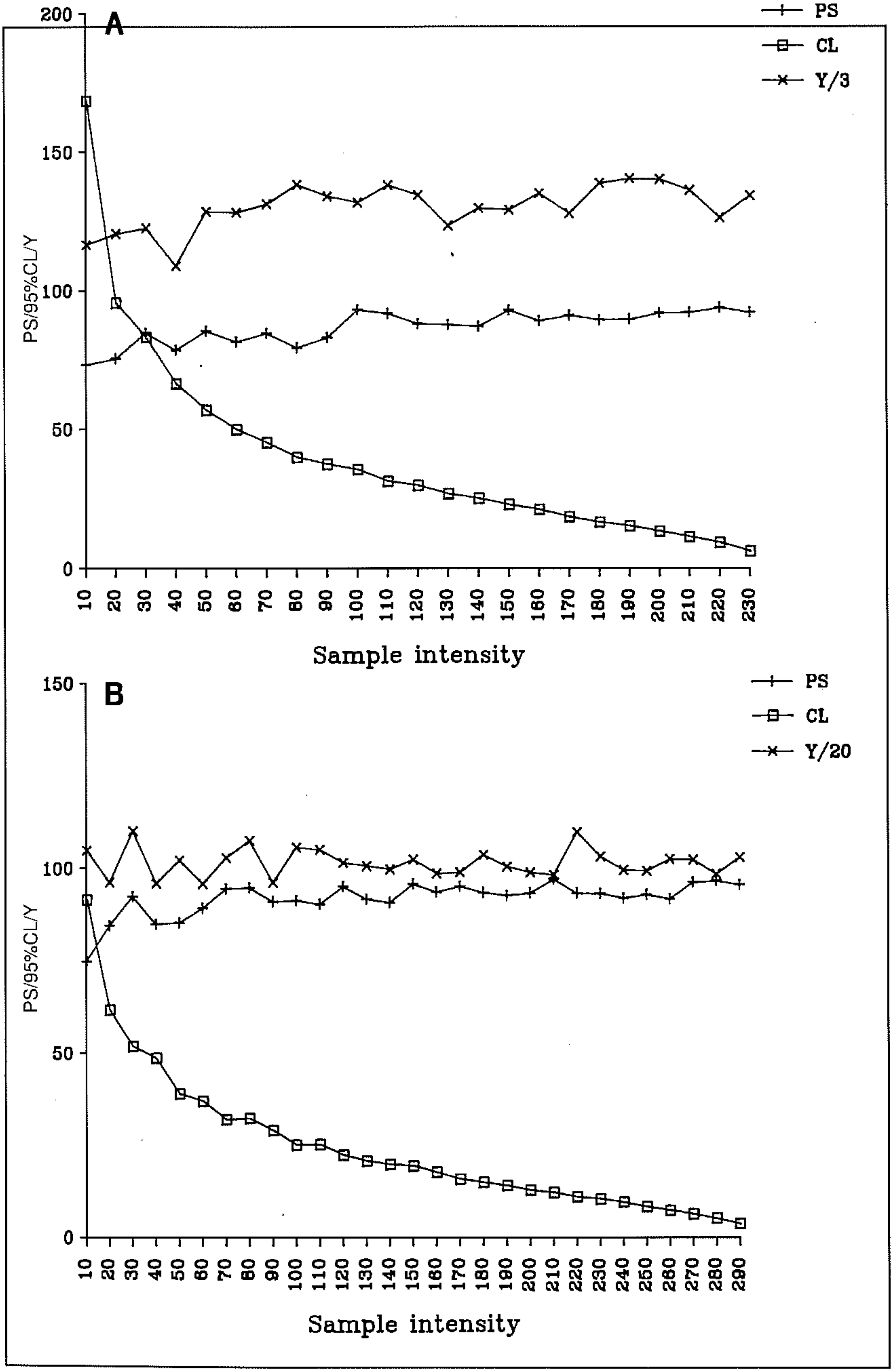

FIGURE 4: Population estimates (Y), percentage similarity (PS) and 95% confidence limits as a percentage of Y (CL) for a simulated random transect sample count of gemsbok in the low (A) and high density (B) strata in Etosha National Park.

RESULTS

Elephant census simulations

The mean (± SE) of the population estimate Y (n = 40), 95% CL (n = 40) and PS (n = 20) of random transect samples (weighted and unweighted) and systematic transect samples for the entire unstratified census area in Etosha in May 1985 are illustrated in Figures 1-3, as an example. Simulations were performed for the shrubland and woodland zones separately, but stratification did not reduce the variances associated with each estimate significantly. Simulations were also performed for an identical census in August 1985, and were similar to the May results and are not illustrated.

Population estimates derived from simulated samples in Figures 1-3 remained acceptably close to the estimate of population size obtained from the total count, but the 95% CL values only reached the <20% range of the population estimate at near maximum sampling intensity. Designing a sample census based on this simulation might therefore yield an accurate population estimate with wide confidence limits and consequently low precision. Random transect sampling (weighted and unweighted) shows a levelling off in precision at 30-40% sampling intensity. About 60-70 transects will therefore be adequate in terms of sampling efficiency, should precision not be an overriding factor. Systematic transect sampling shows greater variance in parameters and should not be used in favour of random sampling, particularly where the danger exists of coincidence with systematically distributed environmental features such as dunes and boreholes.

TABLE 1: Percentage transects required to yield population estimates (Y) with 95% confidence limits of ≤ 20% of Y, and a percentage similarity ≥ 80%, in a simulated random transect sample census of Etosha National Park.

	Sampling intensity at 95% CL ≤ 20% of population estimate, and PS ≥ 80%	
Species[1]	Low density stratum	High density stratum
La	78	67
Sc	59	41
Ct	87	76
Og	65	59
Eb	89	69
Ab	91	88
To	-	97
Am	87	72
Gc	76	55
Ts	87	60
Db	91	71

La = elephant (*Loxodonta africana*), Sc = ostrich (*Struthio camelus*), Ct = blue wildebeest (*Connochaetes taurinus*), Og = gemsbok (*Oryx gazella*), Eb = Burchell's zebra (*Equus burchelli*), Ab = red hartebeest (*Alcelaphus buselaphus*), To = eland (*Taurotragus oryx*), Am = springbok (*Antidorcas marsupialis*), Gc = giraffe (*Giraffa camelopardalis*), Ts = greater kudu (*Tragelaphus strepsiceros*), Db = black rhinoceros (*Diceros bicornis*).

[1] Species subjectively rated in descending order from most visible to least visible.

Multi-species census simulation

Figure 4 A & B illustrates a single simulation of a random sample count for gemsbok (*Oryx gazella*) in the 1987 multi-species census in Etosha as an example. Systematic transect samples were more variable for all species, and are not illustrated. Table 1 presents minimum sampling intensity per species in order to achieve population estimates with confidence limits of not larger than 20% of the population estimates. Low density stratum counts required greater sampling intensity than in the high density stratum for all species. Adequate sampling intensity did not correlate with our ranking of species according to relative visibility. Highly gregarious species seem to require more intensive sampling than those occurring in smaller groups.

Random transect sample censuses in 1990.

Population estimates were more precise than predicted by the simulations performed for a multi-species census when using a sampling intensity of 30% (Table 2). Confidence limits in all cases exceeded the 20% of Y cut-off point, and the population estimates are consequently of little value. Most species occurred in a small portion of the total number of transects flown and their distributions were highly clumped. Only Hartmann's zebras (*Equus zebra hartmannae*) and black-faced impalas (*Aepyceros melampus petersi*) have restricted distribution ranges in Etosha, as determined by habitat and/or range extension since re-introduction. All other species, except gemsbok, occurred in less than 50% of the transects flown (Table 3).

TABLE 2: Population estimates (± SE) and 95% confidence limits (CL) of large game in the transect zone in Etosha National Park in August 1990, using 2 km wide transects, and a sampling intensity of 30%.

Species***	Pop. est. Y ± SE	95% CL as a % of Y	Approx. 95% CL as % of Y predicted by simulations at 30% sampling intensity*
La	1160 ± 208	35.2	40 - 60
Sc	636 ± 91	28.1	30 - 45
Ct	1281 ± 301	46.1	55 - 80
Og	2513 ± 272	21.3	30 - 45
Eb	2664 ± 584	43.0	40 - 70
Ezh**	279 ± 108	75.8	-
Ab	389 ± 111	55.9	60 - 95
To	123 ± 60	95.9	65 - 85
Am	3498 ± 605	33.9	50 - 65
Gc	659 ± 94	28.0	30 - 65
Ts	487 ± 93	37.5	40 - 80
Amp**	212 ± 110	101.4	-
Db	107 ± 20	35.7	50 - 75

* low and high estimates correspond to simulations of counts in high and low game densities respectively, using the 1987 multi-species census in Etosha.

** Ezh = Hartmann's zebra (*Equus zebra hartmannae*), Amp = black-faced impala (*Aepyceros melampus petersi*).

*** See Table 1.

TABLE 3: Sightings per transect of each species during the 30% random transect sample count in Etosha National Park in 1990. (A total of 162 transects were flown).

Species***	2 km transect width*			1 km transect width**		
	no. (%) transects with sightings	total number counted	total number of groups	no. (%) transects with sightings	total number counted	total number of groups
	A	B	C	A	B	C
La	34(21.0)	498	44	22(13.6)	258	24
Sc	75(46.3)	273	121	55(34.0)	187	77
Ct	25(15.4)	550	44	19(11.7)	382	33
Og	103(63.6)	1079	222	83(51.2)	631	140
Eb	57(35.2)	1144	90	37(22.8)	560	48
Ab	16(9.9)	167	18	7(4.3)	63	7
Ezh	7(4.3)	120	17	6(3.7)	78	10
To	6(3.7)	53	6	5(3.1)	51	5
Am	50(30.9)	1502	91	38(23.5)	1003	64
Gc	47(29.0)	283	92	31(19.1)	172	57
Ts	32(19.8)	209	49	24(14.8)	146	37
Amp	5(3.1)	91	5	2(1.2)	51	2
Db	21(13.0)	46	27	12(7.4)	30	15

* using all sightings within c. 1 km from the aircraft
** using all sightings within c. 500 m from the aircraft
*** See Tables 1 & 2

The effects of a clumped distribution on sample estimates is demonstrated by hypothetical samples of 100 individuals counted in 10 equal-sized transects (Table 4). Population estimates derived from transect distributions representing three different degrees of clumping remained constant, but the standard errors and 95% confidence limits declined drastically with increasing homogeneity within a sample. Most species counted in Etosha showed distributions similar to A and B in Table 4, while case C represents an ideal case where eg. stratification had ensured that transects with uniform game densities were sampled together.

TABLE 4: Population estimates (Y ± SE, ± 95% CL as % of Y) of hypothetical sample distributions of 100 individuals in 10 transects of a 33% sample count, representing variable degrees of clumping.

	A	B	C
Transect no.	Total counted	Total counted	Total counted
1	0	0	11
2	0	50	9
3	0	0	10
4	0	0	11
5	100	0	9
6	0	0	8
7	0	30	9
8	0	0	10
9	0	0	11
10	0	20	12
Total	100	100	100
Pop. est. Y	300	300	300
± SE	245	137	10
95% CL as % of Y	185	103	7

The same distributions used in Table 4 are presented in Table 5 but with the number of groups sighted instead of the number of individuals. Population estimates and variances were calculated using the mean group sizes in each sample and were similar in all three cases, as well as to corresponding population estimates and variances in Table 4. Using the number of groups as the sample unit thus did not reduce the variance of the sample. Using sightings of groups instead of actual totals counted, allows correction factors to be used in cases where it is impossible to count groups accurately, eg. densely packed elephant herds or giraffe (*Giraffa camelopardalis*) herds partly concealed by clumps of trees, using independently obtained data on mean group sizes at the time of censusing.

Discarding transects with zero sightings improved the variance of the estimate without biasing the population estimate itself. Table 6 presents two hypothetical samples where population estimates and variances were calculated with and without transects with no sightings of the hypothetical species. In both cases, using case B from Tables 4 & 5, both estimates of variance were reduced following exclusion of transects with no sightings. This procedure is similar to after-the-event stratification discussed in Yates (1960), Sinclair (1972), Bell *et al.* (1973) and Norton-Griffiths (1973, 1975, 1978), and might be useful as an alternative estimator of variance associated with sample estimates of population size. Alternative population estimates with generally reduced sample variances can also be calculated by using the effective strip widths as opposed to intended strip widths (Lindeque & Lindeque 1997), group sizes rather than individuals and excluding transects with zero sightings as in Tables 7-9.

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TABLE 5: Population estimates (Y ± SE, ± 95% CL as % of Y) of hypothetical sample distributions of 100 individuals in 10 transects of a 33% sample count, using the number of groups sighted.

	Transect no.	A	B	C
	1	0	0	1
	2	0	2	1
	3	0	0	1
	4	0	0	2
	5	2	0	1
	6	0	0	1
	7	0	1	1
	8	0	0	2
	9	0	0	2
	10	0	1	3
Total number	10	2	4	15
Mean group size		50.0	25.0	6.7
Groups	Y	6	12	45
	± SE	4.9	5.5	5.5
	± 95% CL as % of Y	184.7	102.1	27.5
Total	Y	300	300	302
	± SE	244.9	135.4	36.7
	± 95% CL as % of Y	184.7	102.1	27.5

TABLE 6: Population estimates (Y ± SE, ± 95% CL as % of Y) of hypothetical sample distributions of 100 individuals in 10 transects of a 33% sample count, using all transects and excluding those with no sightings.

Transect No.	B* Total counted	B* Total groups counted	
1	0	0	
2	50	2	
3	0	0	
4	0	0	
5	0	0	
6	0	0	
7	30	1	
8	0	0	
9	0	0	
10	20	1	
Total	100	4 (Mean group size 25.0)	
Y(n trans. 10)	300	12	300
± SE 137	5	135	
± CL as % of Y	103	102	102
Y(n trans. 3)	300	12	300
± SE 65	3	61	
± CL as % of Y	93	88	88

* Corresponding distributions used in Tables 4 & 5 respectively.

TABLE 7: Population estimates (Y ± SE and 95% confidence limits as % of Y) in the random transect sample census of Etosha National Park (A), corrected population estimate based on effective strip widths (B), and an alternative population estimate (C) based on the exclusion of transects with zero sightings, effective transect widths and using group sizes instead of individuals.

Species *	A Y ± SE; 95%CL as % of Y	B[1] Y ± SE; 95%CL as % of Y	C Y ± SE; 95%CL as % of Y	Non-[2] Transect counts
La	1469 ± 208; 35.2	1469 ± 208; 35.2	1556 ± 88 ; 14.4	309
Sc	681 ± 91 ; 28.1	921 ± 183; 41.1	840 ± 57 ; 14.4	50
Ct	2014 ± 301; 46.1	2532 ± 549; 60.4	2950 ± 331; 31.3	733
Og	2789 ± 272; 21.3	3220 ± 484; 32.2	3514 ± 226; 14.0	276
Eb	4445 ± 584; 43.0	4389 ± 750; 56.4	5405 ± 313; 17.7	1781
Ezh	451 ± 108; 75.8	535 ± 174; 93.6	844 ± 192; 73.3	172
Ab	493 ± 111; 55.9	493 ± 111; 55.9	604 ± 51 ; 21.9	104
To	206 ± 60 ; 95.9	(206 ± 60 ; 95.9)[3]	—	83
Am	5870 ± 605; 33.9	7043 ± 966; 40.5	8456 ± 866; 29.1	2372
Gc	761 ± 94 ; 28.0	897 ± 179; 44.1	818 ± 133; 38.1	102
Ts	516 ± 93 ; 37.5	709 ± 191; 55.2	669 ± 86 ; 27.9	29
Amp	215 ± 110; 101.4	(215 ± 110; 101.4)[3]	—	3
Db	111 ± 20 ; 35.7	144 ± 40 56.4	313 ± 40 ; 26.8	4

* See Tables 1 & 2.

1. Effective transect widths determined following Lindeque & Lindeque (1993) with effective sampling intensities consequently either 30% or 15%. The effective transect width for elephants and red hartebeest was 2 km and 1 km for all others.
2. Additional sightings in non-transect areas were added to the population estimates from transect strata in estimates A, B and C (Norton-Griffiths 1978).
3. Data insufficient to determine effective counting strip width.

TABLE 8: Population estimates (Y ± SE and 95% confidence limits as % of Y) in the random transect sample census of Khaudom Game Reserve based on effective strip widths (B), and an alternative population estimate based on the exclusion of transects with zero sightings, effective transect widths and using group sizes instead of individuals (C).

Species *	B^1 Y ± SE ;95%CL as % of Y	C Y ± SE ;95%CL as % of Y	Non-^{2} Transect counts
La	1208 ± 420; 82.6	918 ± 88 ; 40.4	169
Sc	35 ± 16 ; 92.9	36 ± 5 ; 38.5	0
Ct	190 ± 101; 124.8	296 ± 51 ; 79.6	26
Og	12 ± 12 ; 207.2	44 ± 10 ;280.7	0
Gc	201 ± 55 ; 61.7	230 ± 31 ; 32.7	19
He^3	220 ± 198; 186.5	212 ± 1 ; 6.9	3
Dl^4	—	—	8
Ra^5	—	—	5

* See Tables 1 & 2.

1. Effective transect widths determined following Lindeque & Lindeque (1993) with effective sampling intensities consequently either 30% or 15%. The effective transect width for elephants and red hartebeest was 2 km and 1km for all others.
2. Additional sightings in non-transect areas were added to the population estimates from transect strata in estimates B and C (Norton-Griffiths 1978).
3. Roan (*Hippotragus equinus*)
4. Tsessebe (*Damaliscus lunatus*)
5. Reedbuck (*Redunca arundinum*)

TABLE 9: Population estimates (Y ± SE and 95% confidence limits as % of Y) in the random transect sample census of eastern Bushmanland based on effective strip widths (B), and an alternative population estimate based on the exclusion of transects with zero sightings, effective transect widths and using group sizes instead of individuals (C).

Species *	B^1 Y ± SE ;95%CL as % of Y	C Y ± SE ;95%CL as % of Y	Non-^{2} Transect counts
La	301 ± 188; 173.7	237 ± 90 ; 172.5	13
Sc	371 ± 185; 107.5	372 ± 65 ; 36.7	8
Ct	234 ± 145; 131.1	179 ± 1 ; 0	5
Og	216 ± 162; 158.8	364 ± 70 ; 61.4	8
Ab	18 ± 9 ; 103.0	79 ± 1 ; 0.7	14
Gc	92 ± 44 ; 100.8	96 ± 26 ; 66.2	4
Ts	1443 ± 133; 53.8	496 ± 77 ; 34.4	31
He	—	—	1
Dl	—	—	5
Scaf^3	—	—	14

* See Tables 1 & 2.

1. Effective transect widths determined following Lindeque & Lindeque (1993) with effective sampling intensities consequently either 30% or 15%. The effective transect width for gemsbok was 0.4 km and 1km for all others.
2. Additional sightings in non-transect areas were added to the population estimates from transect strata in estimates B and C (Norton-Griffiths 1978).
3. Buffalo (*Syncerus caffer*)

DISCUSSION

For a conservation agency such as the Namibian Ministry of Environment & Tourism, which is used to working with purportedly exact population estimates derived from "total" aerial censuses, sample estimates might seem vague. Single estimates of population sizes have invariably been produced from "total" censuses, simply because there is no way of measuring bias, variance or error in such censuses (Norton-Griffiths 1978). Sample counts done in northern Namibia in 1990 required only about 10% of the expenditures in finances and effort of total coverage aerial censuses done previously. The price for this reduction in effort required is extensive data processing and manipulation. Population estimates and variances calculated from sample censuses are inevitably more complex and intuitively seem more vague than "total" census arithmetic, but such estimates give numerical estimates to probable ranges, previously recognized to exist but never quantified.

Sample aerial counts are widely used in African conservation areas and elsewhere in the world, and are suitable for most animal species except the very cryptic ones. The methodology and theory of sample counts have been explored exhaustively in Yates (1960), Cochran (1963), Jolly (1969), Norton-Griffiths (1973, 1978), Caughley (1977), Eberhardt & Simmons (1987) and others. Commonly used techniques might, however, require modifications to be suitable for local conditions and different species. Without modifications, sample techniques result in unusable population estimates with unacceptably high confidence limits in censuses of species occurring at low density and/or in a clumped distribution. A critical modification required in future sample counts of virtually all large mammals in northern Namibia is considerable improvements in stratification, where stratification prior to a census should aim to improve the homogeneity of samples. The cost of doing stratification of the census zone by air would probably not exceed the cost of the sample count, and would thus still be much less expensive than a total count. Minor increases in the sampling intensity of a survey will in most cases not reduce the homogeneity of the sample, as predicted by the simulations presented in Figs. 1 - 4 and Tables 1 and 2. A 30% sampling intensity as used in 1990 in northern Namibia already exceeds sampling intensities in large game censuses in neighbouring countries and east Africa.

We have presented population estimates from sample counts subjected to two procedures aimed at reducing variance associated with the estimates, namely removing transects with zero sightings and using groups instead of individuals. Both procedures might be considered questionable, and reducing the heterogeneity of transect samples due to the presence of a majority of transects with zero sightings should rather be attempted through improvements in stratification. Using groups instead of individuals should only be attempted if mean group sizes are determined independently and the variance in group sizes is included in the overall estimate of variance.

By using such modifications, and recognizing that technologies not available to us at present would further improve estimates, we feel that population estimates derived from aerial sample counts in northern Namibia may be at least as good as total count estimates. It is, however, clear that locally rare species or highly aggregated species might require alternative counting procedures. The bias in total aerial counts has not been determined, and population estimates based on such counts cannot be used uncritically to validate sample counts. Recent population estimates of large game in the three census areas are nevertheless presented in Tables 10-12, as well as an indication of which species would require special counting techniques in future, other than a general improvement in stratification. Aerial counting techniques are regarded as unsuitable for only two large game species in Etosha, namely eland (*Taurotragus oryx*) and black-faced impala (other than non-target species such as the large predators). The density of eland in Etosha has reached such a low level that special methods such as mark-resighting will be required, despite the fact that eland are usually adequately visible from the air. Protracted total area coverage censuses will not necessarily be a viable alternative, as eland are highly mobile and groups are unstable in Etosha. Black-faced impalas are not adequately visible from the air and ground counting is required for this species.

Giraffe and kudu (*Tragelaphus strepsiceros*) are both marginally countable from the air, the problem being that observers do not seem to count entire groups, due to partial concealment and differential sightability of different age groups and sexes. Both species usually "freeze" when approached by a fixed-wing aircraft, with kudu bulls and senior adult giraffe bulls often appearing more visible due to the presence of horns or their darker coat colour. Most observers feel that with more time available more individuals will eventually be spotted. It is thus recommended that independent data on group sizes be obtained during a census in order to use mean group size as a correction factor for these two species.

TABLE 10: Recent population estimates based on total aerial censuses inEtosha National Park, compared to an aerial sample count.

Species[1]	Total aerial censuses[2]			15-30% Random transect sample estimate ± 95% CL		Future improvements[4]
	1982	1984	1987	1990 B[5]	1990 C[5]	
La	2202	2464	2021	1469 ± 408	1556 ± 180	Stratify
Sc	1835	1311	1460	921 ± 358	840 ± 114	Stratify
Ct	2195	2253	2617	2532 ± 1087	2950 ± 694	Stratify
Og	5081	3248	2191	3220 ± 948	3514 ± 453	Stratify
Eb	7970	5332	4761	4389 ± 1471	5405 ± 642	Stratify
Ezh	2665	620	449	535 ± 340	844 ± 494	Stratify
Ab	396	486	548	493 ± 218	604 ± 110	Stratify
To	692	353	259	(206 ± 118)	—	Mark-resighting
Am	16011	10722	8162	7043 ± 1892	8456 ± 1770	Stratif
Gc	1184	1376	1129	897 ± 351	818 ± 273	Correct. factor
Ts	1041	1061	970	709 ± 375	669 ± 179	Correct. factor
Amp	93	164	180*	(215 ± 215)*	—	Ground counts
Db	121	150	142**	144 ± 79**	313 ± 83	Ground counts
Total	41486	29540	24889	22773 ± 7860	25969 ± 4992	
Crude Density[3] (n/km²)	(2.3)	(1.6)	(1.4)	(1,3 ± 0.4)	(1.4 ± 0.3)	

1 As in Tables 1 & 2
2 Unpublished data, Ministry of Wildlife, Conservation & Tourism
3. Using c.18000 km² of savanna in Etosha.
4. See text.
5. See Table 7.
* Single-species ground counts indicate a population of 500-1000 in Etosha (F.G. Joubert, pers. comm.)
** Waterhole counts of known individuals indicate a population of c.300 in Etosha (A.D. Cilliers, pers. comm.).

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The successful introduction of *Oreochromis mossambicus* in salt pans along the Namib coast

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ABSTRACT

Twenty four *Oreochromis mossambicus* from the Hardap Dam, Namibia, were introduced during 1986, into salt pans at Swakopmund on the Namib coast. The salt concentration of the salt pans is 42042 mg/l TDS, 16,6% higher than that of seawater. The fish adapted well to the conditions, bred successfully and maintained a healthy population. The population in the Hardap Dam and those in the salt pans show similar growth rates with the Hardap Dam population having a somewhat better length/mass relationship.

INTRODUCTION

The occurrence of *O. mossambicus* in salt water is well documented. According to Kirk (1972) it is assumed that tilapia generally have evolved from a marine ancestor which penetrated fresh water and that this accounts for the large number of euryhaline species. Fowler (1934) reported that *O. mossambicus* occurs in Durban Bay, South Africa, in waters of high salinity. Potts *et al.* (1967) have shown that *O. mossambicus* fry can live and remain healthy in 200% (72000 mg/l TDS) sea water.

Experiments by Brock (1954) with a single brood of *O. mossambicus* divided into two groups, one reared in fresh water and the other in salt water, showed no significant difference in their growth rates and both groups spawned successfully. A similar experiment by Canagartnam (1968) showed that *O. mossambicus* grew better in 100% (36000 mg/l TDS) sea water than in fresh water. They also spawned successfully. This supported his earlier finding that euryhaline fish grow better in a saline medium and can thrive in a wide range of salinities (Canagartnam 1959). Hodgkiss and Man (1977) reported a slower growth rate of tilapia in Hong Kong when salinities decreased.

Whitfield and Blaber (1979) found that *O. mossambicus* could adapt to a salinity range of 0 - 120000 mg/l TDS, which occurred in their study area at Lake St. Lucia, South Africa. Whitfield and Blaber (1979) noted, however, the absence of *O. mossambicus* from most of the estuaries that are permanently open to the sea. They concluded that, while *O. mossambicus* is able to tolerate seawater as well as slow changes in salinity, it is incapable of withstanding rapid changes in salinity. Allanson *et al.* (1971) found that *O. mossambicus* is able to tolerate low temperatures in 5000 mg/l TDS sea water better than in fresh water.

Twenty four *O. mossambicus* were obtained from the Fresh Water Fish Institute at Hardap Dam and introduced into the salt pans at Swakopmund by the owner during the autumn of 1986. The study was initiated to determine the adaptability and to make growth comparisons of the same strain of *O. mossambicus* between high salinity and fresh water.

STUDY AREA AND METHODS

The salt pans (22°37'S;14°29'E) are situated outside Swakopmund, along the Namibian coast (Plate 1). The pans are manmade and are used for salt production. *Oreochromis mossambicus* was introduced and remains confined in pans A and B (surface areas approximately 29 ha and 11 ha, respectively). The depth of the two pans are approximately 2 m with a monthly water flow of 485 333 m^3 from the ocean.

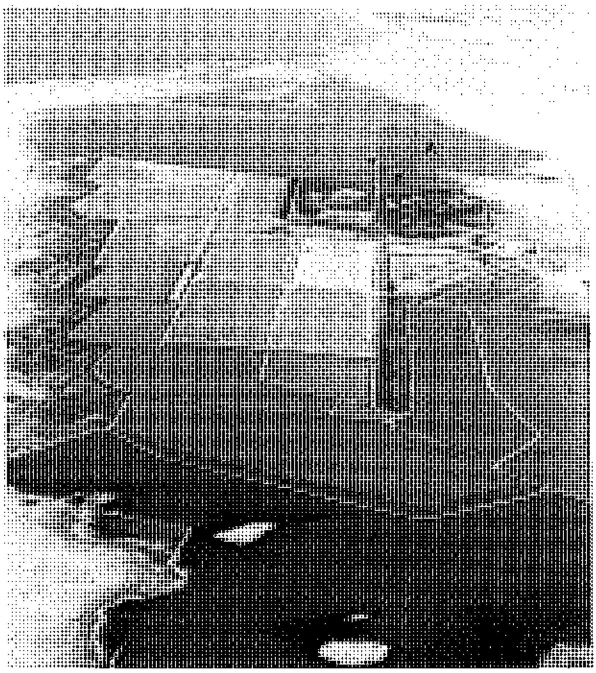

PLATE 1. Aerial photograph of the Swakopmund Salt Pans, Namibia, showing the two pans (A and B) into which *Oreochromis mossambicus* were placed.

A full range of gill-nets consisting of 35, 45, 57, 73, 93, 118 and 150 mm stretch mesh, each 30 m long were used. The nets were set for 72 h and were cleaned every 12 h.

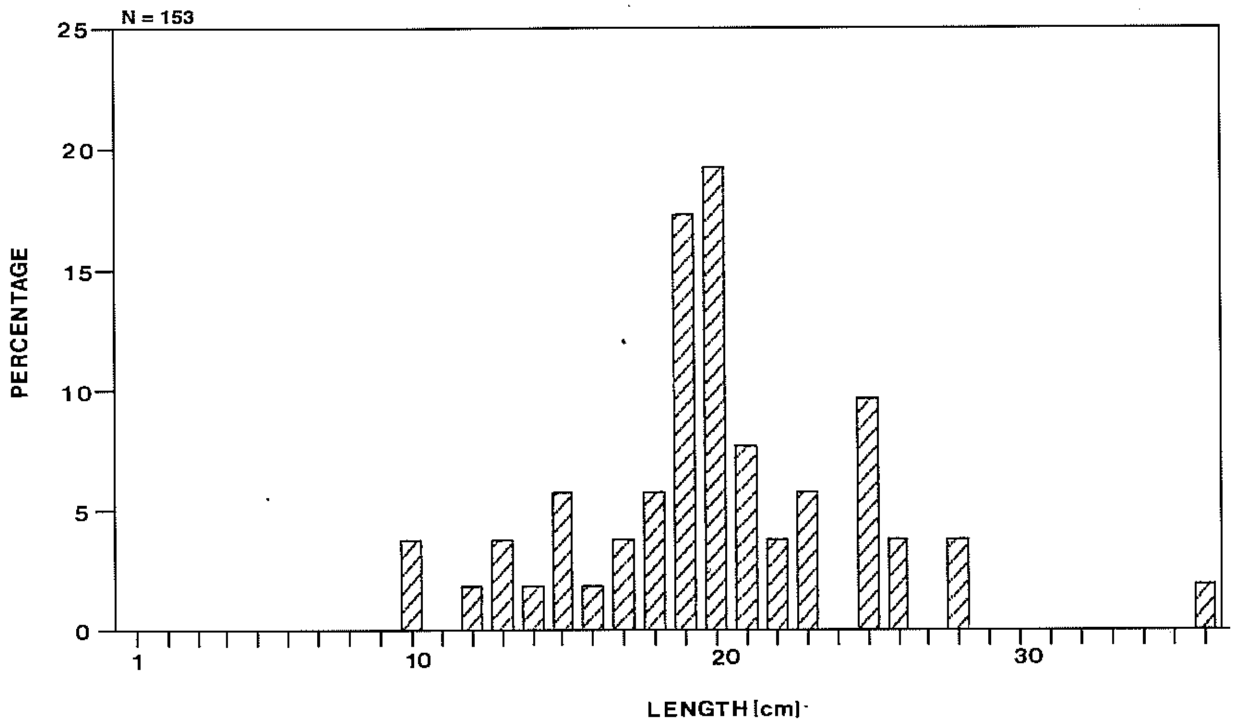

FIGURE 1. Length frequency of *Oreochromis mossambicus* in Salt Pans at Swakopmund.

The fish were weighed with a Mettler P20 balance and their total lengths were measured to the nearest cm. All the fish were sexed by an internal gonad examination. Scales were collected in order to determine annuli. The Bhattacharya method was used to determine cohorts while Munro's method was used to determine the phi prime (Ø) (Sparre *et al.* 1989). The VONBER programme in the LFSA software was used for the determination of the Von Bertalanffy growth parameters (L_∞ = L-infinity, k = curvature parameter). A chi-square test was performed to examine the sex ratio statistically.

RESULTS AND DISCUSSION

The salinity of the salt pans was 42042 mg/l TDS, 16,6 % higher than that of sea water (Table 1). Water quality and water temperature in the salt pans fall within the range for suitable growth for tilapia (Van Zyl 1988). The minimum and maximum critical water temperature for *O. mossambicus* are 10°C and 38,25°C respectively (Allanson 1966; Du Plessis & Groenewald 1953; Lombard 1959; Allanson & Noble 1964; Caulton 1980). Nel (1978) found that *O. mossambicus* survived nitrite concentration up to 8,71 mg/l. According to Muir and Roberts (1982) pH levels between 4,0 and 11,0 are suitable for the survival of *O. mossambicus*. High potassium and magnesium concentrations may influence the taste of the fish. This could be an important factor when aquaculture is considered.

A total of 153 specimens were caught. Their length distribution varied between 10 cm TL and 36 cm TL (Figure 1). The fish had clearly bred successfully in the high salinity pans. Their sex ratio was found to be of 1,5:1,0 (male:female) which does not differ significantly from a 1:1 ratio (Chi-square = 2,283302, DF = 1, p ≥ 0,05). The fish were in good condition and had adapted well to the high salinity in the salt pans.

pH			8,1
Conductivity			6370,0 mS/m
Total dissolved solids (TDS)			42042,0 mg/l
Nitrate			< 0,5 mg/l
Nitrite			< 0,1 mg/l
Chloride			26400,0 mg/l
Potassium			460,0 mg/l
Magnesium			6712,0 mg/l
Turbidity			4,0 NTU
Temperature	(Summer)	Max	27,0°C
		Min	20,0°C
	(Winter)	Max	20,0°C
		Min	12,0°C

TABLE 1. Water quality and water temperature of the salt pans.

Locality	Growth parameters L_∞	k	t_0	PHI prime Ø
Salt Pan (1991)	56,2	0,14	-1,11	6,0980
Hardap Dam (1988)	54,8	0,17	0,51	6,2354

	Length/mass relationship a	b	r	N
Salt Pan (1991)	0,0136	3,0470	0,99	153
Hardap Dam (1988)	0,0105	3,1942	0,99	93

r = correlation coefficient
N = sample size

TABLE 2. Von Bertalanffy growth parameters, PHI prime and the length/mass relationship of *O. mossambicus* from the salt pans and Hardap Dam.

Studies of the annuli on scales, and results of the Von Bertalanffy growth parameters show that *O. mossambicus* in the saltpans grew well but that their weight gain was less than fish in Hardap Dam (Table 2). This is supported by the fact that *O. mossambicus* from Hardap Dam also had a better length/mass relationship (Table 2). The latter is a power curve, where $M = aL^b$ (M = mass, L = total length, a and b = constants). This result differs from the findings of Canagartman (1968). One must bear in mind, however, that the findings obtained by Canagartman (1968) were the result of experimental studies.

Although tilapia culture is limited primarily to fresh and brackish water, it has been widely suggested that euryhaline tilapias could be cultured in higher salinity and marine systems (Watanabe *et al.* 1984). This is also possible in Namibia, with its vast coastline and protected rocky bays at Lüderitz, as well as in the Cuvelai regions with it's brackish groundwater. It is recommended, however, that a study addressing the following factors be done prior to any aquaculture project in saline water: (a) temperature tolerance at different salinities (b) growth experiments, in order to determine the growth rate, food conversion, stocking densities and economical implications.

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Sex and growth rate of *Oreochromis andersonii* x *Oreochromis mossambicus* hybrids using high-protein pellets in an intensive production unit

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ABSTRACT

Male *O. andersonii* and female *O. mossambicus* were successfully cross-fertilized and male hybrid fish were obtained. The growth rates of the hybrids were the same as those of the parent species. Maximum growth from 11,67 g to 82,0 g occurred within 97 days. The maximum individual daily mass increase was 0,90 g. The hybrids were fertile and six back-crosses (with female *O. mossambicus*) were obtained.

INTRODUCTION

Overpopulation caused by the high fecundity of tilapias under conditions of commercial production has long been a problem (Balarin 1979; Caulton 1980; Trewavas 1983). Several solutions have been investigated, one being the use of monosex culture. Male fish grow faster and larger than females, and are therefore the better choice for aquaculture (Balarin 1979; Caulton 1980).

Several methods of producing all-male populations are available (Balarin 1979). The three most commonly used methods are (a) hand sorting of young fish according to sex, which is time consuming, (b) sex reversal of female fry using hormones, and (c) interbreeding of closely related species resulting in male monosex cultures. A search for interspecific crosses yielding all-male hybrids was initiated by Hickling's Malacca Tilapia hybrids (Pruginin *et al.* 1975).

The existing literature concerning hybrids between *O. andersonii* and *O. mossambicus* is conflicting and poorly documented (Wohlfarth & Hulata 1981). Balarin (1979) stated that, according to Thingrav and Gopalakrishnan (1974) crosses between *O. andersonii* and *O. mossambicus* were unsuccessful in producing all-male progeny. However, Thingrav and Gopalakrishnan (1974) themselves stated only that hybrids of *O. andersonii* and *O. mossambicus* were obtained under experimental cultivation in Zimbabwe. A hybrid between *O. andersonii* and *O. mossambicus* has also been found under natural conditions in Zimbabwe (Wohlfarth & Hulata 1981), but no mention is made of hybrids between these two species by Trewavas (1983). It is clear from the literature that very little is known about the hybridisation of *O. andersonii* and *O. mossambicus*.

The aim of this study was to produce hybrids from male *O. andersonii* and female *O. mossambicus*, and to determine whether all male progeny could be obtained. Growth studies were conducted to compare the rates of growth of the hybrids and the parent species.

MATERIALS AND METHODS

Water analysis was done every second week with a HACH DR/EL 4 spectrophotometer to determine the NH_3, NO_2, NO_3, anorganic PO_4 concentrations and pH levels. Dissolved oxygen (O_2) was determined with a YSI 54A oxygen meter and water temperature with a THIES thermograph.

One male *O. andersonii* and seven female *O. mossambicus* were placed in an aquarium (1000 x 600 x 600 mm) in the hatchery at the Fresh Water Fish Institute, Hardap Dam, Namibia. After breeding, the females were transferred to separate aquaria to secure the incubation and hatching of the eggs. The females were returned to the original aquarium after all the fry were swimming outside their mouths.

Two of the crosses were divided into four groups for the growth studies. On 10 of March 1989 four production tanks of 1 m^3 were stocked at densities of 61, 28, 58 and 61 fry per tank. At the start of the study all the fish were tranquilized with MS 222 Sandoz (Methanesulfonate of Meta-Aminobenzoic Acid Ethyl-Esther) and the total length and weight of each fish were determined. This procedure was followed every second week to determine food requirements, calculated from data provided by Gaigher and Geyser (1984). The fish were fed on pellets with a 38% protein content. The experiment was terminated after 97 days and all the fish were individually sexed.

RESULTS

The water quality parameters during the experiment were:
pH (6,7 - 7,1), NO_3 (0,9 - 1,9 mg/l), NO_2 (0,008 - 0,048 mg/l), NH_3 (0 - 0,11 mg/l), PO_4 (0,4 - 1,2 mg/l), O_2 (4,0 - 5,1 mg/l) and temperature (26,0 - 28,5°C)
All four groups of hybrid fish consisted only of males (N = 188). Stocking dates, fish densities, growth rates,

TABLE 1. Stocking dates, fish density, growth rates and mortalities of the hybrids in the hatchery.

DATE	N fish	AVERAGE ORIGINAL MASS (g)	DAILY INDIVIDUAL MASS INCREASE (g)	DAILY INCREASE AS % OF ORIGINAL MASS	FOOD CONVER.
GROUP 1					
10.03.89	61	10,90	—	—	—
13.03.89	61	15,46	0,46	2,25	2,70
11.04.89	60	22,61	0,40	1,45	3,33
29.04.89	59	30,10	0,44	1,30	3,79
10.05.89	58	38,12	0,67	1,58	2,94
23.05.89	57	47,15	0,69	1,38	3,48
06.06.89	56	56,20	0,70	1,17	2,94
17.06.89	56	63,23	0,80	1,19	2,69
GROUP 2					
10.03.89	28	11,67	—	—	—
13.03.89	28	19,31	0,64	4,17	1,51
11.04.89	28	31,30	0,67	2,69	1,93
29.04.89	27	46,60	0,90	2,35	1,55
10.05.89	27	54,70	0,68	1,35	3,56
23.05.89	27	62,51	0,65	1,13	3,09
06.06.89	26	71,80	0,72	1,03	2,92
17.06.89	26	82,00	0,85	1,14	3,10
GROUP 3					
10.03.89	52	9,50	—	—	—
13.03.89	51	14,35	0,40	3,42	2,11
11.04.89	51	20,61	0,35	2,03	3,21
29.04.89	51	29,90	0,55	2,16	2,45
10.05.89	51	37,60	0,64	1,89	2,44
23.05.89	50	44,12	0,50	1,20	3,22
06.06.89	48	50,10	0,46	0,95	3,61
17.06.89	48	57,00	0,69	0,82	3,03
GROUP 4					
10.03.89	61	10,80	—	—	—
13.03.89	61	16,71	0,49	3,67	2,01
11.04.89	61	22,60	0,33	1,66	3,44
29.04.89	59	30,40	0,46	1,73	2,81
10.05.89	59	38,00	0,63	1,90	2,50
23.05.89	58	46,91	0,68	1,60	2,80
06.06.89	58	55,10	0,63	1,22	3,00
17.06.89	58	62,00	0,79	1,33	2,58

mortalities and t- value's are summarised in Table 1 and Table 2. The daily individual mass increase and the daily increase as a percentage of original mass decreases with an increase in body mass (Table 1). The most rapid individual daily growth of 0,90 g took place during April in group 2. The average individual mass increase of 0,730 g in group two is higher than that of the other groups which was found to be 0,594, 0,513 and 0,573 g for group one, three and four respectively. The average food conversion of group two is also better than those of the other groups. The mathematical expression of the growth rates of the four groups are:

Group 1. $M = 7,086 + 0,550T$; $r = 0,989$
Group 2. $M = 9,770 + 0,731T$; $r = 0,999$
Group 3. $M = 7,071 + 0,500T$; $r = 0,996$
Group 4. $M = 7,826 + 0,533T$; $r = 0,990$

where M = mass and T = time.

The growth rate of group two was significantly differen to the other groups from day 50 (Table 2). The mortality rate of the hybrids was low (6,9%) and mortalities were probably caused by handling (Table 1).

DISCUSSION

All the water quality parameters were in the range suitable for normal growth of tilapia (Van Zyl 1988).
The crosses between male *O. andersonii* and female *O. mossambicus* produced all-male hybrids. These hybrids are fertile and therefore cannot be used freely in Namibia for aquaculture, because they could enter natural systems and threaten the genetic integrity of indigenous species.

It is apparent that the high stocking density of group one, three and four negatively influenced the growth rate of the hybrids. Due to the low stocking densities, the growth

TABLE 2. t-value's of the growth rates of the different groups from day 50.

Groups		t-Value
Group 2 X Group 1		
Time (Days)		
	50	DF = 83, t = 3,677, p < 0,001
	61	DF = 83, t = 3,538, p < 0,001
	73	DF = 82, t = 2,920, p < 0,001
	86	DF = 78, t = 3,033, p < 0,001
	97	DF = 78, t = 3,400, p < 0,001
Group 2 X Group 3		
Time (Days)		
	50	DF = 75, t = 4,953, p < 0,001
	61	DF = 75, t = 4,714, p < 0,001
	73	DF = 75, t = 4,454, p < 0,001
	86	DF = 71, t = 5,208, p < 0,001
	97	DF = 71, t = 5,556, p < 0,001
Group 2 X Group4		
Time (Days)		
	50	DF = 84, t = 4,573, p < 0,001
	61	DF = 84, t = 4,492, p < 0,001
	73	DF = 83, t = 3,712, p < 0,001
	86	DF = 82, t = 3,899, p < 0,001
	97	DF = 82, t = 5,520, p < 0,001

rate of group two represents the optimal or near optimal growth rates that can be obtained in the hatchery. Although the growth rate of group two is better than that of the parent species, the growth rates are not significantly different (DF = 14, t = 1,206, p> 0,05; DF = 14, t = 1,097, p > 0,05, Van Zyl 1988). The food conversion is the same as that of the parent species. The hybrids tested did not show any signs of heterosis for growth and food conversion. According to Pruginin *et al.* (1975) reasons for this could be: (a) The hybridisation test was based on a small number of parents. Furthermore, intraspecific genetic variation could also contribute significantly to the results. (b) Dominance including heterosis, is a variable function of environment and may change from additivity to heterosis in the same hybrid when grown in diverse environments.

For the best economical advantage of the hybrids it is necessary to do more progeny tests of paired matings of large samples between *O. andersonii* and *O. mossambicus*.

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Aspects of the ecology of *Barbus hospes* from the Fish River, Namibia

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ABSTRACT

Environmental conditions in the Fish River affect several ecological aspects of *Barbus hospes* which emphasised the importance of the link between populations in the Fish and Orange Rivers. Higher growth and mortality rates were found for this species in the Fish River compared to those in the Orange River. Factors other than temperature seem to stimulate gonad development. The survival of *B. hospes* in the Fish River probably depends on a healthy population in the Orange River.

INTRODUCTION

Barbus hospes is listed in the South African Red Data Book-Fishes as rare in the lower Orange River (Skelton 1987). It is endemic to the lower Orange River and was collected by Cambray (1984) from below the Augrabies Falls to close to the mouth. The distribution of *B. hospes* into Namibia via the Fish River is limited to the lower reaches due to the presence of a waterfall near Witputs (Hay 1991).

The limited information on the biology of *B. hospes* is reported on by Cambray (1984) who concentrated on the effect of stream regulation on the fish fauna in the middle and lower Orange River. Although this author suggested the removal of *B. hospes* from the list of threatened species, it has been included because of its restricted distribution.

In the Fish River *B. hospes* is exposed to severe environmental conditions. The habitat consists mainly of isolated pools interconnected by periodic floods. The biggest threat to this species in the Orange River appears to be further development which increases pollution and siltation (Cambray *et al.* 1986). The aim of the current study was to determine the effect of various environmental conditions in the Fish River on the survival of *B. hospes*.

MATERIALS AND METHODS

Several isolated pools were sampled at Ai-Ais during June 1990. These pools had sandy to clay substrates with limited vegetation and with surface areas of about 200 m^2. The depths were approximately 1,5 m with water temperatures ranging between 13°C and 17°C. A 10 m x 1,5 m mosquito net with a fine mesh size and the fish poison rotenone were used to sample fish.

The length frequencies obtained for the fish from the Orange River as reported by Cambray (1984) were used for the calculation of the growth and mortality rates for the Orange River population.

Growth and mortality parameters were calculated by using the Length-based Fish Stock Assessment (LFSA) and Electronic Length Frequency Analysis (Elefan) software respectively. The methodology for obtaining these parameters is outlined in Sparre *et al.* (1989).

Growth comparison is not reliable when comparing growth parameters separately. Munro's phi prime (Ø) is the combination of the growth parameters which were used to compare the different growth rates (Sparre *et al.* 1989). The higher the phi prime value the better the growth rate. The following growth parameters are used for the determination of Munro's phi prime:

Lα = the mathematical asymptote of the curve.
K = a measure of the rate at which the growth curve according to the growth formula approaches the asymptote.

The formula for Munro's phi prime (Ø) is as follows:

$$\varnothing = \ln k + 2 \times \ln l\alpha$$

Total mortality is defined as follows (Sparre *et al.* 1989):

$$Z = F + M$$

Where : Z = Total mortality
F = Fishing mortality
M = Natural mortality

With limited exploitation taking place at Ai-Ais, the natural mortality was taken as the total mortality (Z = M). The chi-square test was used to determine the significance of the deviation from a one to one sex ratio.

RESULTS AND DISCUSSION

Length frequency

A total of 341 specimens were collected with a minimum and maximum fork length of 3 cm and 7 cm respectively

(Figure 1). The length frequency peaked at the 5 cm and 6 cm length classes. Juveniles were absent at all the collecting sites. Maximum length for both sexes was the same. The minimum lengths however differed with lengths of 4 cm and 6 cm for the males and females respectively.

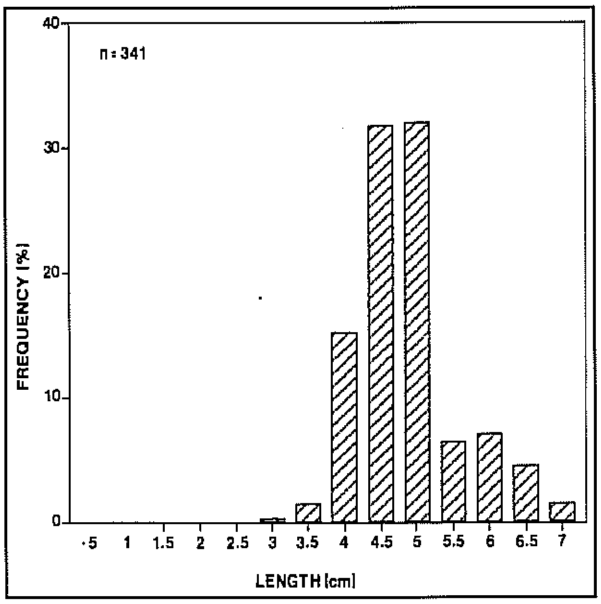

FIGURE 1: Length frequency of *Barbus hospes* from the Fish River.

Growth and Mortality

The Fish River population appears to have a higher growth rate than the Orange River population (Table 1). The growth rate for the females was slightly higher than for the males for the Fish River population (Table 1).

TABLE 1: Growth and mortality rates of *Barbus hospes* based on length frequency, sampled at Ai-Ais, Fish River (June 1990) and the Orange River (Cambray 1984).

	Fish River (June)	Fish River Males (June)	Fish River Females (June)	Orange River (March)	Orange River (September)
Lα	7,4	7,8	7,0	8,5	6,4
K	0,82	0,73	1,01	0,19	0,37
to	- 0,32	- 0,45	- 0,15	- 0,83	- 0,56
Ø	3,80	3,79	3,90	2,62	2,72
Z	1,28	1,35	1,11	0,90	0,63

The mortality rate of the Fish River population appeared somewhat higher than the Orange River population (Table 1) with a predicted survival of 28% after the first year compared to 41-53% in the Orange River (Table 2). The data suggests that males from the Fish River had a higher mortality than the females (Table 1).

Sex ratio

The population had a one to 1,73 male to female sex ratio which differs significantly from an expected one to one sex ratio (Table 3). This correlates with the results of Cambray (1984) who found a male to female ratio of 1:1,82 in the Orange River. The 4-4,5 cm length classes were the only length classes to differ significantly ($P \leq 0,05$) from a 1:1 sex ratio (Table 3).

TABLE 2: Percentage survival rate per year of *Barbus hospes* at Ai-Ais, Fish River, and the Orange River (Cambray 1984).

Year	Fish River (June)	Fish River Males (June)	Fish River Females (June)	Orange River (March)	Orange River (September)
1	27,8%	25,9%	33,3%	40,7 %	53,3 %
2	7,7%	6,7%	11,1%	16,5 %	28,4 %
3	2,2%	1,7%	3,7%	6,7 %	15,1 %

TABLE 3: The sex ratio of *B. hospes* at different length classes, sampled at Ai-Ais, Fish River, June 1990.

Length (cm)	N Fish	N♂	N♀	♂:♀	X^2	Significance level
3	1	0	1	-	-	-
3.5	5	0	5	-	-	-
4.0	51	5	46	1 : 9.2	32.960	$p \leq 0,05$
4.5	107	31	76	1 : 2.45	18.926	$p \leq 0,05$
5.0	108	54	54	1 : 1	0	$p \geq 0,05$
5.5	22	14	8	1 : 0.57	1.636	$p \geq 0,05$
6.0	24	8	16	1 : 2	2.667	$p \geq 0,05$
6.5	15	8	7	1 : 0.88	0.067	$p \geq 0,05$
7.0	5	4	1	1 : 0.25	1.8	$p \geq 0,05$
Total	338	124	214	1 : 1.73	23.964	$p \leq 0,05$

Minimum length at sexual maturity

None of the fish sampled in June had ripe gonads while 76% of the males and 21% of the females possessed developing gonads. The minimum length for male and female fish with developing gonads was 4 cm and 3,5 cm respectively. The highest percentage of developing gonads in males was present in the 5 cm length class and in females in the 6 cm length class. Gonad development was observed in water with temperatures as low as 13°C.

Stomach contents

Although no detailed analysis was done, the stomach contents contained mainly algae and sand grains. The sand grains indicate that *B. hospes* is predominantly a substrate feeder. The analysis may have been biased as the isolated pools contained a limited diversity and supply of food.

Relative abundance

Barbus hospes constituted 23,9% of the species collected at Ai-Ais, approximately the same as *B. paludinosus* (22,2%). Only *Mesobola brevianalis* (Boulenger 1908) was more abundant, at 41% (Table 4).

Figure 1 indicates that limited or no recruitment took place at Ai-Ais during the 1989/90 season. According to Cambray (1984) *B. hospes* prefers riverine conditions which have benefited from the river regulation and it breeds at localised sites along the entire lower Orange River. The fact that the Fish River flows seasonally might influence breeding success. If the assumption by Cambray (1984) is correct that *B. hospes* spawns twice during a season, the 3 cm and 3,5 cm length classes shown in Figure 1 might have been the survivors of limited early breeding during the 1989/90 season.

TABLE 4: The relative abundance (percentage, n = 1427) of all the species sampled at Ai-Ais (June 1990).

Species	Relative abundance (%)
Barbus aeneus	1.89
Barbus hospes	23.90
Barbus paludinosus	22.21
Barbus trimaculatus	0.35
Clarias gariepinus	0.07
Labeo capensis	6.94
Mesobola brevianalis	40.93
Oreochromis mossambicus	3.71

The high growth rate in the Fish River population may be an adaptation to reach maturity in a short time period, to counteract the relatively high mortality in the Fish River, which was twice as high as that in the Orange River in September.

In the Fish River the development of the male gonads of *B. hospes* seem to start earlier in the season and have a much higher percentage development rate than those of the females. The stimulant for gonad development can be attributed to factors other than temperature since developing gonads were collected in fish at low water temperatures. The minimum length at which sexual maturity was reached (Fish River population), coincided with the Orange River population.

Barbus hospes was found to be abundant at Ai-Ais although no juveniles were collected. Migration from the Orange River may account for the high relative density at Ai-Ais. The high abundance may also be due to the lack of predators.

Barbus hospes, although abundant, does not appear to have adapted well to the lentic conditions which are present in the Fish River during most of the year. Whether successful breeding can take place during favourable conditions still remains to be seen. The present status of *B. hospes* in the Fish River indicates a possible dependence on the Orange River population for their survival. The protection of *B. hospes* in the Orange River is therefore of the utmost importance if the Fish River population is to survive the environmental conditions which exist in this system. Further studies are, however, required to shed more light on the status of *B. hospes* in the Fish River.

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The effect of the artificial linkage between the Kunene River and the Cuvelai system on the fish fauna in Owambo, Namibia.

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ABSTRACT

A concrete canal, built in 1972 to supply water from the Kunene River to the central parts of Owamboland, is responsible for the transfer of 32 fish species from the Kunene River to Owambo. Most of these fish are at present limited to artificial reservoirs. Only one cichlid species has so far successfully invaded the oshana system. Turbidity is believed to be the main factor preventing the invasion of Kunene River fish into the oshanas. A total of 22 species have been collected in the oshanas of which five species are considered to be permanent inhabitants. *Oreochromis mossambicus* is present in the Ondangwa reservoir and individuals may be present in the surrounding waterbodies.

INTRODUCTION

The Cuvelai originates near the Sierra Encoco mountains between the upper reaches of the Kunene and Okavango Rivers (Figure 1). It is not a perennial river as was believed, but permanent waterbodies do exist in the upper reaches (Stengel 1963). The system in Owambo mainly consists of oshanas which are large shallow grassy depressions. The Etosha Pan acts as a sump during heavy summer floods (known locally as efundja) and receives water mainly via the Oshana Ekuma in the north-western side and Oshana Oshigambo in the north-east. A small volume of water is transferred to the pan via Oshana Owambo in the east.

The water flows southwards along the oshanas and into Etosha Pan. The water comes from local precipitation and from the Cuvelai System in Angola, not from the Kunene River as was once believed (Wellington 1955). The first to discover this was Dufour in 1880, but it was only in 1926 that Schedtler and Volkmann conclusively proved this fact (Stengel 1963). The Cuvelai drainage basin is therefore a system separate from the Kunene and Okavango Rivers with its own characteristics and fish fauna (Figure 1).

A canal system became operational in 1972 for the transfer of water from the Calueque Dam on the Kunene River just inside Angola to the interior of Owambo (Figure 2). The Calueque-Olushandja component was put out of action during the late 1970's due to hostilities in the area. It was opened again in 1991. During this period water was pumped from Ruacana. The Calueque-Olushandja component consists of a 3 km pipeline and a 21 km concrete lined canal (Figure 2). The Olushandja Dam has a southern and northern embankment. Water is transferred into the Dam via the concrete canal at the northern embankment. A pipeline exists between

TABLE 1: Descriptions of fish collecting sites in Owambo, February 1991 (See Figure 2).

No.	Collecting site	Substrate	Vegetation	Flow rate	Mean Depth (m)
1	Cuvelai oshana Oshakati	Clay	None	Strong	1,0
2	Cuvelai oshana Oshakati	Clay	Aquatic	Slow	1,5
3	Cuvelai oshana Okatana	Clay	Marginal	Medium	2,0
4	Cuvelai oshana Oshakati	Clay	Aquatic	None	1,5
5	Cuvelai oshana Oshakati	Clay	Aquatic	Slow	1,0
6	Cuvelai oshana Oshakati	Clay	Aquatic	Slow	0,2
7	Cuvelai oshana Oshakati	Clay	Aquatic	None	0,4
8	Earth canal Ombalantu	Clay	Marginal	None	0,5
9	Concrete canal Ombalantu	Cement	None	Strong	1,5
10	Earth canal Oshakati	Clay	Marginal	Medium	0,5
11	Ondangwa reservoir	Sandy	None	None	2,0
12	Oshakati reservoir	Sandy	Marginal	None	3,0
13	Olushandja Dam	Muddy	Aquatic	Slow	1,0

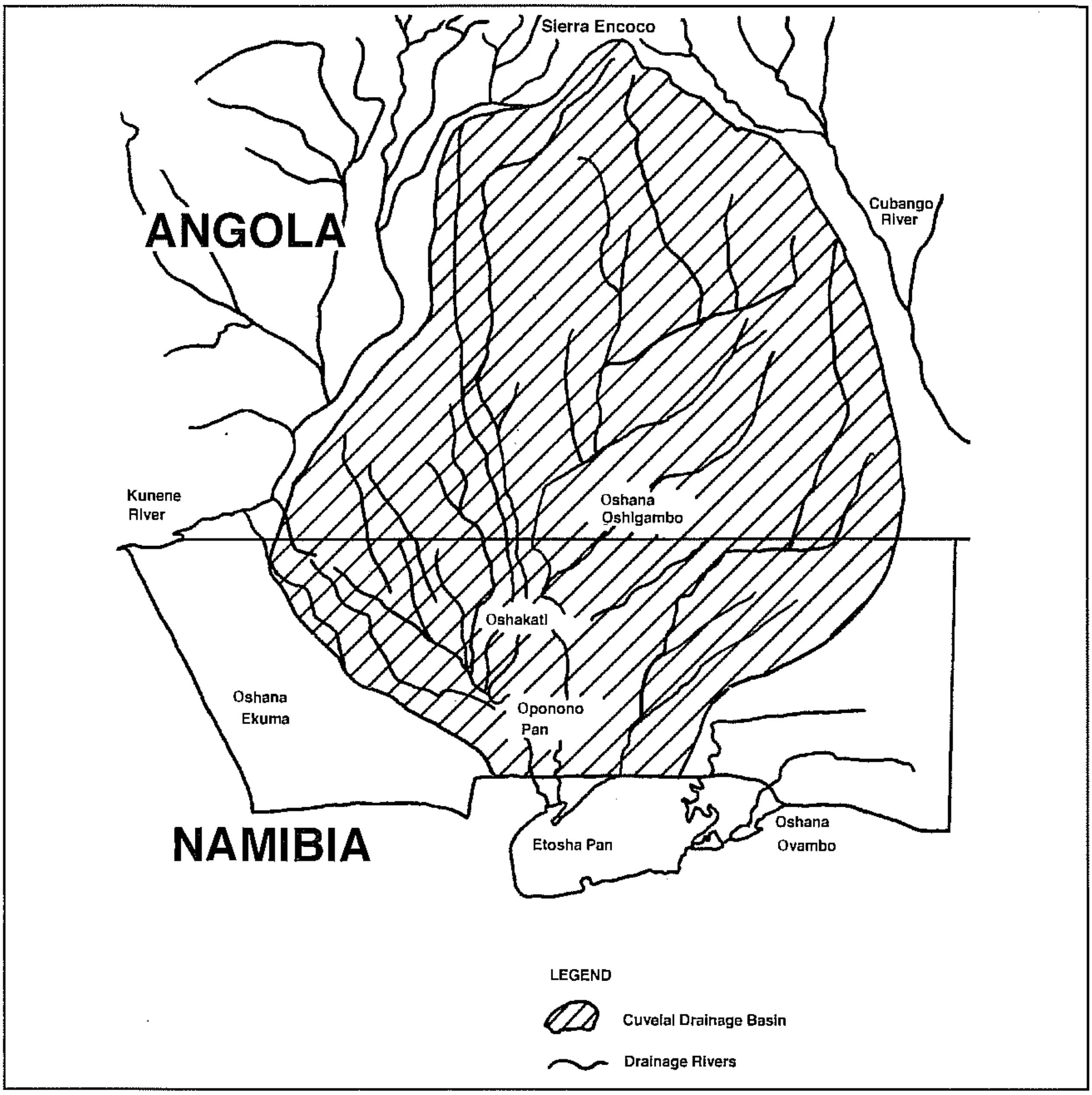

FIGURE 1: The Cuvelai Drainage Basin.

Olushandja and Okahau (60 km) as well as an unlined earth canal (Etaka canal) from the southern embankment of Olushandja Dam. This canal is situated in the Oshana Etaka. The dam provides balancing storage, or is used to release water into the Oshana Etaka. A concrete-lined canal transfers water from Olushandja to the purification works at Ogongo (70 km). Run-off water is collected in an unlined earth canal between Ombalantu and Ogongo. A pipeline transfers water from Ogongo to Oshakati. An unlined earth canal is also present that branches at Oshikuku to Elim. This canal also collects run-off water that supplements the Calueque-Ogongo system. The earth canals were constructed across the oshanas so as to capture water into the canals (Lukowski pers. comm.). These earth canals become flooded when the Cuvelai System flows, and fish species move freely between the oshanas and the canals.

COLLECTING SITES AND EQUIPMENT

Brief descriptions of the collecting sites are listed in Table 1.

The following equipment was used at the collecting sites.

a. A series of gill nets, each 30 m long, with the following stretch mesh sizes: 35, 45, 57, 73, 93, 118 and 150 mm.

b. A 30 m X 1 m seine net with a 12 mm stretch mesh.

c. The fish poison, rotenone.

RESULTS AND DISCUSSION

Water quality and water temperature

The pH in the reservoirs and earth canal was neutral but the Olushandja Dam was slightly acidic (Table 2). The abundance of vegetation in Olushandja Dam is probably the main reason for the low pH and low conductivity. The conductivity and total dissolved solid concentration was slightly higher in the oshanas.

The oshanas and earth canal have a very high turbidity (Table 2). Cyrus (1988) classified a NTU value of 80 as a very high turbidity. Bruton (1988) reported that turbidity reduces egg and larval survival, interferes with breeding behaviour, reduces food availability, growth rates, habitat diversity and may clog the gill filaments of fish. This will be a major ecological barrier that will determine the species diversity in the oshanas. Tilapia species have a high turbidity tolerance that enable them to be more capable of invasion in turbid systems than less tolerant species (Balarin 1979 ; Philippart & Ruwet 1982).

TABLE 2: Chemical water analysis and water temperature of reservoirs and the Cuvelai oshanas in Owambo, February 1991.

Parameter	Oshakati Reservoir	Ondangwa Reservoir	Olushandja Dam	Cuvelai Oshana	Earth Canal
pH	6,9	6,9	6,3	6,4 - 7,3	6,7 - 7,1
Conductivity mS/m	65,2	34,0	5,8	15,9 - 116,4	21,4 - 22,8
TDS* mg/l	430,0	224,0	38,0	105,0 - 768,0	141,0 - 150,0
Nitrate as N mg/l	< 0,5	< 0,5	< 0,5	< 0,5 - 1,3	< 0,5
Nitrite as N mg/l	< 0,1	< 0,1	< 0,1	< 0,1 - 0,7	< 0,1
Chloride as Cl mg/l	48	24	2	20 - 335	7 - 8
Total Alkalinity mg/l	94	74	28	32 - 128	60 - 102
Turbidity** NTU	20	0,8	24	120 - 470	160 - 350
Water temperature °C	27	28	30,5	25 - 38	30 - 31,5

* TDS = Dissolved Solids
** NTU = Nephelometric Turbidity Units

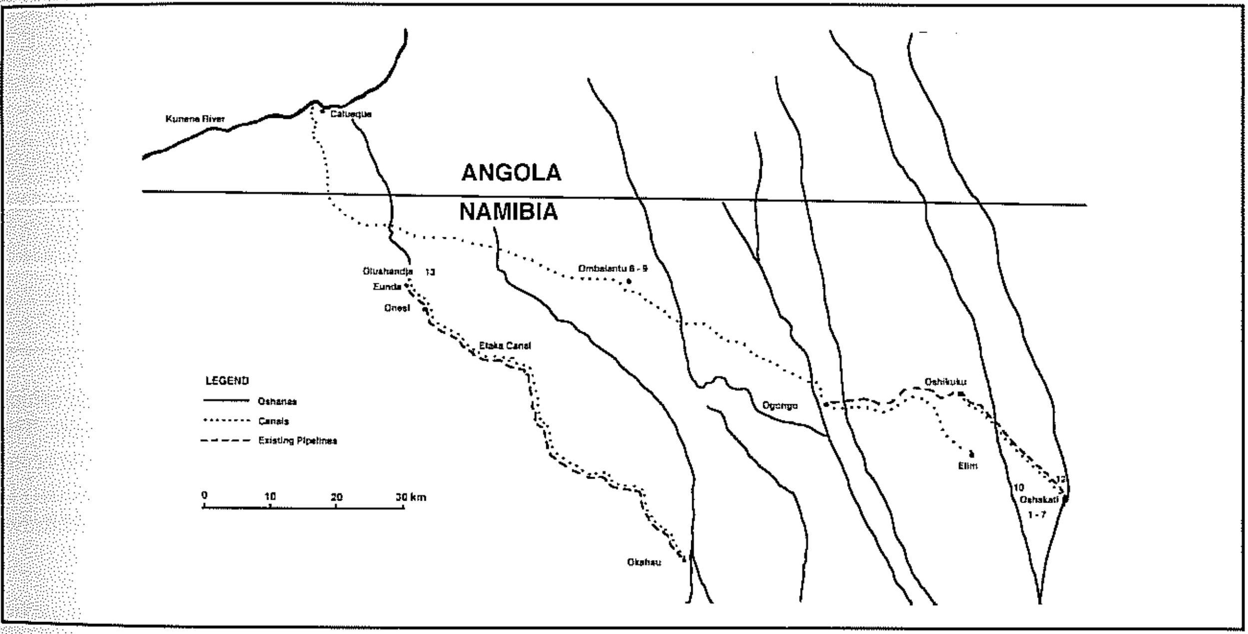

FIGURE 2: The water canal system in Owambo and collecting sites.

Oreochromis macrochir, *Barbus paludinosus* and *Clarias gariepinus* have been collected in the oshanas with temperatures as high as 38°C. The average temperature in the oshanas however is much lower and would not prevent species from entering them. Minimum temperatures do not pose a threat as Owambo has a temperate climate (Van der Merwe 1983). Mean monthly temperatures at Ondangwa vary between 26,1°C in December and 17,5°C in July (Marsh & Seely 1992).

Fish species collected before the building of the canal system.

A total of 13 species had been collected in Owambo before the canal system became operational (Table 3) which were dominated by the families Cyprinidae, Mormyridae, Clariidae and Cichlidae. Species collected were *A. johnstoni*, *B. paludinosus*, *B. mattozi*, *C. gariepinus*, *C. ngamensis*, *M. macrolepidotus*, *M. brevianalis*, *O. andersonii*, *O. macrochir*, *P. castelnaui*, *P. catostoma*, *S. intermedius* and *T. sparrmanii*. *Barbus paludinosus*, *C. gariepinus* and *S. intermedius* were abundant in the Oshana Ekuma while *C. ngamensis* was found to be rare (Bloemhoff 1971). A survey by M. Penrith (unpublished) in Oponono Lake and the Cuvelai System showed that *B. mattozi* and *C. gariepinus* were abundant while *M. macrolepidotus*, *P. catostoma* and *T. sparrmanii* were rare. *Schilbe intermedius* was found to be uncommon (Bloemhoff 1971). *Tilapia sparrmanii* was collected by Penrith mainly on the eastern side of Ondangwa. Several of these species, *A. johnstoni*, *B. mattozi*, *M. macrolepidotus*, *P. castelnaui*, *P. catostoma* and *T. sparrmanii* have never since been collected in the oshanas. Members of the family Mormyridae have also been absent from the oshanas in subsequent surveys and are considered to be present only during large efundjas. The absence of *B. mattozi* is a mystery as Penrith reported it to be abundant in the oshanas prior to the canal system (Bloemhoff 1971). *Barbus mattozi*, *M. macrolepidotus* and *T. sparrmanii* however, seem to have established viable populations in several reservoirs in Owambo. These species are known for their pool habitat preferences (Gaigher 1969, 1973).

TABLE 3: Fish species collected in oshanas and Oponono Lake in Owambo.

Species	Van der Waal Oponono 1991	Van der Waal oshanas 1991	Present study Oshanas	Present study Earth canal	State Museum Windhoek 1971	Bloemhoff 1971 Oponono, oshanas
M. macrolepidotus					X	X
P. catostoma					X	
P. castelnaui					X	X
M. acutidens		X				
B. barnardi				X		
B. paludinosus	X	X	X	X	X	X
B. poechii/trimaculatus		X	X			
B. bifrenatus		X				
B. radiatus		X				
B. lineomaculatus		X				
B. mattozi						X
M. brevianalis	X				X	
S. intermedius		X			X	X
A. johnstoni					X	
C. gariepinus	X	X	X	X	X	X
C. ngamensis		X				X
P. philander	X	X	X			
O. andersonii	X	X	X	X	X	
O. macrochir			X	X		X
T. rendalli		X		X		
T. sparrmanii						X
Th. buysi				X		

Fish species collected in reservoirs in Owambo

Table 4 lists the species collected in several reservoirs in Owambo that are interconnected with the canal system. Several of these species have established viable populations, including *B. paludinosus*, *C. gariepinus*, *M. brevianalis*, *O. andersonii*, *O. macrochir*, *P. philander* and *T. rendalli*. *Oreochromis andersonii* and *O. macrochir* have not yet invaded the Ondangwa reservoir though both species are present in the Oshakati reservoir. *Barbus paludinosus*, *C. gariepinus*, *M. brevianalis* and *P. philander* have a natural distribution south of the Kunene River in Namibia. *Orthochromis machadoi*, *T. buysi*, *T. albolabris* and *S. coulteri*, which are all endemic to the Kunene River, have also been collected in Owambo. *Coptostomobarbus wittei* is the only species collected in Owambo that has not yet been sampled in the Kunene River, though further collections in the Kunene River may reveal its presence (Hay *et al.* 1995). Several species present in the Kunene River but which are unlikely to disperse to Owambo due to specialised habitat preferences are *B. codringtonii*, *B. eutaenia*, *B. puellus*, *Chiloglanis neumanni* and *Kneria maydelli*. Swamp loving species present in the Kunene River which have the potential to survive in Olushandja Dam are *B. afrovernayi*, *B. thamalakanensis*, *Clarias theodorae*, *C. stappersii*, *P. castelnaui* and *H. multifasciatus* with *P. castelnaui* being collected in Owambo only once. These swamp loving species may increase in diversity and abundance as water is pumped from Calueque which consists mainly of swamp and floodplain habitats. The previous pump station used is situated below the Ruacana Falls in rapid-like habitat. The current species diversity in Owambo may be influenced by these two different draw-off points from the Kunene River.

The greatest species diversity has been found in the Olushandja Dam where 39 species have been collected. This can be attributed to (i) the presence of aquatic vegetation which increases the different habitat types, and (ii) the perennial water conditions resulting from the fact that Olushandja Dam is the first draw-off point from the canal. The species diversity is not constant due to the fluctuation in water level which influences food availability, habitat diversity and protection from predators. *Oreochromis mossambicus* constitutes 47,2% of the total number of fish caught in the Ondangwa reservoirs. The other species present are *B. paludinosus*, *C. gariepinus*, *M. brevianalis*, *P. philander* and *T. rendalli* (Table 4). The presence of *O. mossambicus* is undesirable as interbreeding is possible with the closely related species, *O. andersonii*, which is a permanent resident of the oshanas. Hybrids had been observed in nature by Mortimer (1960) while fertile offspring, all males, were produced in a closed system by Van Zyl (1997). The presence of *O. mossambicus* in Owambo may jeopardise the genetic purity of the cichlids in this region including the Kunene and Okavango Rivers.

TABLE 4: Fish species collected in reservoirs in Owambo.

Species	Van der Waal (1991) Reservoirs	Present study Olushandja (1991)	Present study Ondangwa Reservoir (1991)	Present study Oshakati Reservoir (1991)
H. ansorgii	X			
M. macrolepidotus	X			X
M. lacerda	X			
P. catostoma	X			
B. lateralis	X			
M. acutidens		X		
R. maunensis	X			
H. odoe	X			
H. machadoi	X			
B.barnardi	X	X		
B. bifrenatus	X			
B. mattozi	X			
B. paludinosus	X	X	X	X
B. poechii / trimaculatus	X			
B. radiatus	X			
B. kerstenii	X			
B. unitaeniatus	X			
C. wittei	X			
M. brevianalis	X	X	X	X
L. ansorgii	X			
C. gariepinus	X	X	X	X
C. ngamensis	X			
S. intermedius	X			
S. leopardinus	X			
S. macrostigma	X			
S. woosnami	X			
A. johnstoni	X			
O. andersonii	X	X		X
O. macrochir	X	X		X
O. mossambicus			X	
T. rendalli	X	X	X	X
T. sparrmanii	X	X		
Or. machadoi	X			
Th. buysi	X	X		
Th. albolabris	X			
Ph. acuticeps	X			
S. codringtonii	X			
S. greenwoodi	X			
S. coulteri	X	X		
S. giardi	X			
S. angusticeps	X	X		
S. macrocephalus	X			X
S. thumbergi	X			
P. philander	X	X	X	

Fish species collected in the oshanas, Oponono Lake and Etosha Pan

The dominant species in the oshanas are *B. paludinosus*, *C. gariepinus*, *O. andersonii*, *O. macrochir* and *P. philander*. These species can be considered as permanent residents and are included in the first order families, being characterised by species encountered where no other fishes occur (Roberts 1975). *Barbus paludinosus*, *B. barnardi*, *C. gariepinus*, *O. andersonii*, *T. rendalli*, and *T. buysi* were present in the earth canal at Ombalantu and Oshakati (Table 3). *Oreochromis macrochir* is listed for the first time as being present in the Cuvelai System. Van der Waal (1991) terms this a late coloniser with specific habitat requirements that is not expected to colonise the Cuvelai System. Philippart and Ruwet (1982) regard this species as a specialised feeder, a characteristic that will probably limit its distribution. Despite these views, *O. macrochir* was found to be common in the oshanas and surrounding waterbodies in Owambo.

Barbus paludinosus and *C. gariepinus* were collected at all the collecting sites in the oshanas. *Pseudocrenilabrus philander* had a preference for vegetation in stagnant pools while *O. andersonii* was collected in deep pools (1,5 m). *Oreochromis macrochir* had a preference for lotic conditions in the oshanas.

An increase of 32 species are listed for Owambo since the establishment of the canal. *Mormyrus lacerda* and *P. philander* were collected by Pellegrin (1936) at Mupa some 200 km north of Oshakati in Angola, but not in Owambo before the canal system became operational. The invasion of fish and presumably other aquatic species could have been avoided altogether if more thorough surveys and better planning had been done in Owambo before the initiation of the canal system.

Several species already present in the reservoirs have the potential to infiltrate the oshanas during the next major flood. Examples of these species are *B. unitaeniatus*, *M. acutidens M. brevianalis*, *S. leopardinus* and *T. buysi*. Active predators such as *Hepsetus odoe*, *Serranochromis angusticeps* and *S. macrocephalus* are not likely to establish populations due to the high turbidity. The dug - out aquifers hold water for a much longer period of time, which may result in the survival of species in these semi-permanent waterbodies throughout the year.

The earth canal added two species to the list during the 1991 survey namely *B. barnardi* and *T. buysi* (Table 3). *Barbus barnardi* has specialised habitats which will hinder further invasions into the oshanas. *Thoracochromis buysi* was found to be abundant in a variety of habitats in the Kunene River (Hay *et al.* 1995) and together with *T. rendalli* may have the potential to find its way to the upper reaches of the Cuvelai System with the next major flood.

The artificial reservoirs in Owambo are used as a step-off point by several species for the invasion of the Cuvelai System. A major flood event is needed for species to migrate to the head waters of the system where permanent pools exist. It is not possible to determine which of the 46 species listed in Owambo are exotic to the Cuvelai System, except *O. mossambicus*, as very little data is available concerning surveys done in the upper reaches prior to the canal system. A link between the Cuvelai and Kunene Systems in the past is a possibility as *B. mattozi* was collected in the Cuvelai before the canal system became operational. *Barbus mattozi* is present in the Kunene River but is absent from the Okavango River (Cubango in Angola) that is the eastern neighbouring system of the Cuvelai (Figure 1). One of the main factors in the oshanas that limit the species composition is turbidity which in turn will effect the habitat diversity and food availability. The highly seasonal and episodic nature of the Cuvelai System is also likely to affect the species diversity in Owambo.The origin of *O. mossambicus* in the Ondangwa reservoirs is not known but it can be assumed that it was introduced artificially. The nearest population of this species is in the Otjikoto Lake, some 250 km south of Ondangwa, where it is slowly becoming the dominant species. This population had in turn been introduced, probably by local farmers. The Ondangwa population of *O. mossambicus* is not isolated and it could be present in the surrounding waterbodies. *Oreochromis mossambicus* is very likely to become a permanent member of the fish fauna of the Cuvelai system and, together with *O. andersonii* and *O. macrochir* in this system, the outcome of possible hybridisation is not known.

The dominant families in the oshanas are Cichlidae, Clariidae and Cyprinidae. Specimens of the families Mormyridae and Cyprinodontidae have not been collected in the oshanas since the establishment of the canal system. The reason for this phenomenon is unknown. Characidae is the only family of which specimens were collected in the oshanas that was not present before the establishment of the canal system. This however, is seen only as a temporary invasion.

Van der Waal (1991) reported *T. rendalli* as a species that successfully invaded the oshanas near the canal. However this species was recorded only in the earth canal during the February 1991 survey.

Pseudocrenilabrus philander is the only permanent inhabitant in the oshanas resulting from invasion along the canal system. *Oreochromis macrochir* increased in abundance due to the canal system as it was previously collected only in the Etosha Pan.

The Owambo canal plays a positive role in supplying this area with a valuable protein source that can be utilised by the local people especially during the wet season. The canal system facilitates the transfer of fish into Owambo during the wet season and also ensures the availability of fish in reservoirs during the dry season. The invasion of *O. mossambicus* from the Cuvelai System to the Kunene River is a possibility as the movement of fish in the canal will be difficult to control.

The 1991 survey was done during an average rainy season. The species diversity in the oshanas is expected to increase during high rainfall seasons when efundja events occur, but whether more species will in fact become permanent inhabitants still remains to be seen.

RECOMMENDATIONS

1. The population of *O. mossambicus* in the Ondangwa reservoirs must be destroyed as soon as possible to prevent any genetic pollution in the region. Methods to eliminate the species, are the fish poison, rotenone, seine netting or by draining reservoirs.

2. Fish species not indigenous to either the Kunene or Okavango Rivers should not be kept or released in Owamboland to prevent the dispersal of exotic species from the Cuvelai System to the Kunene and Okavango Rivers.

3. The transfer of species from the Cuvelai System to either the Kunene or Okavango Rivers must be prohibited by all means as the genetic purity of certain species in

Owamboland, especially the cichlids, cannot be guaranteed.

4. Electrophoretic analysis of selected fish species is recommended to determine the taxonomic status of the populations in Owamboland.

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Observations on Dik-Dik *Madoqua kirkii* in the Namutoni area of Etosha National Park

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ABSTRACT

Observations were made on a population of dik-dik in Etosha National Park from 1983 to 1986. Most sightings were of an adult pair or a pair and one offspring. More family groups and single females were seen in the cold-dry season than during other seasons. Birth of lambs usually occurred in December and January. Sightings suggest that there are two breeding seasons in a year, although only two juveniles were seen in the winter months. Mortalities were low in the study population, with only 2 animals dying from vehicle injuries. No mortalities from disease were found.

INTRODUCTION

Of the five species of dik-dik found in Africa, only *Madoqua kirkii* (Günther 1880) occurs in the southern African subregion. *Madoqua kirkii* has six subspecies of which *Madoqua kirkii damarensis* is found in Namibia (Skinner & Smithers 1990). The dik-dik is a small antelope weighing approximately 5 kg with a shoulder height up to 45 cm (Tinley 1969).

In Namibia, where it is a protected species, dik-dik can be found from the Kunene River south to Mount Brukkaros and from the Pro-Namib east to Grootfontein. They are common in Etosha National Park in areas of suitable habitat: stony surfaces which support woodland or dense vegetation, at the pediment of hills or at the foot of outcrops (Tinley 1969).

STUDY AREA AND METHODS

This study was done in the stony *Terminalia-Spirostachys* woodland area (le Roux 1980) east of Namutoni camp in Etosha National Park (Fig. 1), where the density of dik-dik is high. The study area (8 500 ha) was surveyed throughout the year as part of the ranger's duties by driving all roads in the area and by foot patrols of 1-6 h. duration.

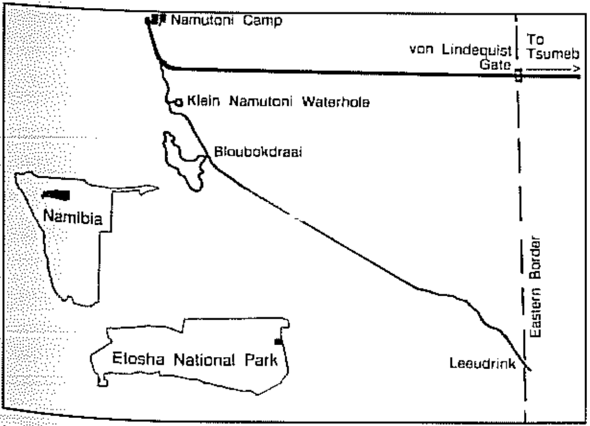

FIGURE 1: Map of study area in the Namutoni area of Etosha National Park, Namibia.

RESULTS AND DISCUSSION

In total, 323 sightings of dik-dik were recorded over the three-year period (1983-86). Observations included group size and composition, mating behaviour, reproductive status of females and the identification of items eaten whenever possible. For convenience, observations were grouped into the three climatic seasons recognized in Etosha: the hot-wet season from January to April; the cold-dry season from May to August; and the hot-dry season from September to December (Berry 1980).

There were an estimated 160 animals in the study area, but the majority concentrated within an area of 1 000 ha of preferred habitat. While the density for the study area was estimated at 0.02 animal per ha, the density in the concentration area was estimated to be 0.16 animal per ha. Animal numbers decreased by approximately 50 percent in the hot-wet season, when dik-dik frequently left their preferred territory (personal observations, this study). Otherwise, the population appeared stable.

The largest number of sightings of dik-dik (152; 47%) was of an adult pair (97; 30%) or one adult or pair and one offspring (55; 17%) (family group) which occupied and defended a definite territory (Table 1). Such a family is considered the most typical social unit (Tilson & Tilson 1986; Estes 1991). Of the 16 sightings of a single parent and offspring, 12 were of females and 4 were of males with a juvenile or subadult. The remaining sightings were of solitary subadults (smaller than adult size &/or with short horns—less than 4 cm) or adults, and groups of two to four individuals. No solitary juvenile animals (less than half the average adult size) were seen.

More family groups and single females were sighted in the cold-dry season than during the other seasons. Presumably this is because offspring born in December-January are larger by May and more easily seen as they join the activities of their parents, and females were neither hiding to lamb nor with newborn offspring. It could also be due, in part, to reduced foliage which increased sightability in the winter months. By the end of

TABLE 1: Number of sightings (total =323) of different social groups and total number of individual juvenile and subadult dik-dik by season.

	Number of sightings							No. of animals		
Season	Single M	Single F	M/F Pairs	Families[1]	Groups[2]	SA[3]	TOTAL	Juv[4]	SA[4]	TOTAL
Hot-wet	31	12	29	20	16	0	108	15	5	20
Cold-dry	17	18	38	34	10	6	123	2	41	43
Hot-dry	21	12	30	1	21	7	92	0	15	15
TOTAL	69	42	97	55	47	13	323	17	61	78
PERCENT	21	13	30	17	15	4				

[1] Families: Male or female or mated pair plus juvenile or subadult.
[2] Groups: 2 or more adults, excluding mated pairs.
[3] SA (subadults: smaller than adult size &/or with horns <4 cm): one or more subadults in absence of adults.
[4] Juv (juveniles: < 1/2 adult size), SA: total numbers seen, with adults, alone or with other SA.

the hot-dry season and into the beginning of the hot-wet season, these offspring are maturing and most leave their families to establish their own territories. Females seem to be less visible at this time due to hiding out for lambing and nursing. Therefore, families were seen less often and single males were seen more often than in the cold-dry season.

Using a Chi-squared test, we found the group compositions to be significantly different between the three seasons ($x^2 = 43.23$, df = 10, $p < 0.001$). Comparing two seasons at a time, the greatest difference was found between the cold-dry and the hot-dry seasons ($x^2 = 33.11$, df = 5, $p < 0.001$).

Although other researchers described groups of up to six adults (Tinley 1969; Tilson & Tilson 1986), the reason for such a grouping remains unclear. They suggested these were temporary aggregations of neighboring groups, perhaps related, along common boundaries. Skinner and Smithers (1990) and Tinley (1969) report up to six animals may be seen during the dry season. In this study the largest group seen was four.

Observations indicate that the usual reproductive cycle begins during May and June with "courtship," when a male sniffs a female's urine to detect estrous. If the female is in estrous, then the male, with the crest hairs on his head erect, approaches her from behind and taps her hindquarters with his foreleg to determine her readiness for mating. Pregnant females are apparent from October through December (Fig. 2). Birth occurs from December into January, although juveniles are only observed later due to the habit of dik-dik to hide their young for the first few weeks of life (Estes 1991).

There were, however, two sightings of pregnant females in June and one of a lactating female in July as well as courtship behaviour in February during the course of the study. These sightings suggest that there are two breeding seasons in a year, although the success of the second birth period is not known. It appears the majority of females produce young once a year in December and January, and only a few females have offspring during the winter months. Only two newborn lambs were sighted in the cold-dry season (one each in May and June); it may be due to the low number of lambs produced at that time in the

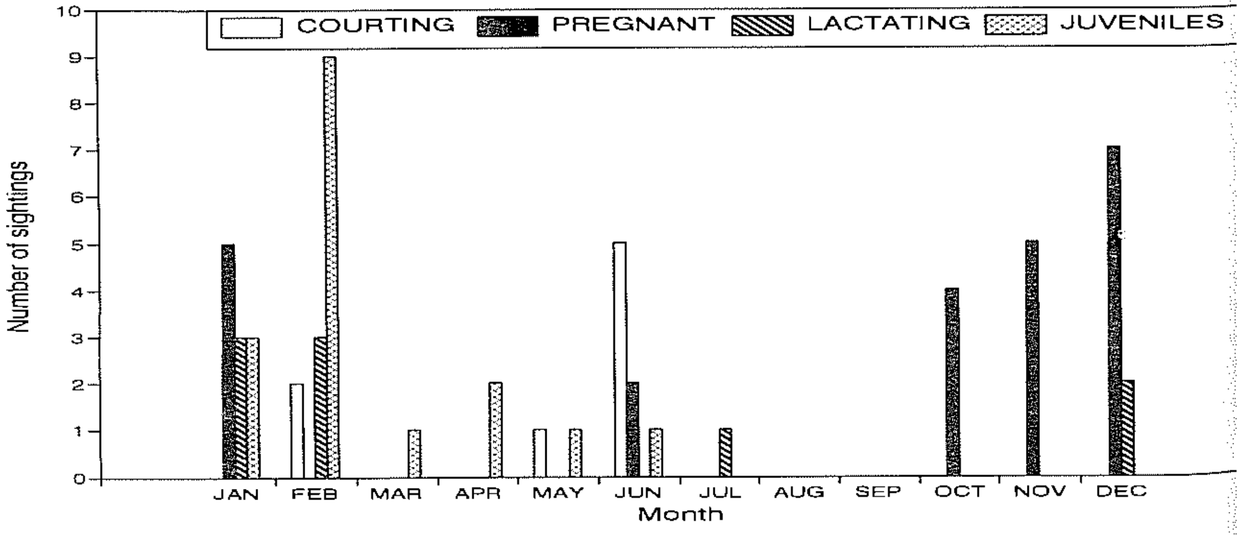

FIGURE 2: Numbers of sightings (total=57) of dik-dik indicating reproductive activities by month.

entire population, thus decreasing the chances of sightings, or due to high mortality among these lambs. In East Africa dik-dik reportedly produce two offspring a year, at the beginning and end of the rains (Kellas 1955; Estes 1991). Juveniles with one or both parents were sighted predominantly from January through April (Table 1), while subadults were seen throughout the year, but predominantly from May through December (56 of 61 animals).

Dik-dik pairs are believed to occupy the same territory throughout their lifespan (Tilson & Tilson 1986). In the Namutoni area, however, several pairs were observed to abandon their territories temporarily if the habitat were submerged during the rainy season. The varying areas occupied were referred to as winter and summer territories (69 percent of the rain occurs January through March – unpublished data, Etosha Ecological Institute). Once the rains ended and the preferred territory was again dry, the dik-dik returned. Tinley (1969) also noted seasonal movement of pairs from their usual territory, but he ascribed this to the growth of grasses which potentially obstructed the animals' view of danger.

Males fight with other males which intrude into their territory. These fights have been described as consisting of chasing and stabbing at each other with their horns without actual contact, called "air cushion fights" (Estes 1991). During this study actual horn-to-horn contact could be heard distinctly on several occasions when two males were observed fighting. Several of the known individuals had irregular, skew or broken horns, possibly due to intraspecific aggression. Otherwise, no bodily injury was ever observed and the fights were not considered life threatening. Females were never observed fighting.

Dik-dik communicate vocally with each other in several ways. To call its mate, the male or female sounded a single whistle. On several occasions, a dik-dik answered the observer's imitation of this whistle, most likely out of curiosity about a possible intruder. When frightened, or as an alarm, they made a quiet, soft trilling noise. When bounding away in fright, they emitted at each impact the 'sik-sik' sound for which they are said to be named. It sounded like a rapid exhalation of air on each impact, and is presumed to signal to other dik-dik the exact location of the fleeing animal. A visual signal of alarm, excitement or courtship behaviour is the raised rufus crest on top of their heads (Tinley 1969). Normally the crest lies flat on their foreheads between their ears.

Within the study area is an abundance of shrubs and trees which provide preferred food for dik-dik. Being predominantly browsers, the tiny ruminants were seen eating the leaves, flowers and fruit predominantly of *Acacia*, *Boscia* and *Croton* species, *Dichrostachys cinerea* and *Terminalia prunioides* (Table 2). Only young *Spirostachys africana* plants and the flowers of *Tribulus terrestris* were selected as food, while primarily dropped pods and leaves of *Acacia tortilis* and *Mundulea sericea* were chosen. Occasionally, when tender new green grass appeared with the rainy season, dik-dik were seen grazing *Enneapogon cenchroides* and *Setaria verticillata*. Dik-dik were never seen eating *Colophospermum mopane*. Once, when one of these water-independent animals (Tinley 1969) looked as if it were about to drink at a waterhole, it actually ate the algae from the water's surface. As reported in Estes (1991), dik-dik were never observed drinking.

TABLE 2: Seasonal variation in plant species eaten by dik-dik in the Namutoni area of Etosha National Park by number of sightings per species (total sightings=64).

Trees, shrubs, herbs	Hot-wet (Jan-Apr)	Cold-dry (May-Aug)	Hot-dry (Sept-Dec)
Acacia spp.	6	3	6
Boscia spp.	0	4	1
Croton spp.	3	0	4
Dichrostachys cinerea	4	5	2
Grewia spp.	0	0	1
Legume (unidentified)	2	0	0
Maytenus senegalensis	0	0	2
Mundulea sericea	1	1	0
Spirostachys africana	1	2	0
Terminalia prunioides	6	2	2
Tribulus terrestris	2	0	0
Grasses			
Enneapogon spp.	1	0	0
Eragrostis spp.	1	0	0
Setaria verticillata	1	1	0

The same vegetation which provides food also provides cover for the antelopes, which depend on both flight and hiding to escape predators (Estes 1991). On two separate occasions, dik-dik were seen leaping under the protective branches of acacia shrubs to escape the diving attacks of a Giant Eagle Owl *Bubo lacteus* and a Martial Eagle *Polemaetus bellicoses*. The birds were forced to abandon their attacks by the thorny, thick vegetation. The only known successful attack on a dik-dik by a Giant Eagle Owl was photographed by a tour guide in 1990.

One observation was made of a dik-dik pair away from this normal protective habitat. At the edge of Etosha's barren pan near Twee Palms, at least three kilometres from the nearest suitable habitat, a male and female were sighted on 15 August 1983. They were observed walking in the direction of a tamboti *Spirostachys africana* woodland. The reason for their being in such a vulnerable, unlikely area and their subsequent fate remained unknown.

The only known mortalities in the dik-dik population during the study were two adults hit by vehicles on the tar road. Previously, 10 mortalities were reported between March 1976, when mortality records were first available in Etosha, and October 1981: one attributed to lion predation, three to leopard predation and six killed by vehicles. Since the study, only six mortalities have been reported among dik-dik: two hit by vehicles; one broken neck from running into a fence; one presumably killed by a Martial Eagle; one killed by a Giant Eagle Owl; and one dead of apparent starvation.

CONCLUSIONS

From behavioural observations spanning the three years of the study, several conclusions affecting possible management activities in the dik-diks' range were reached. Burning as a veld management practice was considered of little consequence to dik-dik because of their rocky habitat with normally little ground cover to burn. Only if the canopy were destroyed would fire affect the animals, which seldom move very far from their territories (Tilson & Tilson 1986) and thus might have difficulty finding sufficient food and shelter. Changes in the water supply likewise were seen as having no impact on the dik-dik, except where water would attract other species which could reduce canopy cover.

Additionally, it was felt bush encroachment would benefit the browsing animals, as would the occurrence in their territories of larger browsers such as kudu *Tragelaphus strepsiceros*, black-faced impala *Aepyceros melampus petersi*, rhinoceros *Diceros bicornis*, giraffe *Giraffa camelopardalis* and elephant *Loxodonta africana*. These herbivores break down tall vegetation normally out of reach of the tiny dik-dik and drop plant material they are eating, thus making available additional food. Again, only if these animals destroyed the canopy would they adversely affect the dik-dik. In the Namutoni area, however, sufficient vegetation was considered to be available to all browsing species, even during the dry seasons.

Lastly, mortalities due to two endemic and highly fatal diseases, anthrax and rabies, have not been recorded in dik-dik, even though their habitat lies within an area with a high incidence of both diseases (unpublished data, Etosha Ecological Institute) and they potentially are susceptible to both diseases. Therefore, a vaccination program appears unnecessary.

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The high incidence and origin of two-egg clutches in a Damara Tern colony in southwestern Namibia

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ABSTRACT

Damara Terns *Sterna balaenarum* laid two-egg clutches in less than 0.9% of over 500 nests reported in coastal Namibia since 1975. In 1991, during renewed efforts to completely survey Damara Tern population throughout Namibia, a colony was re-discovered at Hottentot Bay in southwestern Namibia. Of 12 nests with eggs, at least 4 (33%) had two eggs. We argue that this unexpectedly high incidence probably arises from enhanced food resources in the Lüderitz area rather than release from predator-influenced clutch limitation. Further study in this area would greatly assist in our understanding of the evolution of single-egg clutches in Damara Terns.

INTRODUCTION

The Damara Tern *Sterna balaenarum* is one of only five terns that regularly lays a single egg clutch (Frost & Shaugnessy 1976, Cramp & Simmons 1985) and in this respect it differs from its presumed closest relative the same-sized Little Tern *Sterna albifrons*, which lays two eggs. Laying two eggs appears unrelated to body mass (see Fig. 1) as both large and small species lay more than one egg per clutch (Cramp & Simmons 1985). Instead it has been suggested the trait may be related to the Damara Tern's noncolonial habits and vulnerability to predation (Frost & Shaugnessy 1976, Clinning 1978). Alternatively it may arise from an inability to rear more than two young due to ephemeral or limited food resources (cf. Nisbet 1977, Monaghan *et al.* 1989). One way of testing these ideas is to seek areas in which Damara Terns lay two eggs and compare ecological factors there with areas in which they lay single eggs. Here we report on a small colony with an unusually high incidence of two-egg clutches in southwestern Namibia.

RESULTS

During regular monitoring of this globally vulnerable and near-endemic breeding seabird, Namibian nature conservation officials have recorded over 500 Damara Tern nests between 1975 and 1988. These nest records, deposited with the Ministry of Environment & Tourism in Windhoek, indicate that two-egg clutches occurred in just five of 511 nests. Since then, a further 66 nests, all single eggs, have been recorded from two areas: the West Coast Recreation Area (S. Rohm and R. Norris-Jones) and from a coastal survey of terns from the Cunene River to Sandwich Harbour (Simmons 1993). In total, just 5 of 577 Damara Tern nests recorded in Namibia to date, had two-egg clutches, a frequency of 0.87%.

During renewed efforts to census terns throughout Namibia, the coastal area north of Lüderitz was surveyed in December 1991. On 18 December, 12 nests were located on a large isolated salt pan which runs 24 km south from Hottentot Bay, some 40 km north of Lüderitz. Centred on 26°15'S, 15°00'E, the elongated pan is *c.* 6 km at its widest point and varies from 0 to *c.* 3 km from a coast which comprises a series of small sandy and rocky bays. In the east it is bordered by the Namib sand sea. The dry brown pan is topographically flat but is criss-crossed in some areas with large salt ridges where the salt crust has buckled. Birds were found nesting in these raised areas, and were first reported here in 1977 (Siegfried & Johnson 1977).

Eleven tern nests all with eggs, were checked in a small colony which may have comprised more birds, approximately 10 km south of Hottentot Bay and 1 500 - 2 500 m from the coast. Nearest active nests were only 20 m apart (range 20 - 80 m) and communal mobbing occurred during the nests. Another nest was discovered about 6 km SSE from the colony but was not checked for contents. Of the 11 colonial nests, nine were checked for contents and four had two-egg clutches; a frequency of 44%. All other nests were c/1. When first reported in 1977, nine pairs were recorded breeding, all with single eggs (n = 8) or chicks (Siegfried & Johnson 1977).

Egg volume (Length x breadth 2 x 0.48) (Monaghan *et al.* 1989) was not calculated for these eggs, but they have been for a larger sample of Damara Tern eggs throughout coastal Namibia (Nest record scheme). We then plotted egg volume against body mass for a sample of terns for which data on both were available (Cramp & Simmons 1985), and compared those species regularly laying two eggs with those laying one (Fig. 1). Terns laying single eggs laid increasingly larger eggs as body mass increased. However, for Damara Terns, a single large egg was not evident: egg volume was identical to that of several same-sized two-egg species (Fig. 1).

This argues against the idea that single eggs are an adaptive strategy enabling the laying of larger better quality eggs for reasons of increased hatchability, or chick growth (Parsons 1970, Nisbet 1978, Williams 1980). Instead it suggests some constraint to laying a second egg which is occasionally overcome in some areas.

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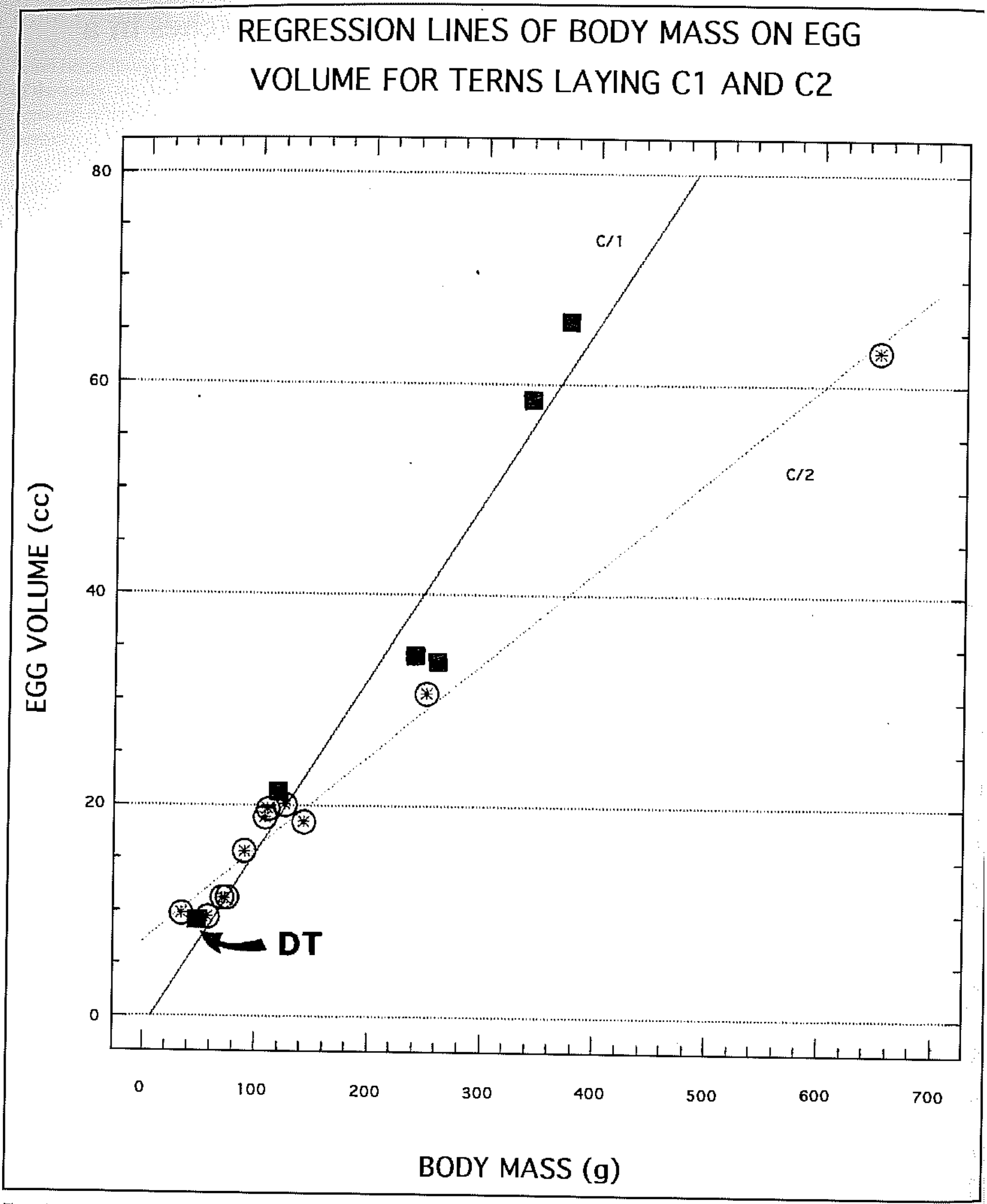

Figure 1: The difference in egg volume of terns laying one-egg clutches (cl) and two-egg clutches (c2), relative to body mass. Damara Terns (DT) lay eggs no larger than same-size congeners laying two eggs.

DISCUSSION

Relative to national averages (< 0.9%) the 1991 findings represent a very high frequency indeed. The most likely explanation is that the large clutches may reflect very favourable food resources since tern clutches are closely related to male food provisioning rates (Nisbet 1977, Monaghan *et al.* 1989). The Lüderitz area is also well known for its large near-shore Benguela upwellings (Shannon 1985) where fish availability is increased due to increased nutrient availability (Crawford *et al.* 1987). Damara Terns in this area, therefore, may enjoy a relatively dependable and enhanced food resource relative to other terns along the Namibian coast. This would tie in with the finding that egg size has not increased among Damara Terns (relative to same sized congeners) as an evolutionary response to increase growth and survival of chicks. Instead birds appear to be constrained to a single in most cases.

The alternative, that clutches in some species are thought to be an adaptation to increase growth rate and thus reduce the time that chicks remain vulnerable to predation (Frost & Shaugnessy 1976, Clarke & Wilson 1981) is unlikely in view of the lack of increase in egg size (Fig. 1). However, predation pressure is virtually non-existent on this highly isolated pan, and nests were unusually closely situated relative to averages from elsewhere (57 - 200 m: Frost & Shaugnessy 1976, Clinning 1978, Simmons & Braine 1994). Hence release from predation-limited clutch size may have had some bearing on the large clutches found at Hottentot Bay.

Other explanations for the two-egg clutches such as two females laying in one nest cannot be ruled out, but it seems unlikely in view of the vast amount of breeding habitat available on this and other salt pans.

If enhanced food resources from the Lüderitz upwelling cell contributed to the larger clutches, one would predict that more two-egg clutches should occur in south western Namibia. There are too few other nests known from the southern edge of the Damara Tern's Namibian range to assess whether two-egg nests are more common there. Geographic analyses however, indicate that only one c/2 has ever been recorded from the Skeleton Coast Park (n =286: Simmons & Braine 1994) while R. and S. Braby (in litt.), found no c/2 nests in 214 nest records from the same area. Only two pairs of adults feeding two chicks in 180 nests (1.1%) were recorded by Tarr (in prep.), and none in 40 nests were recorded by Clinning (1978), in the West Coast Recreation Area, south of the Skeleton Coast. Only single-eggs have been reported in clutches from South Africa (Randall & McLachlan 1982) and the Elizabeth Bay colony in Namibia (Siegfried & Johnson 1977).

That terns in this southerly colony sometimes lay two eggs is therefore unexpected. Further records of clutch size in this area combined with observations of food resources, courtship feeding, chick growth, predation pressure and population density would shed light not only on the reasons for two-egg nests at Hottentot Bay but also the evolution of the unusual one egg clutch of the Damara Tern.

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Cape Fur Seal predation by Brown Hyaena in the Namib-Naukluft Park, Namibia

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ABSTRACT

A single brown hyaena *Hyaena brunnea* was found on the fresh carcase of a Cape fur seal *Arctocephalus pusillus* in the Meob Bay area of the Namib-Naukluft Park, Namibia. Evidence showed that the hyaena approached the seal and killed it by biting and crushing its skull. Although no previous records of this type of predation could be traced, brown hyaena may hunt seals more commonly than is known.

INTRODUCTION

Brown hyaena *Hyaena brunnea* occur commonly on the Namib Desert coast where their scats reflect prey abundance in the area they frequent (Skinner & van Aarde 1981; Skinner & Smithers 1990). The Cape fur seal *Arctocephalus pusillus* is abundant along this coast where it congregates in breeding and non-breeding colonies of tens of thousands, and brown hyaenas closely associate with such colonies (Skinner & van Aarde 1981). One non-breeding aggregation, which regularly hauls out on the beach, is located between Meob Bay and Conception Bay at approximately 14°30'E, 24°15'S. Single seals frequently occur along the beach to the north and south of this aggregation. These may be healthy individuals resting and sleeping or they may be injured, diseased or debilitated. As can be expected from a seal population of this magnitude, natural mortality accounts for many of the carcases which are found ashore, but it is well known that seals often are fatally injured or destroyed by boat fishermen along the entire Namibian coast. There is consequently no shortage of food for a medium-sized scavenger like brown hyaena, which is also the largest resident terrestrial carnivore on the Namib-Naukluft Park's coast.

RESULTS AND DISCUSSION

On 10 June 1992 at 08h45 we located a full grown brown hyaena on a seal carcase 10 km north of the Lange Wand in the Meob area (c. 14°37'E, 24°30'S). The seal, a female, was not fully grown judging from the unworn teeth and body mass which we estimated at 50 kg (*vide* 75 kg given by Smithers 1983). It had been killed by a bite on top of the head which crushed the cranium; the brain was eaten and the anal area slightly fed on (Figure 1). There were also tooth marks on the back, presumably made when the hyaena tried to carry off the carcase at our approach; instead it dropped its kill and ran to shelter among neighbouring dune hummocks. The blood was still fresh and the carcase warm, indicating the kill had occurred shortly before our arrival. There was no evidence that the seal was sick or debilitated.

Tracks showed that the seal had hauled out of the sea, probably after the most recent high tide, which occurred about midnight the previous evening. It moved 40 m above the high water mark to a dune hummock, where it rested and possibly slept. Hyaena tracks were found approaching the beach from the inland. The tracks crossed the seal's drag marks whereupon they followed the

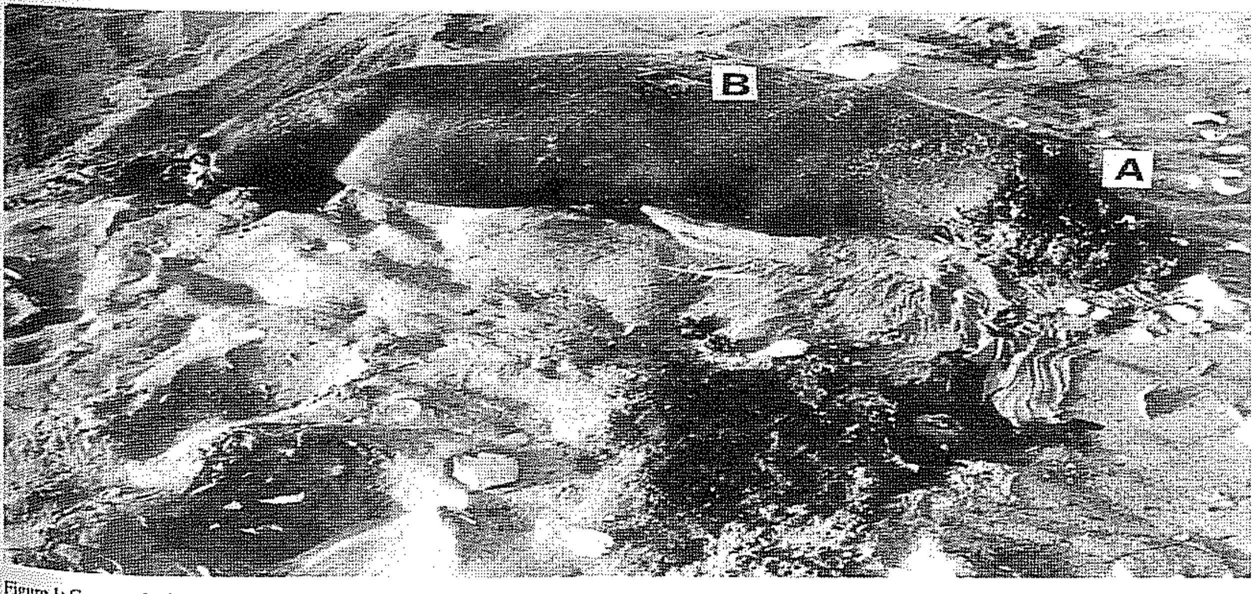

Figure 1: Carcase of a Cape fur seal killed by brown hyaena, showing "A" the crushed skull, and "B" marks on the back where the hyaena attempted to carry the carcase.

marks, diverting to an adjoining dune hummock where the hyaena lay down about 5 m from the resting seal. According to the signs, the hyaena attacked the seal where it lay, killed it after a struggle, then began to feed on the brain.

We left the carcase and returned the following morning to find the seal had been dragged about 150 m inland to a shallow depression between vegetated dune hummocks. Approximately 90% of the carcase had disappeared, leaving portions of the skin and skeleton remaining. There were numerous hyaena and black-backed jackal *Canis mesomelas* tracks around the remains. In the same depression we found evidence of earlier scavenging in the form of three seal skulls and one skull and horns of gemsbok *Oryx gazella*. These skulls were all from fully grown animals, and it is unlikely they were carried there by jackal. Several old hyaena scats were present, indicating a latrine (Skinner & van Aarde 1981), although no signs of a den in the immediate area could be found.

Brown hyaenas are predominantly scavengers, their kills being largely restricted to small mammals, birds, reptiles and insects, although they are known to kill sheep, goats and calves (Skinner & Smithers 1990). While brown hyaenas in the Kalahari spend little time and energy hunting prey, with no records of large herbivores being hunted (Mills 1990), they will indulge in a brief chase and grab at their prey, quickly giving up if unsuccessful (Owens & Owens 1978). Their close association with seal colonies is for scavenging benefits, with 75% of coastal brown hyaena scats containing seal remains (Skinner & van Aarde 1981). These authors raise the possibility of live seals being killed by brown hyaena although they never record this. We have subsequently seen a video recording where a brown hyaena attacks, kills and carries off a newly born seal pup which was separated from its mother.

We contacted eight persons who collectively spent 60 years as workers and nature conservators in the Skeleton Coast Park to the north of the Namib-Naukluft Park, where brown hyaenas and seals also occur commonly. They had no records of seal predation by brown hyaenas, although they on several occasions located the latter on seal carcases. Together with our own experience of 15 years, this is the first instance of such predation recorded on the Namib coast. However, because the secretive nature of the brown hyaena plus the isolation and restricted access to 80% of the 1 400 km Namibian coastline which is either proclaimed game reserve or protected diamond area, it is possible that brown hyaena kill seals more commonly than is presently known.

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Frost damage to wild sycamore fig trees in the Namib-Naukluft Park, Namibia

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ABSTRACT

Wild sycamore figs *Ficus sycomorus* suffered extensive frost damage in 1989, being the first known occurrence in 25 years. Twenty-five fig trees were moniroted for 21 months and the effects of frost were related to minimum temperatures in the riverbed. Sub-zero temperatures affected 20 of the trees and caused up to 90% frost damage to leaves. Foliage affected by frost remained moribund and attached to the branches for the monitoring period. Frost may limit the distribution of sycamore figs in the Namib.

INTRODUCTION

Wild sycamore figs *Ficus sycomorus* L. form part of the riverine woodland community in the lower Kuiseb River in the Namib-Naukluft Pa;rk, a conservation area of the Namib Desert in Namibia. During winter 1989 extensive leaf damage by frost was noted on these fig trees (M>K> Seely, pers. comm.) This initiated a study (1989-91) aimed at investigating and quantifying the damage, as well as monitoring the degree of recovery.

STUDY AREA

A 15 km section of the Kuiseb River in the vicinity of the Namib Research Institute at Gobabeb was selected (Fig. 1). The Namib is a cool, coastal desert extending in a narrow strip of about 200 km wide and 2 000 km long from Mocamedes in Angola to the Olifants River in South Africa (Seely 1987). The Kuiseb River rises in the central Khomas Hochland area of Namibia. It has a catchment area of approximately 15 000 km^2 and traverses the Namib for a length of about 440 km before ending at the Atlantic at Walvis Bay (Huntley 1985). Gobabeb lies on the middle section of the Kuiseb River (23°34'S, 15°03'E) at an altitude of 407m. The annual average rainfall (n = 30 years) is 18,8 mm (Weather Office records). About 37 days of fog occur per year (Lancaster, Lancaster & Seely 1984).

The Kuiseb is an ephemeral river that flows sporadically past Gobbeb during the period January to April of most years. The riverine woodland comprises *Faidherbia albida, Acacia erioloba, Salvadora persica, Euclea pseudebenus, Tamarix usneoides* and *Ficus sycomorus*. The latter species is sparsely distributed along the river, with only 25 trees occurring within the 15 km liner study area. The riverine vegetation is utilized by domestic stock

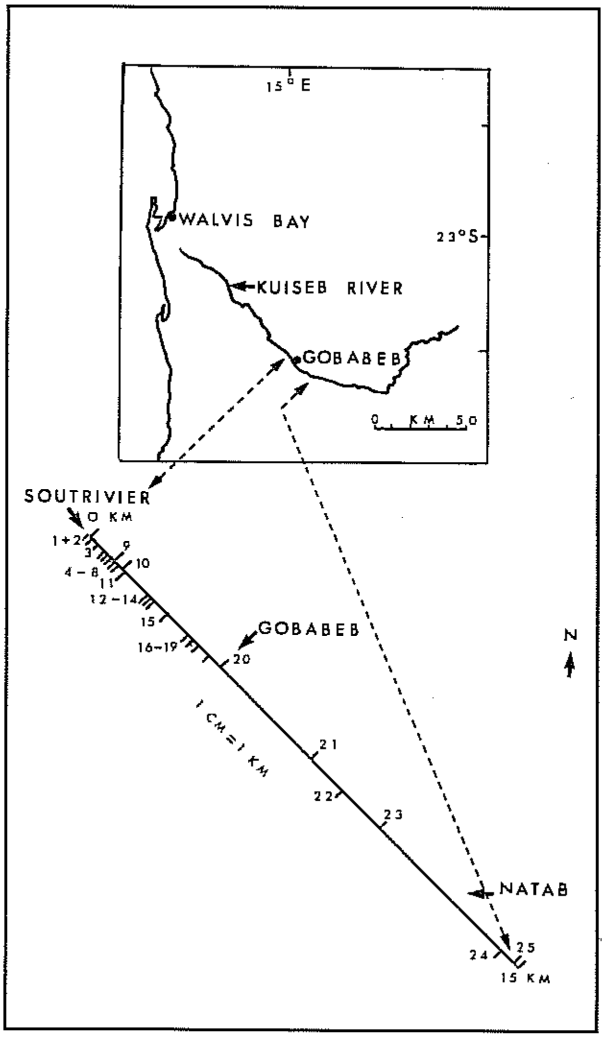

FIGURE 1: Map of the central Namib region showing the study area in the Kuiseb River (inset), together with a detailed, schematic diagram of the location of 25 fig trees which were monitored for frost damage.

belonging to communities of Topnaars – goats, sheep, cattle and donkeys – as well as gemsbok *Oryx gazella*, springbok *Antidorcas marsupialis*, steenbok *Raphicerus campestris* and ostrich *Struthio camelus*. In addition to excessive grazing and browsing pressure on most of the riverine vegetation, goats inflict additional damage to fig trees by feeding on their bark.

METHODS

All fig trees occurring in the study area were monitored at irregular intervals from September 1989 to May 1991. Twenty-five trees were tagged and numbered with plastic strips. Five large specimens, ranging from 5-15 m in height, which showed no frost damage served as controls. The height of each tree was subjectively estimated to the nearest metre. Frost damage was assessed by estimating the total amount of foliage killed on each tree according to a rating of 0-10 where:

0 = no damage
1 = <10%
2 = 11-20%
3 = 21-30%
4 = 31-40%
5 = 41-50%
6 = 51-60%
7 = 61-70%
8 = 71-80%
9 = 81-90%
10 = 91-100%

The extent of damage in relation to the circumference of the tree's canopy was estimated and expressed as a percentage of 360°. The height of the dead foliage above ground level was recorded as well as its position in relation to the river-bed. To assess re-growth, trees were rated on a scale of 0-4, based on fresh foliage production, where 0 - no re-growth, 1 = trace, 2 = low, 3 = medium, 4 = high. Because neighbouring trees may protect fig trees from frost by shielding or forming a protective canopy over the fig trees, the distance of neighbouring species from the fig trees and the extent to which they protected the fig trees was expressed as a percentage.

Absolute maximum and minimum screen temperatures and absolute grass minimum temperatures were obtained from Gobabeb. Taking these data for the period when the frost was throught to have occurred in winter 1989, the minimum temperatures for the river-bed at this time were estimated. This was achieved by comparing absolute minimum grass temperature at the weather station with that measured in the river-bed.

RESULTS AND DISCUSSION

The measurements of 25 fig trees, their damage by frost and subsequent re-growth, and their relationship to other tree species are given in Table 1. Twenty out of 25 fig

TABLE 1: Frost damage and other parameters measured on 25 fig trees in the Kuiseb River, Namib-Naukluft Park (1989-91)

Tree no. and location (N or S)	Estimated height (m)	Average rating (0-10)	Frost Damage degree (% of 360°)	Frost Damage height (m)	Percentage protection	Re-growth of foliage (0-4)	Distance from other trees (m)
1 S	15	0	0	0	25	Control	8
2 S	10	0	0	0	0	Control	8
3 S	9	1	25	3-6	0	2	2
4 S	9	1	15	2-5	0	3	6
5 S	15	1	50	1-5	25	3	8
6 S	8	1	25	1-5	0	3	5
7 S	10	1	50	1-7	0	3	4
8 S	10	1	40	2-7	0	3	3
9 N	4	5	100	2-4	100	3	0
10 N	9	2	50	2-7	50	2	1
11 S	7	5	100	0-7	0	2	1
12 S	8	0	0	0	100	Control	3
13 S	5	0	0	0	100	Control	5
14 S	9	0	0	0	0	Control	1
15 S	6	2	15	2-3	50	1	2
16 S	10	2	60	2-6	100	3	0
17 S	10	3	50	1-8	50	3	1
18 S	12	2	50	0-5	100	3	1,5
19 S	10	1	5	4-6	0	3	3
20 N	5	3	50	2-5	0	3	25
21 N	6	2	50	1-5	50	3	2
22 S	6	1	50	2-5	0	3	5
23 N	6	9	100	1-6	0	4	15
24 S	8	1	15	1-7	50	3	1
25 N	10	2	50	0-8	50	4	3

trees (80%) showed some degree of frost damage. After two years of monitoring, leaves killed by frost were still attached to the fig trees. Estimated frost damage for most fig trees during the monitoring period varied from 0 to 90%. The tree with the highest frost damage recorded (No. 23), namely 81-90% had no protection from other trees. The greatest extent of leaf damage occurred on those parts of the trees facing the river, but three trees showed frost damage on their entire circumference of foliage. One of these trees (No. 11) had complete canopy protection whereas the two remaining trees had none. Another tree (No. 20), which grew 25 m from the nearest other tree, showed frost damage to 50% of its circumference. Consequently it appears that the shelter provided by other trees did not decrease the amount of frost damage. Frost damage did not occur above the height of 8 m in any of the trees. Although medium to high regrowth rates occurred on 16 of 20 trees, complete recovery from frost damage was not recorded in any of the affected fig trees when monitoring ended 21 months later. The effect which frost may have had on fruiting could not be established because of the highly subjective nature of estimating fruit production and subsequent shedding of fruit.

TABLE 2: Comparison between sub-zero minimum grass temperatures in the Kuiseb river-bed and Gobabeb weather station (May '91 to October '91)

Date	Min. grass temp. (°C)		Difference (°C)
	River-bed	Weather Station	
28 June	-1,1	2,7	3,8
19 Aug.	-2,7	-1,1	1,6
20 Aug.	-1,0	1,1	2,1
Mean	-1,6	0,9	2,5

Sub-zero grass minimum temperatures were measured at the weather station on two occasions in winter 1989: -0,8°C in June and 01,5°C in July. Since grass minimum temperatures in the river-bed were on average 2,5°C lower than those at the weather station (Table 2), frost damage was probably severest during June/July 1989 when the lowest temperatures occurred and may have declined to -3,3°C and -4,0°C in the river-bed. Similarly, a second episode of frost may have occurred during August 1990 when an absolute grass minimum of -0,5°C was measured at Gobabeb's weather station, indicating an absolute grass minimum of -3,0°C in the river-bed. This makes it possible to predict frost damage to fig trees in the river-bed when grass minimum temperatures at Gobabeb approach zero.

The mustard bush *Salvadora persica*, which is abundant in the study area, and sycamore figs, which are the least common of the riverine trees, are the only broad-leafed tree species of the Kuiseb riverine community. Both *S. persica* and *F. sycomorus* showed severe frost damage, whereas the remaining tree species have greatly reduced leaf surface area, which rendered them less susceptible to frost. No frost damage was evident in these remaining tree species.

CONCLUSIONS

Frost damage to wild figs in the Kuiseb river-bed is an infrequent phenomenon and has been observed once in the period 1967-91 (M.K. Seely, pers. comm.). Therefore frost in this region of the Namib Desert can be considered an episodic event which may exert considerable stress on fig trees. For example, frost events may kill seedling fig trees and it is noteworthy that no seedlings were recorded in the study area. Since the smallest fig tree measured 4 m in height (Table 1), it appears likely that recruitment to the population is curtailed by periodically unfavourable weather conditions, one of which could be frost. This would affect tree species composition in the river-bed by favouring narrow-leafed species which appear more tolerant to frost. From the observations made in the river-bed, it can also be predicted that the distribution of sycamore fig trees in the Namib may be limited to areas where frost is infrequent or absent.

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Analysis of the 1990 and 1991 Namibian pelagic fishing seasons

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ABSTRACT

This paper examines some of the more important characteristics of Namibia's commercially important pelagic fish stocks exploited during the 1990 and 1991 seasons. Comparisons of landings in recent years and some broad speculations on the future state of the Namibian pelagic fish stocks are made. Species considered are pilchard *Sardinops ocellatus*, anchovy *Engraulis capensis*, horse mackerel *Trachurus capensis* and round herring *Etrumeus whiteheadi*. A total of 242 901 t pelagic fish was landed during the 1990 pelagic fishing season, while 171 094 t was landed during the 1991 season. These landings were of a similar magnitude to the mean since 1979. The landings of both seasons were largely based on a single strong cohort for all species, spawned during the austral spring and summer period of 1988/89. Indications are that recruitment of all pelagic stocks was poor during the 1989/90 breeding period.

INTRODUCTION

The marine ecosystem in the exclusive economic zone (EEZ) of the Republic of Namibia is, biologically, a highly productive system (Crawford *et al* . 1987). This region supports large populations of pelagic and demersal fish, as well as several invertebrate species, which are utilised for commercial purposes.

Owing to its economic importance to Namibia and the Walvis Bay enclave, considerable effort is placed on obtaining biological information on Namibia's pelagic fish stocks. This information is used primarily to assist the authorities in managing these stocks to provide an optimal sustainable benefit to the fishing community and to the Namibian economy. Benefit can be defined as a combination of total fish biomass landed, economic yield, and some level of socio-economic benefit (eg. number of people employed, foreign exchange earned, etc.). This directed research effort has resulted in a database of biological parameters and catch statistics on pelagic fish covering more than 25 years and represents one of the major time-series of biological information available in Namibia.

Annual reports and reviews of the multi-species pelagic fishery off Namibia can be found in the International Commission for the Southeast Atlantic Fisheries collection of scientific papers (Butterworth 1979, 1980; Butterworth & Le Clus 1979; Hewitson 1988; Hewitson *et al.* 1989a; Hewitson *et al.* 1989b; Katsuyama 1984; Le Clus 1984, 1986; Le Clus *et al.* 1987; Le Clus & Melo 1981, 1982, 1983; Le Clus & Thomas 1981, 1982; Melo 1984a, 1985; Melo & Thomas 1985; Newman & Schülein 1974; Schülein 1986; Schülein *et al.* 1978; Thomas 1981, 1983, 1984, 1986; Thomas & Boyd 1985; Wysokinski 1981) and other sources (Crawford *et al*. 1985; Moorsom 1984; Payne & Crawford 1989).

Pelagic shoaling fish are normally considered unsuitable for human consumption in an unprocessed form. Namibian pilchard is canned and thus has a higher economic value than the other species which are processed into fish meal for animal feed and fish oil for use in the chemical industry. Catches of a mixed species composition including pilchard are processed into fishmeal and oil, and such pilchard is considered as "by-catch". Fishermen are expected to limit this pilchard by-catch. The management of pelagic horse mackerel is complicated by the fact that this species, on reaching maturity, migrates offshore to form an important component of the deep-sea trawling industry.

The 1990 and 1991 pelagic seasons both commenced on 1 March and closed on 31 August. The initial 1990 pilchard canning quota was set at 40 000 t, but an additional quota of 20 000 t was granted in mid-July. By-catches were not included in the quota. In 1991 a total pilchard quota of 60 000 t, including by-catches, was allocated. Anchovy, horse mackerel and round herring catches were not subjected to quota restrictions, however landings were closely monitored to ensure that the by-catch of pilchard and especially juvenile pilchard was kept to a low level. A high bycatch of juvenile pilchard must be avoided to realize an optimum long-term yield for this species.

The 11 mm mesh-size net and the purse-seine catching technique are of such a nature that little size selectivity of fish within shoals occurs. It should be noted, however, that purse-seining is a non-random sampling procedure as shoals of larger-sized fish are usually targeted. The data presented, therefore, do not reflect the state of the entire population but merely the portion targeted by the fishing industry. These data are, however, comparable to previous years, as fishing gear and techniques and target populations have essentially remained unchanged since the late 1960's with the introduction of hydro-acoustical fish finding techniques and hydraulic power-blocks to assist net-hauling. The data can thus be used to indicate trends within the pelagic fish populations.

METHODS

A fleet of thirty-eight purse seiners was licensed to catch pelagic fish within Namibia's Exclusive Economic Zone during the two years under review. Skippers of all vessels were required to supply information on the locality and date of catches made. On off-loading at the processing factories all landings were weighed using bucket-type or band-type industrial mass meters.

Fish samples were collected by fisheries inspectors from all vessels during off-loading at intervals of approximately 20 minutes, or more frequently in the case of small landings. These samples were obtained from the chutes between the vessel and the factory and were used to determine the species composition of the total catch.

Samples for biological analyses (*viz.* measuring length, weighing, ageing, sexing and describing the reproductive state) were collected in a similar manner from a maximum of six vessels each day. Vessels sampled were selected randomly. The number of landings made and samples collected are presented in Table 1. Each sample was grouped according to species and specimens were analyzed as above.

In 1990, pilchard, anchovy and round herring were selected at random and the caudal length (L_c) recorded to the nearest 0,5 cm. Measuring continued until 50 fish of each species had been assigned to any one of the 0,5 cm length classes, resulting in a sample size of approximately 100 fish per landing. As problems determining the precise posterior position of the caudal column were experienced, total length (L_t) was measured in 1991. The difference between these two measurements, the tail flukes, appear to grow isometrically, therefore simple conversion factors could be applied to convert the 1990 caudal lengths to total length for comparison with the 1991 data. The factor calculated for each species was:

Pilchard $L_T = 1.18\, L_C + 0.3$
Anchovy $L_T = 1.10\, L_C + 0.7$
Round herring $L_T = 1.11\, L_C + 1.1$

Horse mackerel were measured to total length (L_T) in both years under review.

Otoliths were used for ageing pilchard and anchovy, the methods applied being similar to those described by Melo (1984b) and Thomas (1985). In 1990 an index of the age structure of the catch was obtained from 20 fish in each length class per month. Sampling was randomised in 1991; 10 fish per sample were selected randomly.

Namibian horse mackerel were until recently not actively managed and therefore otoliths, whilst collected, have not been analyzed. Owing to the normal economic insignificance of round herring no data for ageing were collected.

RESULTS

Landings

Pelagic landings from 1964 to 1991 are summarised in Table 2.

The pilchard catch for 1990, 89 215 t, was the highest since 1977. The canning quota was exceeded by 50%. A large proportion of this excess pilchard was caught due to target misidentification, which resulted in pilchard being netted while vessels were searching for anchovy and/or horse mackerel. The 1991 pilchard catch of 68 607 t, while about 25 % less than the 1990 catch, reflected the stricter control imposed by the authorities in keeping landings within the quota, rather than the availability of pilchard.

A total of 51 506 t of anchovy was caught in 1990 and 17 537 t in 1991. Landings have thus maintained a downward trend since the peak harvest of 376 000 t in 1987 and indeed the 1991 harvest represents one of the lowest since the anchovy industry started in 1967.

Pelagic horse mackerel landings totalled 85 180 t during the 1990 season and 83 250 t in 1991. Although these landings were equal or better than most previous harvests, they were only half of the 1988 catch. With the decline in anchovy landings since 1982 and the depleted state of the pilchard stock, juvenile horse mackerel has become an important component in Namibian pelagic catches (Le Clus *et al*. 1987).

TABLE 1: Number of samples collected from purse-seine vessels during the 1990 and 1991 pelagic fishing seasons.

	Year	Pilchard	Anchovy	H.Mackerel	R.Herring
Directed landings	1990	938	462	599	26
(>50% of catch)	1991	706	173	412	
Samples collected	1990	266	89	170	39
	1991	245	19	125	2
Length measurements	1990	58 565	8 407	26 417	4 299
	1991	24 469	1 900	12 550	200
Fish aged	1990	1 478	811	0	0
	1991	2 125	174	0	0

TABLE 2: Catch statistics from 1964 to 1991 in tonnes (x 1000)

Year	Pilchard	Anchovy	H.Mackerel	Other	Total
1964	636	1			637
1965	666	1			667
1966	719	3			722
1967	926	24			950
1968	1387	161			1584
1969	1110	226			1336
1970	514	189			703
1971	325	185	140	5	655
1972	374	137	22	2	535
1973	408	296	12	4	720
1974	562	249	60	2	843
1975	561	186	14	8	769
1976	452	88	23	8	571
1977	200	133	81	1	415
1978	46	355	9	1	411
1979	34	277	28	6	245
1980	11	187	35	1	234
1981	52	187	3	2	254
1982	51	84	67	1	203
1983	44	184	107	4	339
1984	56	14	87	3	160
1985	54	51	22	3	130
1986	52	16	83	1	152
1987	66	376	34	1	476
1988	62	117	169	0	348
1989	78	79	31	0	188
1990	89	51	85	18	243
1991	68	18	83	2	171

Round herring, historically an insignificant contributor to the Namibian pelagic catch, represented 7.2% of the total pelagic catch in 1990, but returned to a more usual level of 1 700 t, 1.0% of the total catch, in 1991.

Temporal and spatial distribution of catches

The pattern for pilchard catches during 1990 was similar to previous years (Hewitson *et al.* 1989a; Hewitson *et al.* 1989b) with most of the pilchard caught early in the season (Figure 1). A further period of increased catches occurred towards the end of the season. The area between 22°00'S and 24°00'S accounted for 81.0% of the total pilchard catch taken (Figure 2). Catches in this area were high from the end of March until the end of April, contributing largely to filling the initial quota of 40 000 t. Fishing then ceased until a further quota of 20 000 t was granted in mid-July. This additional quota was taken almost entirely north of 23°00'S. Pilchard-directed fishing started later in 1991, most of the catch being taken in mid-season between 21°00'S and 23°00'S.

The overall temporal trend of anchovy catches in 1990 was similar to that of 1989 (Hewitson *et al.* 1989b), although catching started almost a month later in 1990 with maximum catches occurring from mid-March to the end of April (Figure 1). Very little anchovy was caught after this period in either year. In 1991, as in 1988 (Hewitson *et al.* 1989a), large amounts of newly recruited juvenile anchovy were caught late in the season. These recruits were not available in the intervening seasons. Seventyfour per cent of the total anchovy catch was taken between 22°00'S and 24°00'S in 1990 compared to 82% in 1991. The balance was caught further north (Figure 2).

The pelagic horse mackerel harvest was exceptionally high during March in both seasons, while the remainder of the catch was spread throughout the rest of the season in 1990, but mostly caught in April in 1991 (Figure 1). Horse mackerel was caught south of 22°00'S early in the 1990 season, while a large proportion of the remaining catch was made between 20°00'S and 22°00'S (Figure 2). In previous years most of the harvest was taken further north. In 1988, for example, the highest yields were recorded between 20°00'S and 22°00'S, while in 1987 and earlier years most of the catch was made north of 20°00'S (Hewitson 1988). The 1991 catch, which was almost entirely from north of 21°00'S, reflected a return to the more common distribution of the pelagic horse mackerel stocks.

Round herring was caught mainly in April 1990 between 22°00'S and 24°00'S, in shoals mixed with anchovy and juvenile horse mackerel. The temporal and spatial trends of catching, therefore, were very similar to those of anchovy and horse mackerel (Figures 1 & 2). Few round herring were caught in 1991.

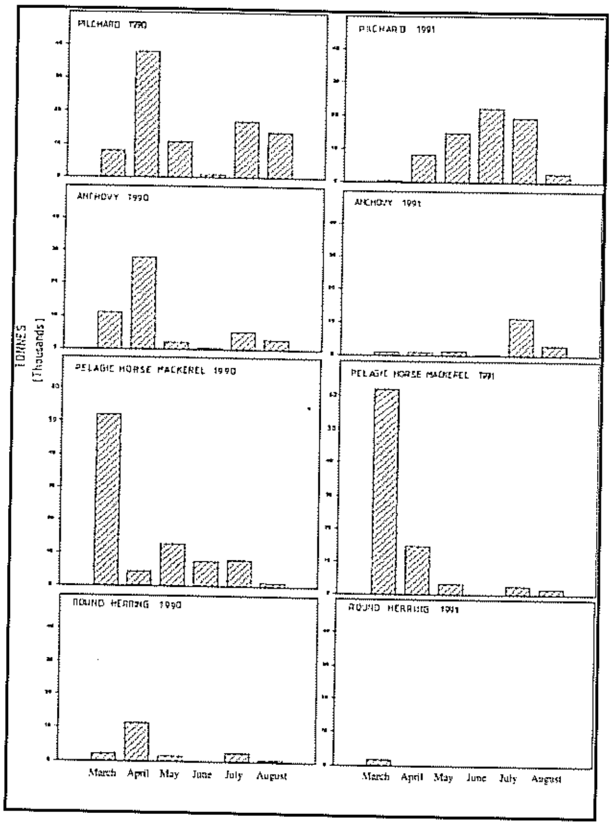

FIGURE 1: Monthly catches of a) pilchard, b) anchovy, c) pelagic horse mackerel and d) round herring in 1990 and 1991 (March to August).

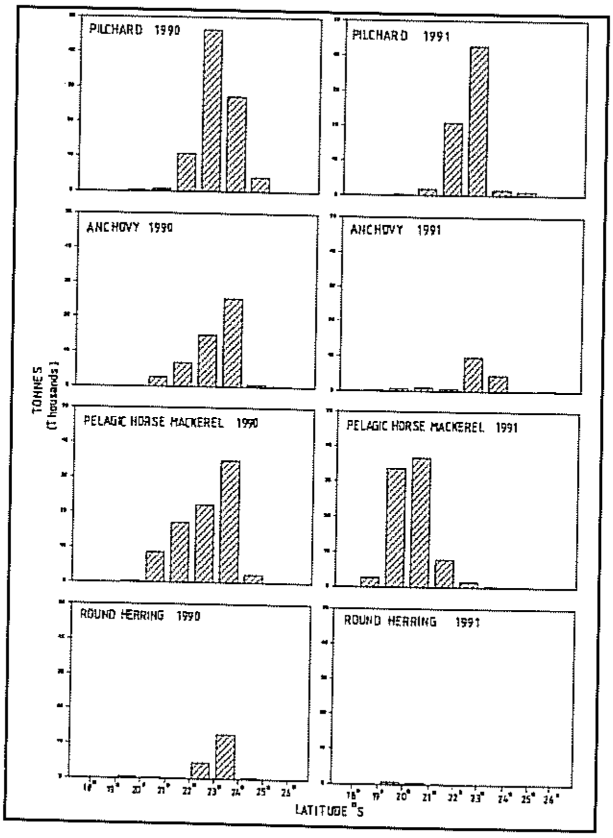

FIGURE 2: Spatial variation of a) pilchard, b) anchovy, c) pelagic horse mackerel and d) round herring catches in 1990 and 1991.

Length and age frequency

Length-frequency analysis of the pilchard landed in 1990 shows that 80% were between 20.0 cm and 24.0 cm L_t (Figure 3), while in 1991 91% were between 21.0 cm and 25.0 cm. Pilchard of less than 19.0 cm L_t, mostly 0-year olds, represented less than 19% of the total number of fish sampled in 1990 and only 5% in 1991. In the previous three years the percentage of fish smaller than 16 cm L_c (approximately 19.2 cm L_t) was considerably higher than in 1990 and 1991. Percentages of 65.9, 58.2 and 63.7 were recorded in 1989, 1988 and 1987, respectively (Hewitson 1988; Hewitson *et al.* 1989a; Hewitson *et al.* 1989b).

Age data obtained from commercial catches confirmed the paucity of 0-year old pilchard in the landings during these two years (Table 3). 0-year old fish were caught in all months except May, but accounted for only 6.4% by number of the total 1990 pilchard harvest and less than 3% in 1991. The age data, therefore, indicated that during 1990 and 1991 the pilchard population was founded on a single cohort which was spawned during the austral spring/summer period of 1988/1989. Pilchard from earlier cohorts were almost entirely absent from the landings during these two seasons.

TABLE 3: Frequency (percentage) of pilchard in each age-group caught during the 1990 and 1991 pelagic fishing seasons

		Year-Class			
Year	Month	0	1	2	3
1990	March	13.3	85.5	1.2	0.1
1990	April	8.0	88.9	2.6	0.4
1990	May	0.7	96.3	2.5	0.5
1990	June	11.8	86.5	0.6	1.0
1990	July	5.6	92.3	1.9	0.1
1990	August	3.0	93.4	3.4	0.1
1990	March-August	6.4	90.8	2.4	0.3
1991	March	-	-	-	-
1991	April	2.6	13.1	81.9	2.4
1991	May	2.6	22.5	72.5	2.4
1991	June	4.8	41.4	53.0	0.8
1991	July	0.2	33.8	65.0	1.0
1991	August	5.8	46.1	46.8	1.3
1991	March-August	2.9	28.3	67.1	1.7

The age distribution of the anchovy caught during 1990 was dominated by one-year and two-year old fish (Table 4), with a modal length (L_t) of 12.0 cm to 14.0 cm (Figure 3). This was of a similar age structure to the 1989 catch (Hewitson *et al.* 1989b). The proportion of 0-year old fish represented in the catches in these two years was the lowest ever recorded. The anchovy caught in 1991 were, in comparison, smaller with a length of 9.0 cm to 12.0 cm, of which almost half was 0-year old fish. This was similar to the catches made in 1987 and 1988 when the modal length (L_c) of fish landed was 10 cm (approximately 11.9 cm L_t) (Hewitson *et al.* 1989a; Hewitson *et al.* 1989b).

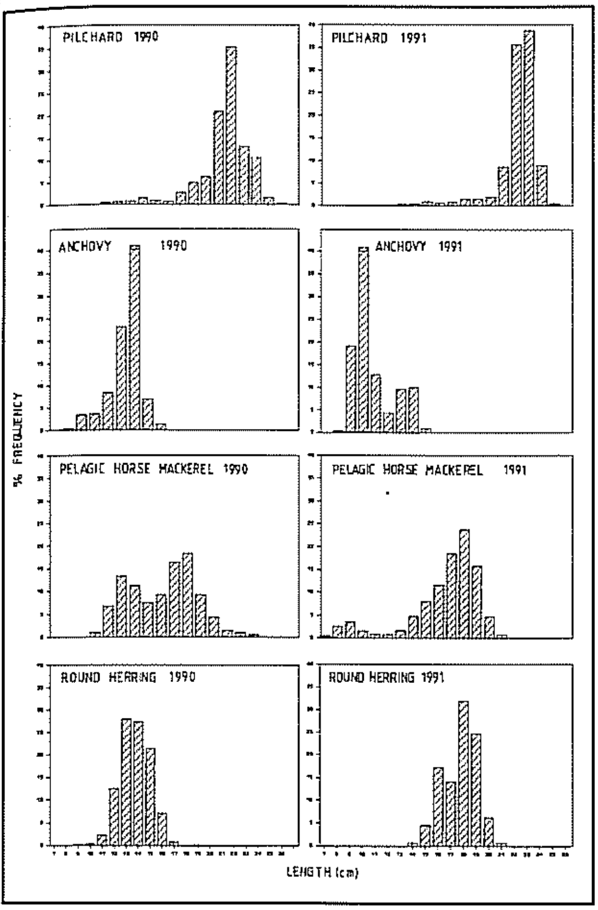

FIGURE 3: Length-frequency distribution of a) pilchard, b) anchovy, c) pelagic horse mackerel and d) round herring catches in 1990 and 1991.

TABLE 4: Frequency (percentage) of anchovy in each age-group caught during the 1990 and 1991 pelagic fishing seasons

		Year-Class			
Year	Month	0	1	2	3
1990	March	1.5	46.7	46.1	5.8
1990	April	1.0	59.7	37.6	1.7
1990	May	1.9	54.5	43.3	0.2
1990	June	23.7	42.9	29.6	3.8
1990	July	64.4	24.8	10.0	0.6
1990	August	23.0	53.4	21.9	1.5
1990	March-August	12.9	50.6	34.1	2.4
1991	March	5.3	21.0	73.7	0
1991	April	20.0	10.0	60.0	10.0
1991	May	10.7	60.7	21.4	7.2
1991	June	0	60.0	20.0	20.0
1991	July	64.8	3.7	22.2	9.3
1991	August	69.8	13.2	13.2	3.8
1991	March-August	44.8	21.3	27.0	6.9

Pelagic horse mackerel landed in 1990 had a bimodal length distribution, the larger fish being 16.0 to 18.0 cm L_t (Figure 3). This was similar to previous years, for example, the modal length (L_t) for 1986, 1987 and 1988 was 17.5 cm, 17.5 cm and 16.5 cm, respectively (Hewitson *et al.* 1989a). A modal length (L_t) of 13.0 cm was, however, recorded in 1989 (Hewitson *et al* . 1989b). Horse mackerel caught early in the season, up to mid-May, displayed a bimodal length distribution with peaks at 12.0 cm and 17.0 cm. In 1991 the modal peak was between 16.0 and 20.0 cm, representing a more normal pelagic horse mackerel catch.

Only small round herring was harvested during 1990, with a modal length (L_t) of 12.0 to 16.0 cm (Figure 3), while the few round herring caught in 1991 were about 4 cm larger. This is presumed to represent growth in the intervening period.

DISCUSSION

The total pelagic fish landings of 243 000 t for the 1990 fishing season (March to August) represents a 29% increase compared to the previous season. This catch is of a similar magnitude to the mean catch of the previous 13 years, namely 273 000 t. Most of the fish caught in 1990 were from a single strong cohort for all species, probably the result of favourable environmental conditions for egg and larval survival during the spring and summer period of 1988/89. The 1991 catch was also largely dependant on the 1988/89 cohort, but at 173 000 t, it was one of the smallest catches of the Namibian pelagic fishery since modern purse seining began. This was largely due to the strict limitation on pilchard catches, the small size of the adult anchovy stock and the subsequently failure of the anchovy recruit run.

Landings peaked in the early part of both seasons under review followed by a generally lower catch for the rest of the season (Figure 4). The fleet concentrated their efforts on horse mackerel in March of both years, but catches of pilchard and anchovy, which were relatively good in April 1990, were poor in 1991. Moderate catches of pilchard and horse mackerel were made in May 1990, but fishing was stopped entirely for much of June owing to the mixture of juvenile pilchard with adult fish. An additional pilchard quota issued in June allowed further good catches of pilchard to be made in July and August in 1991. Pilchard catches sustained the fleet through May, June and July, until the quota was filled, while a small catch of anchovy recruits in July was also made. Little fish was available in August 1991 and the industry stopped fishing voluntarily some ten days before the official end of the season.

Catches of all species shifted some 100 nm from 21°-24°S northwards to 19°-23°S (Figure 4) in the two years under review compared to the catches in the years immediately preceding this period. Few environmental data are available to indicate the causes of this shift in distribution.

The 1990 pilchard catch was composed of predominantly one-year old fish recruited from the 1988/89 cohort. These fish were of uniform size (modal L_t 20.0 - 24.0 cm) and were ideal for canning. Very few older fish were present, and data from both commercial sampling and research cruises indicated that few juveniles were present. During 1989 about 50% of the pilchard catch were 0-year old fish (Hewitson *et al.* 1989b), indicating a very successful 1988/89 spawning season. During 1990 only 6.4% (by number) 0-year old fish were present, it was therefore not surprising that the 1991 pilchard catches were again reliant on the 1988/89 cohort. A similarly strong cohort sustained the industry between 1984 and 1986 (Le Clus *et al.* 1987) indicating that this situation may not be unusual.

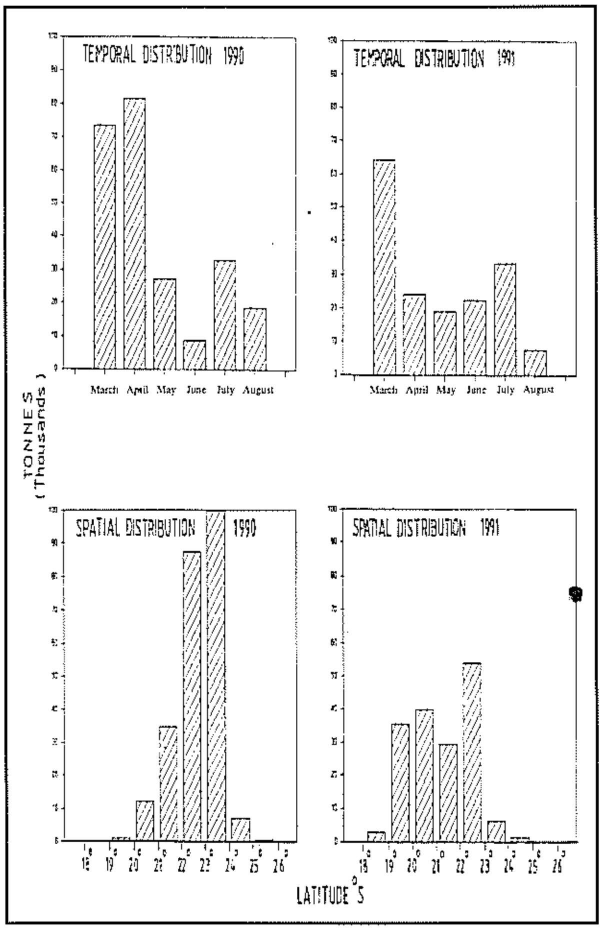

FIGURE 4: Temporal and spatial distribution of the total pelagic catch in 1990 and 1991.

The age distribution of pilchard caught over the last three decades shows considerable change from the predominantly 2-year and older fish population in the sixties (Thomas 1986), to a mixed population in the seventies (Butterworth 1980). During the eighties the population structure was dominated by 0-year old fish. Almost no 3-year or older pilchard were caught during the last decade (Le Clus *et al.* 1987) (Figure 5). There has therefore been a tendency for the development of an increasingly younger pilchard population over the last three decades. This is probably due to too high fishing mortalities during this period. Despite relatively high availability of the pilchard stock, and a reported increase in total biomass (DCB, unpub. data), the pilchard population is dominated by a single year-class and must therefore still be considered vulnerable.

Traditionally, adult anchovy are caught north of Walvis Bay early in the season, with the bulk of the anchovy catch based on the recruit run which normally peaks from July to August south of Walvis Bay. Although this trend was maintained early in the 1990 season, the recruit run failed to materialise and anchovy recruits contributed only 12% to the total number of anchovy landed. The anchovy catch consisted of predominantly 1 and 2-year old fish and for this short-lived species these relatively old fish are assumed to have suffered high natural mortality rates which resulted in a poor adult anchovy harvest early in the 1991 season. A small recruit run developed late in 1991, but still resulted in one of the lowest anchovy catches recorded since the late 1960's.

The success of the Namibian anchovy fishery is mainly determined by the strength of the recruitment run. This juvenile class normally forms the basis of the adult stock for the following year. Following the poor recruit run in 1989, the low adult harvests of 1990 and 1991 were to be expected. Conversely the correlation between the strength of recruitment and the size of the adult breeding stock has been shown to be poor for the Namibian anchovy (Le

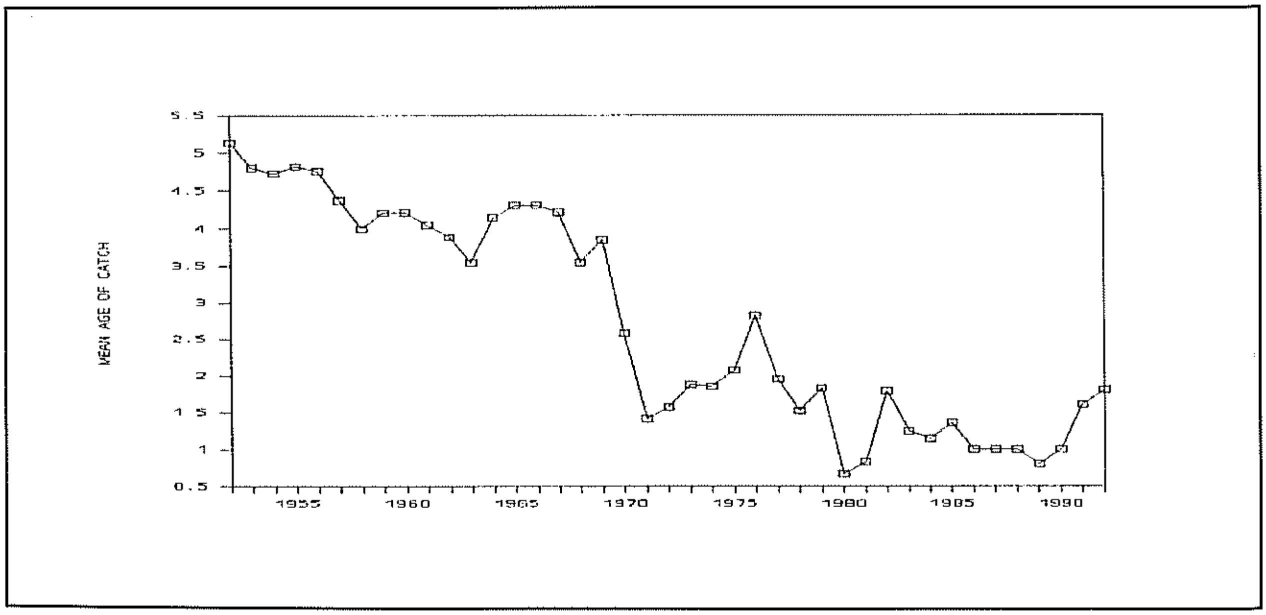

FIGURE 5: The age-distribution of pilchard catches during the last three decades.

Clus 1986), as well as for northern anchovy *(Engraulis mordax)* (Peterman *et al.* 1988). It is therefore not possible to make predictions concerning the harvest of juvenile anchovy during the latter part of the 1992 season. Further recruitment failures will, however, lead to continued reduction of the adult stock and could cause the total collapse of the anchovy fishery off the Namibian coast.

A bimodal length distribution for the Namibian pelagic horse mackerel fishery has often been recorded (Katsuyama 1984). Kenmuir and Kinloch (1985) suggested that these bimodal peaks may represent separate successful year classes. From age-length data (Katsuyama 1984), it can be deduced that the 1990 horse mackerel landings consisted of two year classes, namely 1-year old and 2-year old fish. The 1991 horse mackerel length distribution suggest that these two cohorts have converged to form one strong modal peak, but the 1990 recruit cohort was relatively weak.

Despite its relatively large contribution to the 1990 pelagic catch, catches of round herring must be considered as incidental in the Namibian pelagic fishery, due to round herring's close behavioral association with anchovy and pelagic horse mackerel.

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A survey of the fishes of the Kunene River, Namibia

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ABSTRACT

A survey of fishes of the Kunene River along the Namibia-Angola border in 1990-1991 resulted in a total of 69 freshwater and 19 marine species being recorded. Previously Bell-Cross (1982) reported 70 species, Bethune and Roberts (1991) 69 species and Van der Waal (1991) 63 species. The absence of several species not collected during the survey is attributed to the limited sampling done in floodplain and swampy areas. Several records from previous reports are questioned. The Epupa and Ruacana Falls do not appear to serve as effective isolation barriers to separate species in the Kunene River. Habitat preference is the major factor limiting the dispersal and distribution of fish species.

INTRODUCTION

The Kunene River is the second largest river in Angola and originates at Boas Aguas near Huambo (Nova Lisboa) in the highlands of Angola (Figure 1). It flows southwards for 650 km, plunges over the Ruacana Falls and then heads westwards, forming the boundary between Namibia and Angola. It reaches the Atlantic Ocean 1 050 km from it's headwaters.

Between Ruacana Falls and the Atlantic Ocean the Kunene River is narrow, fast flowing, and characterised by many small rapids. A second waterfall, Epupa Falls (Quedas Mortenegro), is present 130 km downstream of Ruacana Falls. From Epupa Falls the river flows through the Bains Mountains before it reaches the Namib Desert where it flows between sand dunes.

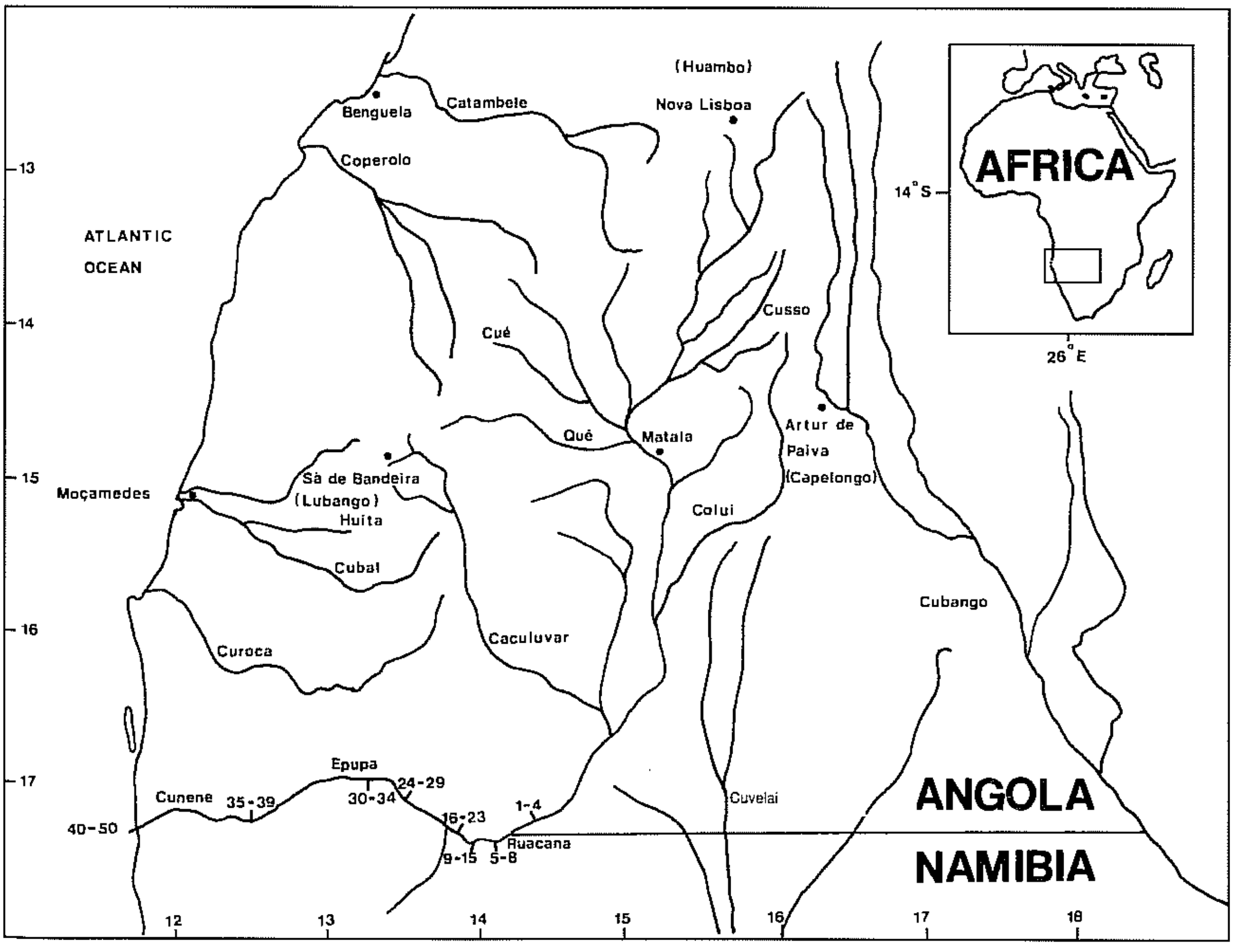

FIGURE 1: The Kunene River in relation to Namibia and collecting sites. Details of the collecting sites and location names are given against collecting site numbers in Table 4.

Climate

The rainfall ranges from over 1500 mm per annum in the highlands of Angola to less than 50 mm per annum in the Namib Desert (Van der Merwe 1983). More than 80% of the rainfall in Kaokoland occurs between October and March with a maximum during January and February. Streamflow is correlated with rainfall which peaks between February and May and is lowest in September and October. December is the hottest month in Kaokoland. Mean maximum temperatures range from 35°C in the east to about 30°C in the west (Van der Merwe 1983).

Hydrology

The Kunene River has a total catchment area of 106500 km^2 (Midgley 1966). The headwaters lie between 1700 and 2000 m above sea level. A small portion of the upper catchment area is hilly with a relatively high runoff. Tributaries include the Caculuvar, Cului and Cassava. The mean annual runoff for the Kunene River calculated at the river mouth is 5800 million m^3 per annum. Towards the central reaches the gradient declines (1:4500) to form widening marshy plains (Midgley 1966).The portion between Calueque and Ruacana (1:215) is characterised by a series of rapids followed by a vertical drop of 120 m at the Ruacana Falls.The channel from Ruacana to the sea is steeply graded (1:447) with distinct falls and rapids (Epupa and Ondorusu).

Temperature

The water temperature varies between 18,5 °C in July and 28,5 °C in February (data provided by SWAWEK). Water temperature tends to increase from east to west. There is a decrease in water temperature with depth near the mouth (Table 1). This, however, is likely to be the influence of the cooler sea water. Temperature of surface water in the lagune is cooler than the water at the bottom. This is probably due to wind induced cooling.

TABLE 1: Water temperature (°C) at various localities on the Kunene River, December 1990.

Depth (m)	Temperature (°C) at Locality No. (see Fig 1)								
	5	10	18	24	30	35	41	45	49
0	20	20	20	20	21	22,5	21,8	20,0	25,5
0,5	20	20	20	20	21	22,5	22,3	20,0	25,4
1,0	20	20	20	20	-	22,5	22,5	20,0	24,8
1,5	20	20	20	20	-	22,5	22,7	-	23,8
2,0	20	20	20	20	-	22,5	23,0	-	-
2,5	20	-	20	-	-	22,5	23,2	-	-
3,0	20	-	20	-	-	22,5	23,3	-	-

Water quality

The pH values of the Kunene are more or less neutral (Table 2). Conductivity is low except for the mouth.

The turbidity in the Kunene River is low except for the areas near the mouth (Table 2).The lagune widens near the mouth with a decrease in depth.Wave, wind and tidal action in these areas are responsible for the increased turbidity. Locality 40 is situated near a rapid that increases the water turbulence and therefore also the turbidity.The lower turbidity at localities 49 and 50 is influenced by sea water that generally has a low turbidity.

TABLE 2: Water analysis at various localities on the Kunene River, December 1990.

Locality	pH	Conductivity mS/m	Total dissolved solids mg/l	Chlorine mg/l	Turbidity NTU
1	6,4	3,8	25	1	6
5	6,4	3,9	26	1	9
10	7,1	4,2	28	1	3
24	7,0	4,1	27	1	3
30	8,2	8,9	59	1	3
35	7,4	6,4	42	1	3
40	7,2	8,3	55	4	27
41	7,7	8,6	57	8	25,0
44	7,1	8,2	54	34	26,0
46	8,0	99,5	657	160	5,9
48	7,4	400,0	2640	1160	23,0
49	7,9	5190,0	34254	19800	12,0
50	7,6	5210,0	34386	20000	6,7

Oxygen

No oxygen stratification was detected in the river (Table 3).

TABLE 3: Oxygen content (mg/l) of the water at various localities on the Kunene River, December 1990.

Depth (m)	Hippo Pool	Opkoron Gombe	Ondozo	Otjim Bundu	Epupa	Otjinungwa
0	8,9	3,1	3,7	4,0	7,4	5,4
1	8,9	3,1	3,7	4,8	-	5,8
2	8,9	3,0	3,6	-	-	5,8
3	8,6	-	3,4	-	-	-

Previous collections from the Kunene

The earliest documented collection of fish species from Angola comes from Steindachner (1866) and Boulenger (1898, 1910-1916). Further expeditions were made by Nichols and Boulton (1927), the Vernay-Lang Kalahari expedition (Fowler 1930), Dr. Jordan (Trewavas 1936), Pellegrin (1936), Ladiges and Voelker (1961), Ladiges (1964) and Poll (1967). One of the earliest recorded species from the Kunene system is *Pelmatochromis welwitschi* (Boulenger 1898), the synonym for *Chetia welwitschi* (Boulenger 1898), that was collected by Dr. Welwitsch at Fluila (Boulenger 1898). Fluila is probably the misspelt form of Huila that is close to the Huila River, a tributary of the Kunene (Bell-Cross 1975). A survey done by Penrith (1978) included several marine species that were sampled in the mouth and lagune of the Kunene River. In 1982 an additional 13 species from southwestern Angola, mainly from the Kunene basin, were added by Penrith. Bell-Cross (1982) listed 70 species from the Kunene in his biogeography of the Zambezi River fish fauna. The most recent lists are by Van der Waal (1991) totalling 63 species and Bethune and Roberts (1991) with 69 species from the Kunene River.

TABLE 4: Description of the fish collecting sites on the Kunene River

Figure 1 Ref. no.	Sites	Substratum	Vegetation	Flow rate	Mean depth	Sampling methods
1	Calueque floodplain	Sandy	Marginal	Slow	2m	Gill-net series
2		Sandy	Marginal	Slow	3m	Gill-net series
3		Clay	Aquatic	Slow	1m	Seine net
4		Rocky	None	Slow	0.5m	Rotenone
5	Hippopool	Rocky	None	Slow	4m	Gill-net series Rotenone
6		Rocky & Sandy	*Phragmites* sp.	Strong	2m	Gill-net series
7		Sandy	*Phragmites* sp.	Slow	1m	Seine & mosquito net
8		Sandy	Marginal	Slow	2m	Gill-net series
9	Opkorongombe	Sandy	Marginal	Strong	2m	Gill-net series
10		Sandy	Marginal	Strong	2m	Gill-net series
11		Clay	None	Slow	2m	Mosquito net
12		Clay	*Phragmites* sp.	None	1m	Seine net
13		Clay	Aquatic	Slow	0,4m	Rotenone
14		Clay	None	Slow	1m	Mosquito net
15		Clay & Rocky	None	None	1m	Seine net
16	Opatyamaungu	Clay & Sandy	None	Slow	1m	Seine net
17	Kunene Stein	Clay	None	None	0,5m	Mosquito net
18	Ondozo rapid	Rocky	Aquatic	Medium	0,4m	Rotenone
19	Ondozo	Clay	None	Slow	2m	Casting and Mosquito net
20		Clay & Sandy	None	Strong	2m	Gill-net series
21		Clay & Sandy	Marginal	Strong	2m	Gill-net series
22	Ondorusu falls (rapid)	Rocky	None	Strong	0,5m	Rotenone
23		Clay & Rocky	None	None	1m	Rotenone
24	Otjimbundu	Rocky & Sandy	None	Medium	3m	Gill-net series
25		Sandy	None	Slow	1,5m	Casting and Mosquito net
26		Sandy	None	None	0,3m	Mosquito net
27		Sandy	None	Strong	1m	Mosquito net
28		Sandy	*Phragmites* sp.	Slow	0,2m	Mosquito net
29		Sandy	None	Medium	1,5m	Mosquito net
30	Epupa	Rocky & Sandy	None	Slow	2m	Rotenone
31		Rocky & Sandy	None	None	0,5m	Rotenone
32		Sandy	None	Strong	2m	Casting and Mosquito net
33		Sandy	None	Strong	1m	Rotenone
34		Sandy	None	Strong	1m	Mosquito net
35	Otjinungwa	Sandy	None	Medium	2m	Seine, mosquito, casting nets, traps & angling
36		Sandy	Marginal	Strong	2m	Gill-net series
37		Sandy	Marginal	Strong	2m	Gill-net series
38		Sandy	Marginal	Strong	2m	Gill-net series
39	Rapid	Rocky	None	Strong	0,5m	Rotenone
40	Seven km from Mouth	Clay & Sandy	*Phragmites* sp.	Slow	3,5m	Gill-net series
41	Six km from mouth	Clay	*Phragmites* sp.	Medium	1,5m	Gill-net series
42	One km from mouth	Sandy	None	None	1m	Mosquito net
43	Lagune	Sandy	Marginal	Strong	3m	Gill-net series
44	Lagune	Sandy	None	Strong	0,5m	Water sample
45	Isolated pool	Sandy	Aquatic	None	1m	Rotenone
46	Isolated pool	Sandy	None	None	1,5m	Rotenone
47	Rapid	Rocky	None	Medium	0,4m	Rotenone
48	Lagune	Sandy	None	Strong	1,5m	Gill-net series
49	Mouth	Sandy	None	Strong	4m	Angling,Seine
50	Sea	Sandy	None	Strong	2m	Water sample

Grid references of the collecting sites:

Calueque Floodplain:	17° 16'S14° 30'E
Hippopool:	17° 23'S14° 12'E
Opkorongombeo:	17° 25'S14° 04'E
Opatyamaungu:	17° 25'S14° 02'E
Kunene Stein:	17° 21'S13° 59'E
Ondozo:	17° 24'S13° 57'E
Ondorusu Falls:	17° 24'S13° 56'E
Otjimbundu:	17° 17'S13° 45'E
Epupa:	17° 00'S13° 15'E
Otjinungwa:	17° 15'S12° 15'E
Mouth:	17° 15'S11° 45'E

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5	Hippopool	Rocky	None	Slow	4m	Gill-net series Rotenone
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7		Sandy	*Phragmites* sp.	Slow	1m	Seine & mosquito net
8		Sandy	Marginal	Slow	2m	Gill-net series
9	Opkorongombe	Sandy	Marginal	Strong	2m	Gill-net series
10		Sandy	Marginal	Strong	2m	Gill-net series
11		Clay	None	Slow	2m	Mosquito net
12		Clay	*Phragmites* sp.	None	1m	Seine net
13		Clay	Aquatic	Slow	0,4m	Rotenone
14		Clay	None	Slow	1m	Mosquito net
15		Clay & Rocky	None	None	1m	Seine net
16	Opatyamaungu	Clay & Sandy	None	Slow	1m	Seine net
17	Kunene Stein	Clay	None	None	0,5m	Mosquito net
18	Ondozo rapid	Rocky	Aquatic	Medium	0,4m	Rotenone
19	Ondozo	Clay	None	Slow	2m	Casting and Mosquito net
20		Clay & Sandy	None	Strong	2m	Gill-net series
21		Clay & Sandy	Marginal	Strong	2m	Gill-net series
22	Ondorusu falls (rapid)	Rocky	None	Strong	0,5m	Rotenone
23		Clay & Rocky	None	None	1m	Rotenone
24	Otjimbundu	Rocky & Sandy	None	Medium	3m	Gill-net series
25		Sandy	None	Slow	1,5m	Casting and Mosquito net
26		Sandy	None	None	0,3m	Mosquito net
27		Sandy	None	Strong	1m	Mosquito net
28		Sandy	*Phragmites* sp.	Slow	0,2m	Mosquito net
29		Sandy	None	Medium	1,5m	Mosquito net
30	Epupa	Rocky & Sandy	None	Slow	2m	Rotenone
31		Rocky & Sandy	None	None	0,5m	Rotenone
32		Sandy	None	Strong	2m	Casting and Mosquito net
33		Sandy	None	Strong	1m	Rotenone
34		Sandy	None	Strong	1m	Mosquito net
35	Otjinungwa	Sandy	None	Medium	2m	Seine, mosquito, casting nets, traps & angling
36		Sandy	Marginal	Strong	2m	Gill-net series
37		Sandy	Marginal	Strong	2m	Gill-net series
38		Sandy	Marginal	Strong	2m	Gill-net series
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44	Lagune	Sandy	None	Strong	0,5m	Water sample
45	Isolated pool	Sandy	Aquatic	None	1m	Rotenone
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47	Rapid	Rocky	None	Medium	0,4m	Rotenone
48	Lagune	Sandy	None	Strong	1,5m	Gill-net series
49	Mouth	Sandy	None	Strong	4m	Angling,Seine
50	Sea	Sandy	None	Strong	2m	Water sample

Grid references of the collecting sites:

		Ondozo:	17° 24'S13° 57'E
Calueque Floodplain:	17° 16'S14° 30'E	Ondorusu Falls:	17° 24'S13° 56'E
Hippopool:	17° 23'S14° 12'E	Otjimbundu:	17° 17'S13° 45'E
Opkorongombeo:	17° 25'S14° 04'E	Epupa:	17° 00'S13° 15'E
Opatyamaungu:	17° 25'S14° 02'E	Otjinungwa:	17° 15'S12° 15'E
Kunene Stein:	17° 21'S13° 59'E	Mouth:	17° 15'S11° 45'E

METHODS

Equipment and description of collecting sites

Collections were made during August 1990, December 1990 and December 1991; two summer and one winter surveys. Calueque is the only locality with mainly floodplain and swamp habitats as the river below the Ruacana Falls consists of rapids and fast flowing water. There are few isolated pools and side streams in the middle and lower reaches of the river. The survey at Calueque was limited in time which probably effected the species composition of fish captured. Collecting sites were selected to include all habitat types of the river. Sampling in the lower reaches was hampered by rugged terrain.

The following equipment were used to sample fishes during the surveys:

1. A series of gill nets with the following stretch mesh sizes:35, 45, 57, 73, 93, 118 and 150 mm (30 m each) were used in the main stream and at Calueque. Gill nets were also used in the lagune at the river mouth.
2. A 30 m x 1 m seine net with a 12 mm stretch mesh size was used in shallow water. Side streams and floodplains at Calueque were also sampled with this gear.
3. A 10 m x 1 m mosquito mesh seine net was used for streamlets.
4. Rotenone was used in isolated pools, rapids and vegetated areas.
5. Angling was used in the river mouth.
6. Traps, 45 x 41 x 18 cm, covered by a 12 mm mesh size net and with four inlets were used in deep water habitats and vegetated areas.
7. A 2 m diameter casting net with a 35 mm stretch mesh size was used in rapids and fast flowing currents.

Temperature

Temperature was measured at 10h00 at each collecting site.

Water quality

Water was sampled and kept as cool as possible. The analysis was done by the Department of Water Affairs, Windhoek.

Oxygen

An YSI54A oxygen meter was used for the determination of the Oxygen content.

The descriptions of the collecting sites are listed in Table 4.

RESULTS AND DISCUSSION

Forty-three freshwater species were collected from the Kunene River during these surveys. Most of the species were from the family Cyprinidae followed by the Cichlidae (Table 5). The absence of the families Bagridae, Distichodontidae and Kneriidae during these surveys can be attributed to specialised habitats as well as to their being uncommon in the Kunene River. Although no species separation is apparent in the Kunene River, several species do indicate restricted distribution such as *Barbus breviceps* (Trewavas 1936), *Kneria maydelli* (Ladiges & Voelker 1961), *K. polli* (Trewavas 1936), *Labeo ruddi* (Boulenger 1907) and *Synodontis thamalakanensis* (Fowler 1935) (Table 5). These species were not found above the Ruacana Falls.The majority of the species are present above the Ruacana Falls with a decline in species numbers towards the river mouth. Greater habitat diversity, in the upper reaches is likely to be the reason for this. It is unlikely that the major waterfalls prevent the downriver movement of fish. Another factor is that fewer surveys have been conducted in the lower reaches of the river compared to the upper reaches.

Barbus breviceps and *K. polli* are new records from the Kunene River. Although not in the main stream, they were collected in a southerly tributary of the Kunene River. Common species in the Kunene River are *Brycinus lateralis* (Boulenger 1900), *Micralestes acutidens* (Peters 1852), *Barbus fasciolatus* (Günther 1868), *B. mattozi* (Guimaraes 1884), *B. radiatus* (Peters 1853), *B. poechii/trimaculatus*, *B. unitaeniatus* (Günther 1866), *Mesobola brevianalis* (Boulenger 1908), *Schilbe intermedius* (Linnaeus 1762), *Oreochromis macrochir* (Boulenger 1912), *Pseudocrenilabrus philander* (Weber 1897) and *Thoracochromis buysi* (Penrith 1970). Dominant species during night sampling were *Aplocheilichthys johnstonii* (Günther 1893), *B. fasciolatus*, *B. lateralis* and *M. acutidens*.

TABLE 5: Fish species from the Kunene River and their distribution in relation to the Epupa and Ruacana waterfalls.

X - denotes species present in the Kunene River.
? - denotes dubious or unconfirmed records.
* - species not recorded during present surveys, but additionally recorded by previous collectors.

Species	Below Epupa	Epupa-Ruacana	Above Ruacana
MORMYRIDAE			
Hippopotamyrus ansorgii		X	X
* *H. discorhynchus*			X
Marcusenius macrolepidotus	X	X	X
Mormyrus lacerda	X	X	X
Petrocephalus catostoma	X	X	X
Pollimyrus castelnaui	X	X	X
KNERIIDAE			
* *Kneria maydelli*		X	
* *K. angolensis*			X
* *K. polli*	X		
CHARACIDAE			
Brycinus lateralis	X	X	X
Micralestes acutidens	X	X	X
* *Rhabdalestes maunensis*			X
HEPSETIDAE			
Hepsetus odoe	X	X	X

Species	Below Epupa	Epupa-Ruacana	Above Ruacana
DISTICHODONTIDAE			
* *Hemigrammocharax machadoi*		X	X
* *H. multifasciatus*			X
CYPRINIDAE			
* *Barbus afrovernayi*	X		X
* *B. barotseensis*		X	X
B. barnardi		X	X
* *B. bifrenatus*		X	X
* *B. breviceps*	X		
* *B. codringtonii*	?	?	?
B. eutaenia	X	X	X
B. fasciolatus	X	X	X
* *B. lineomaculatus*			X
B. mattozi	X	X	X
* *B. multilineatus*			X
B. paludinosus	X	X	X
B. radiatus		X	X
B. kerstenii	X		X
B. thamalakanensis			X
B.poechii/trimaculatus	X	X	X
B. unitaeniatus	X	X	X
* *B. dorsolineatus*			X
* *B. puellus*	?	?	?
Mesobola brevianalis	X	X	X
Labeo ansorgii	X	X	X
L. ruddi	X	X	
AMPHILIIDAE			
* *Leptoglanis rotundiceps*		X	X
SCHILBEIDAE			
Schilbe intermedius	X	X	X
CLARIIDAE			
* *Clarias theodorae*			X
C. ngamensis		X	X
C. gariepinus	X	X	X
* *C. liocephalus*	?	?	?
C. stappersii		X	X
MOCHOKIDAE			
* *Chiloglanis neumanni*			X
Synodontis leopardinus	X	X	X
S. nigromaculatus	X	X	X
S. vanderwaali	X	X	X
* *S. thamalakanensis*			X
S. macrostigma			X
S. woosnami			X
* *S. macrostoma*			X
CYPRINODONTIDAE			
Aplocheilichthys macrurus	X	X	X
A. johnstonii	X	X	X
* *A. katangae*	X		X
CICHLIDAE			
* *Chetia welwitschi*		X	X
* *Orthochromis machadoi*	X	X	X
Oreochromis macrochir	X	X	X
O. andersonii	X	X	X
Pseudocrenilabrus philander	X	X	X
* *Pharyngochromis acuticeps*	?	?	X
Sargochromis coulteri	X	X	X
S. codringtonii/giardi		X	X
* *S. gracilis*	?	?	?
* *S.greenwoodi*		X	X
Serranochromis angusticeps		X	X
* *S. altus*	?	?	?
S. macrocephalus	X	X	X
* *S. robustus jallae*		X	X
* *S. thumbergi*		X	X
Tilapia rendalli	X	X	X
T. sparrmanii	X	X	X
Thoracochromis buysi	X	X	X
T. albolabris	X	X	X
GOBIIDAE			
Chonophorus guineensis	X		
Nematogobius ansorgei	X		
* *Ctenogobius lepturus*	X		
ELEOTRIDAE			
Eleotris vittata	X		
Batanga lebretonis	X		
EXOCOETIDAE			
Cheilopogon milleri	X		
CARANGIDAE			
Lichia amia	X		
POMADASYIDAE			
Pomadasys jubilini	X		
P. rogeri	X		
SCIAENIDAE			
Argyrosomus hololepidotus	X		
SPARIDAE			
* *Lithognathus aureti*	X		
MUGILIDAE			
* *Liza aurata*	X		
L. falcipinnis	X		
* *L. dumerilii*	X		
Mugil cephalus	X		
POLYNEMIDAE			
Galeiodes decadactylus	X		
ARIIDAE			
Arius latiscutatus	X		
BOTHIDAE			
* *Citharichthys stampflii*	X		
GOBIESOCIDAE			
* *Diplecogaster megalops*	X		

DISTRIBUTION (TABLE 5) AND HABITAT PREFERENCES (TABLE 6) OF SPECIES COLLECTED:

Mormyridae

Hippoptamyrus ansorgii (Boulenger 1905) was not found below the Epupa Falls. It prefers shallow water with a sandy substrate, but was also collected in deep water with a rocky substrate. Bell-Cross and Minshull (1988) reported it from rocky-bottomed habitats with fast flowing water.

Marcusenius macrolepidotus (Peters 1852) has a wide habitat preference and is distributed throughout the system. It was found to be more active during the night. Gaigher (1969) collected it in pools and slow flowing rapids in rivers from the Transvaal, South Africa. It is found in marsh and reed beds in the Okavango River (Bethune 1991).

Mormyrus lacerda (Castelnau 1861) is distributed throughout the system. It was recorded in floodplain as well as deep water habitats and appears to be more active during the night. Van der Waal and Skelton (1984) indicated their habitat preference to be deep standing water while Bell-Cross and Minshull (1988) reported it from deep pools with associated aquatic vegetation.

TABLE 6: Habitat preferences of species from the Kunene River.

Species	Habitat preferences
MORMYRIDAE	
Hippopotamyrus ansorgii	Shallow water, sandy substrate
H. discorhynchus	Larger waterways
Marcusenius macrolepidotus	Wide habitat preference
Mormyrus lacerda	Floodplain, deep water
Petrocephalus catostoma	Floodplain, rocky substrate
Pollimyrus castelnaui	Vegetated areas
KNERIIDAE	
Kneria maydelli	Rocky substrate
K. polli	Rocky substrate
CHARACIDAE	
Brycinus lateralis	Floodplain, main stream
Micralestes acutidens	Open, moving water
Rhabdalestes maunensis	Swampy areas
HEPSETIDAE	
Hepsetus odoe	Floodplain, deep water
DISTICHODONTIDAE	
Hemigrammocharax machadoi	Shallow water, aquatic vegetation
H. mulifasciatus	Shallow water, aquatic vegetation
CYPRINIDAE	
Barbus afrovernayi	Vegetated areas
B. barotseensis	Vegetated areas
B. barnardi	Floodplain, swampy areas
B. bifrenatus	Running water, vegetated areas
B. breviceps	Rocky substrate
B. eutaenia	Rapids, rocky areas
B. fasciolatus	Shallow, slow-moving water
B. lineomaculatus	Wide habitat
B. mattozi	Preference for quiet water
B. multilineatus	Quiet waters, aquatic vegetation
B. paludinosus	Wide habitat
B. radiatus	Swampy areas, Shallow water
B. kerstenii	Floodplain
B. thamalakanensis	Floodplain
B.poechii/trimaculatus	Floodplain, isolated pools
B. unitaeniatus	Floodplain, isolated pools
Mesobola brevianalis	Shallow, quiet water, vegetation
Labeo ansorgii	Shallow, swampy, rocky areas
L. ruddi	Quiet water
AMPHILIIDAE	
Leptoglanis rotundiceps	Shallow water
SCHILBEIDAE	
Schilbe intermedius	Wide habitat
CLARIIDAE	
C. ngamensis	Floodplain
C. gariepinus	Wide habitat
C. stappersii	Shallow water, vegetated areas
MOCHOKIDAE	
Chiloglanis neumanni	Rapids
Synodontis leopardinus	Floodplain, mainstream
S. nigromaculatus	Shallow water
S. vanderwaali	Vegetated areas
S. macrostigma	Floodplain, deep water
S. woosnami	Shallow water, vegetated areas
S. macrostoma	Rocky environments
POECILIIDAE	
Aplocheilichthys macrurus	Shallow water, side stream
A. johnstonii	Wide habitat
CICHLIDAE	
Orthochromis machadoi	Rocky environments
Oreochromis macrochir	Shallow, slow-moving water
O. andersonii	Isolated pools, rapids
Pseudocrenilabrus philander	Wide habitat
Sargochromis coulteri	Shallow water, sandy substrate
Serranochromis angusticeps	Floodplain
S. altus	Wide habitat
S. macrocephalus	Wide habitat
S. robustus jallae	Open water
S. thumbergi	Flowing water
Tilapia rendalli	Main, side streams, rapids
T. sparrmanii	Floodplain, vegetated pools
Thoracochromis buysi	Wide habitat
T. albolabris	Rocky substrate, swampy areas

Petrocephalus catostoma (Günther 1866) is present throughout the Kunene System. This species was collected from floodplain areas covered with aquatic vegetation as well as from areas with a rocky substrate. It is less common in the main stream. It has a wide distribution in the Incomati River (Gaigher1969) and prefers pools in the Limpopo (Gaigher 1973).

Pollimyrus castelnaui (Boulenger 1911) is present throughout the system. It was collected in littoral reaches of the main stream near vegetated banks. Its preferred habitat is vegetated backwaters, but the species may enter fast flowing habitats (Bell-Cross & Minshull 1988). Van der Waal and Skelton (1984) reported it to be abundant in shallow floodplain areas in the Caprivi. *Hippopotamyrus pappenheimi* (Boulenger 1910) as reported from the Kunene River by Poll (1967) is probably a synonym of this species.

Characidae

Brycinus lateralis (Boulenger 1900) is abundant and present throughout the Kunene River. It prefers floodplain and swampy areas, but has also been collected in deep water habitats. This species is listed as rare in the Red Data Book of southern Africa (Skelton 1987), but does not appear to be threatened in Namibia. The preferred habitat in the Caprivi is deep water as well as shallow floodplain areas (Van der Waal & Skelton 1984).

Micralestes acutidens (Peters 1852) was collected from Calueque to the mouth. This species is common in the Kunene River and active during the night. It prefers open, moving waters near the banks, although it is present in a wide range of habitats. Bethune (1991) also reported it to prefer open, flowing water.

Hepsetidae

Hepsetus odoe (Bloch 1794) is present in floodplains, deep water areas as well as rapids throughout the Kunene River. The absence of *Hydrocynus vittatus* (Castelnau

1861) in the Kunene River may have increased the habitat and distribution range of *H. odoe* in this system (c.f. Bell-Cross & Minshull 1988).

Cyprinidae

Barbus barnardi (Jubb 1965) was not found below the Epupa Falls. Its habitat preference is swampy and floodplain areas. It is not common in the Kunene River. It was collected from the Olushandja Dam in the Cuvelai System which consists of floodplain and swampy habitats.

Barbus eutaenia (Boulenger 1904) is present throughout the system, but appears to be uncommon. It was collected in rapids whereas Bell-Cross and Minshull (1988) indicate their preference to be fast flowing water with vegetation. Gaigher (1973) reports that oxygen may limit their distribution.

Barbus tangandensis (Jubb 1954) has been assigned to *B. kerstenii* (Skelton pers. comm.) and is present at the upper and lower reaches of the system in floodplain areas.

Barbus thamalakanensis (Fowler 1935) was collected above the Ruacana Falls from floodplain areas. Bell-Cross and Minshull (1988) reported it to be present in vegetated areas.

Barbus mattozi (Guimaraes 1884) is distributed throughout the river with a preference for quiet water. Gaigher (1973) reported the preference of this species to be deep pools. Bell-Cross and Minshull (1988) also indicated a preference for quiet waters.

Barbus radiatus (Peters 1853) has not been collected below the Epupa Falls. The preferred habitats are swampy areas with aquatic vegetation and shallow water with a clay substrate. Bell-Cross and Minshull (1988) indicated that it has a wide habitat preference which is supported by its wide distribution in the Limpopo System (Gaigher 1969).

The status of *B. trimaculatus* (Peters 1852) and *B. poechii* (Steindachner 1911) requires further investigation (Greenwood 1962). *Barbus poechii* as identified by one dash on the peduncle is present in the Okavango and Upper Zambezi Rivers. *Barbus trimaculatus* with three lateral spots has a much wider distribution that includes the Middle and Lower Zambezi, Zaire, Limpopo and Orange River Systems. Specimens from the Cuvelai System resemble *B. poechii* whereas specimens from the Kunene River have three distinct lateral spots. Van der Waal (1991) collected intermediate forms from the Cuvelai System. The specimens collected from the Kunene River were from floodplain areas, shallow waters and isolated pools throughout the system.

Barbus unitaeniatus (Günther 1866) is common throughout the system. This species was collected in floodplains and shallow water. Our results were similar to those of Gaigher (1973) who reported it to have a wide distribution in the Limpopo system, and Bell-Cross and Minshull (1988) who also indicated it to have a wide habitat preference.

Barbus fasciolatus (Günther 1868) is distributed throughout the system but is more common in the lower reaches. This species was collected in shallow, slow-moving water. It was also collected during the night in a variety of habitats. Van der Waal and Skelton (1984) recorded it from floodplain areas.

Barbus paludinosus (Peters 1852) is present along the entire river.It was sampled from rocky and sandy substrates in sidestreams, floodplains as well as the main stream. It was found to be abundant in the Vernay collection from the Kunene River (Fowler 1930). Although common, it was found not to be abundant during our surveys.

Labeo ansorgii (Boulenger 1907) is evenly distributed from Calueque through to the mouth. It has a wide habitat tolerance from shallow swampy areas covered with aquatic vegetation with a sandy substrate to deep water areas with a rocky substrate and rapids. It was more active during the day than at night. *Labeo cylindricus* (Peters 1852) and *L. molybdinus* (du Plessis 1963) have been listed by previous authors from this system, but specimens identified as these species are now assigned to *L. ansorgii* (Skelton pers. comm.). This is the dominant species of the two *Labeos* found in the Kunene River.

Labeo ruddi (Boulenger 1907) has not yet been collected above the Ruacana Falls. It has a more limited distribution than the previous species and prefers quiet water. It prefers pools in the Limpopo River (Gaigher 1973).

Mesobola brevianalis (Boulenger 1908) is distributed throughout the river. Shallow quiet waterwith aquatic vegetation is preferred. It is abundant in the Limpopo River with a wide habitat preference (Gaigher 1973).

Schilbeidae

Schilbe intermedius (Linnaeus 1762) was collected throughout the Kunene River and has a wide habitat preference. Reizer (1974) reported that it is restricted by elevated salinity.

Clariidae

Clarias gariepinus (Burchell 1822) is distributed throughout the system with a wide habitat preference.This species is known to have a wide distribution (Gaigher 1973; Van der Waal & Skelton 1984; Bell-Cross & Minshull 1988).

Clarias ngamensis (Castelnau 1861) was not collected below the Epupa Falls. It is primarily a floodplain species.

Clarias stappersii (Boulenger 1906) has not yet been collected below the Epupa Falls. It appears to prefer shallow water with vegetation. *Clarias stappersii* had previously been confused with *C. submarginatus* (Peters

1882) which only occurs in Cameroon (Skelton & Teugels 1991).

Mochokidae

Our collections confirm the presence of *Synodontis leopardinus* (Pellegrin 1914) in the Kunene River although it was not reported from this system by Skelton and White (1991). Re-examination of the specimens is therefore needed before these records can be confirmed. It preferred the floodplains, but was also collected in the main stream and rocky areas.

Only one specimen of *S. nigromaculatus* (Boulenger 1905) was collected in shallow water with a sandy substrate. Pellegrin (1936) and Ladiges (1964) recorded *S. melanostictus* (Boulenger 1905) from the Kunene River which is regarded as a junior synonym. Their specimens need to be critically re-examined (Skelton pers. comm.). Poll (1967) and Bell-Cross and Minshull (1988) also reported *S. nigromaculatus* from the Kunene River.

Synodontis woosnami (Boulenger 1911) appears to prefer shallow water with vegetation and is present above the Ruacana Falls. Van der Waal and Skelton (1984) and Bell-Cross and Minshull (1988) reported it from floodplain areas.

Synodontis vanderwaali (Skelton and White 1990) is distributed throughout the system. It prefers water with vegetation, but has also been collected in the main stream.

Synodontis macrostigma (Boulenger 1911) is present above the Ruacana Falls and in floodplain areas as well as deep water habitats. Van der Waal and Skelton (1984) recorded it from deep water and sandy substrate areas in the Caprivi.

Cyprinodontidae

Aplocheilichthys macrurus (Castelnau 1861) is distributed throughout the system and was collected from shallow water with a rocky substrate and side streams with vegetation. Further investigation is required to confirm the identity of this species in the Kunene River (Skelton pers. comm.).

Aplocheilichthys johnstonii (Günther 1893) is distributed throughout the system. It was collected from side streams with a rocky substrate and in shallow water in the main stream with a rocky substrate. In the Limpopo River System it appears to prefer clear pools and slow flowing sections with vegetation (Gaigher 1973).

Cichlidae

Oreochromis macrochir (Boulenger 1912) is evenly distributed throughout the system. It prefers slow, shallow water, but was also collected in rapids. Van der Waal and Skelton (1984) however listed it from deep water and swamp habitats in the Caprivi.

Oreochromis andersonii (Castelnau 1861) is not common in the Kunene River but was collected throughout the system. It was mainly collected in isolated pools and rapids.

Pseudocrenilabrus philander (Weber 1897) is widely distributed in various habitats which include rapids and vegetated pools. Bruton and Kok (1980) reported it to be abundant in vegetated pans in Maputaland.

Sargochromis coulteri (Bell-Cross 1975) is present throughout the system. It was sampled in slow, shallow water over sandy substrate. Bell-Cross (1975) recorded it from fast flowing water over alternatively stone and soil substrata.

The status of the *S. codringtonii/giardi* complex needs further investigation. Greenwood (1984) considers that at present it is not possible to refer Kunene specimens with certainty to either *S. codringtoni* (Boulenger 1908) or *S. giardi* (Pellegrin 1904).

Serranochromis angusticeps (Boulenger 1907) has not yet been collected below the Epupa Falls. The preferred habitats are shallow water and floodplains. Winemiller and Kelso-Winemiller (1991) indicate the preferred habitat to be vegetated areas and shallow backwaters as well as floodplains.

Serranochromis macrocephalus (Boulenger 1899) is present throughout the system with a wide habitat range, including floodplain areas, deep water and rapids. Trewavas (1964) reported it to be present in open water.

Tilapia sparrmanii (Smith 1840) is distributed throughout the system and was collected mainly from floodplain areas with a preference for well-vegetated pools. Gaigher (1969) reported it to be present in the Incomati River System in vegetated pools.

Tilapia rendalli (Boulenger 1896) is widely distributed throughout the system. It was located in rapids, the main stream as well as side streams. Philippart and Ruwet (1982) considered temperature and salinity to be the major factors limiting the distribution of this species. Gaigher (1969) also reported that temperature and the absence of aquatic vegetation limits their distribution.

Thoracochromis buysi (Penrith 1970) is distributed throughout the system. It was found to be the dominant cichlid, especially in the lower reaches. This species was collected from a wide variety of habitats.

Thoracochromis albolabris (Trewavas and Thys van den Audenaerde) is distributed throughout the system. It was collected in swampy areas, the main stream as well as shallow water with a rocky substrate.

Nineteen marine species are listed from the Kunene River mouth of which 13 species were collected during these surveys. *Arius latiscutatus*, *Cheilopogon milleri* (Gibbs and Staiger 1970), *Galeiodes decadactylus* (Bloch 1795), *Pomadasys jubilini* (Cuvier 1830) and *P. rogeri* (Cuvier 1830) are recorded for the first time from the Kunene River mouth. *Cheilopogon milleri* is an oceanic species and is not considered to be a permanent inhabitant of the river mouth. *Batanga lebretonis* (Steindachner 1870), *Eleotris vittata* (Dumeril 1860), *Chonophorus guineensis* (Peters 1876), *Nematogobius ansorgei* (Boulenger 1910), *Mugil cephalus* (Linnaeus 1758) and *Liza falcipinnis* (Valenciennes) were the only marine species present in fresh water. Except for *L. falcipinnis* the former species were sampled in isolated pools with fresh water as far as eight kilometers upstream of the mouth. They were associated with fresh water species such as *Barbus paludinosus*, *B. trimaculatus/poechii*, *Tilapia rendalli* and *Oreochromis andersonii*.

SPECIES NOT RECORDED DURING PRESENT SURVEY:

Due to limited time spent at Calueque, several floodplain-loving species were not collected including *Aplocheilichthys katangae* (Boulenger 1912), *Barbus barotseensis* (Pellegrin 1920), *B. bifrenatus* (Fowler 1935), *B. multilineatus* (Worthington 1933), *Clarias theodorae* (Weber 1897), *Hemigrammocharax machadoi* (Poll 1967), *H. multifasciatus* (Boulenger 1923) and *Rhabdalestes maunensis* (Fowler 1935). Cichlids such as *Sargochromis codringtonii*, *S. greenwoodi* and *S. robustus jallae* which prefer standing deep water habitats were also not collected. These habitats are uncommon in the lower reaches of the system.

Mormyridae

Hippopotamyrus discorhynchus (Peters 1852) is present above the Ruacana Falls (Namibian State Museum collection). This species needs further confirmation. It's habitat preference appears to be the larger waterways.

Kneriidae

Specimens recently collected by Griffin and Eyre at Okavanje (Freshwater Fish Institute NHF 425a), in a southern tributary of the Kunene River, had been identified as *Kneria polli*. *Kneria polli* was described by Trewavas (1936) from Mt. Moco, Angola, in the Cuvo River System. Poll (1967) also recorded it from Serra do Chela with neither being part of the Kunene River System. *Kneria maydelli* was described by Ladiges and Voelker (1961) from the type locality Ruacana. Bell-Cross (1982) listed *K. angolensis* (Steindachner 1866) from the Kunene River and it has also been given in the Okavango/Upper Zambezi River System by Ladiges (1964), Bell-Cross (1966) and Poll (1967). An unidentified *Kneria* sp. is listed in the Namibian State Museum collection and was collected from the Ondato River, a southern tributary of the Kunene. Thus three *Kneria* spp. are listed from the Kunene River, but re-examination of the specimens is required to establish their identification.

Characidae

Brycinus humilis (Boulenger 1905) is listed by Ladiges(1964), Poll (1967) and Bell-Cross (1982) but the status of this species is still not certain and it is currently assigned to *B. lateralis* (Skelton pers. comm.).

Bethune and Roberts (1991) listed *Hydrocynus vittatus* from the Kunene River. However this is an error as the species was not taken during the present survey nor is there any other known records of it in the Kunene River.

Micralestes argyrotaenia (Trewavas 1936) is listed by Ladiges(1964), Jubb (1967), Poll (1967) and Bell-Cross (1982), but is currently assigned to *Micralestes acutidens* (Skelton pers. comm.).

Rhabdalestes maunensis has only been collected above the Ruacana Falls (Van der Waal 1991). It has been reported to have a preference for swampy areas. Van der Waal (1991) sampled it in the Olushandja Dam (Cuvelai System) which consists of swamp and floodplain habitats.

Distichodontidae

Hemmigrammocharax machadoi(*Nannocharax monardi*) has not yet been collected below the Epupa Falls. Preferred habitat appears to be shallow water with dense aquatic vegetation (Bell-Cross & Minshull 1988).

The distribution of *Hemmigrammocharax multifasciatus* (*Nannocharax fasciolaris*) appears to be limited to above the Ruacana Falls (Nichols & Boulton 1927). The habitat preference is shallow water with dense aquatic vegetation (Bell-Cross & Minshull 1988).

Cyprinidae

Barbus afrovernayi (Nichols and Boulton 1927) is present below the Epupa and above the Ruacana Falls and prefers vegetated areas of rivers and swamps and requires well oxygenated waters.

The record of *B. barotseensis* is dubious. *Barbus annectens* (Gilchrist and Thompson 1917), which is currently assigned to *B. barotseensis*, is listed by the State Museum of Namibia. Jubb (1967) also pointed out the close similarity between these species. Vegetated areas appear to be the preferred habitat.

Barbus bifrenatus is absent below the Epupa Falls. This species was taken mainly in running water with vegetation. Van der Waal (1991) collected it from running oshanas in the Cuvelai System, but considers it as an unsuccessful invader of the oshanas in Owambo.

Barbus breviceps was sampled at Okavanje in a stream south of the Kunene River by Griffin and Eyre (Freshwater Fish Institute NHF 425b). The stream forms permanent pools and therefore will reach the Kunene River after sufficient rains. The species is only known from the type locality which is 100 km south-east of Quibala, Angola, in the Longa River System (Trewavas 1936). Pellegrin (1936), Ladiges (1964) and Poll (1967) identified *B. burgi* (Boulenger 1911) from the Kunene River. *Pseudobarbus burgi* is confined to the south-western Cape and listed in the Red Data Book-Fishes (Skelton 1987) and has been misidentified from the Kunene River (Skelton pers. comm.). Another closely related species, *B. anoplus* (Weber 1897), was reported from the Gaub River which is a tributary of the Kuiseb River (Dixon & Blom 1974). Re-examination of *B. anoplus* is required to confirm its identity.

Barbus codringtonii (Boulenger 1908) has only been listed from the Kunene River by Ladiges and Voelker (1961), Jubb (1967) and Poll (1967). *Barbus codringtonii* was not found during these surveys. The occurrence of *B. codringtonii* in the Kunene River requires confirmation.

Barbus lineomaculatus (Boulenger 1903) has only been collected above the Ruacana Falls (Poll 1967). It appears to have a wide habitat tolerance. This species was collected in well oxygenated water in the Limpopo River System (Gaigher 1973).

Barbus multilineatus has been collected above the Ruacana Falls (Namibian State Museum collection) and prefers quiet waters with dense aquatic vegetation (Bell-Cross & Minshull 1988).

Barbus dorsolineatus (Trewavas 1936) is listed by Bell-Cross (1966, 1982) from the Kunene River. The type locality is from a tributary of the Catumbela River. Ladiges (1964) and Poll (1967) reported it from the Angolan basin, but not from the Kunene River.

Barbus puellus (Nichols & Boulton 1927) was described from Chitau in Angola which forms part of the Quanza drainage basin (Nichols & Boulton1927). AlthoughBell-Cross (1966, 1982), Jubb (1967) and Poll (1967) listed this species, its presence in the Kunene River is questioned.

Barbus argenteus (Günther 1868) is listed by Farquharson (1962), Ladiges(1964), Jubb & Farquharson (1965),Poll (1967) and Bell-Cross (1982) from the Kunene River. Skelton (pers. comm.) suspects that juvenile *B. mattozi* in the Kunene River have been mistaken as *B. argenteus* by earlier collectors as the latter species was not collected during the present survey. Boulenger (1910-1916) also indicated the closeness of *B. mattozi* and *B. argenteus*.

Coptostomobarbus wittei (David and Poll 1937) was collected by Van der Waal (1991) from the Olushandja Dam in the Cuvelai System which is artificially connected to the Kunene River. Although it has not yet been collected from the Kunene River it is likely to be present. The preferred habitat is floodplains and it is therefore expected to be collected in the upper reaches.

Amphiliidae

Leptoglanis rotundiceps (Hilgendorf 1905) has not yet been collected below the Epupa Falls (Namibian State Museum collection). This species is restricted to shallow water with a sandy substrate (Bell-Cross & Minshull 1988).

Clariidae

Clarias theodorae has only been collected between the Ruacana and Epupa Falls. Skelton and Teugels (1991) reported it to have a wide distribution and it is therefore expected to be present throughout the Kunene River. It is often collected in shallow water with vegetation as well as in rapids (Bell-Cross & Minshull 1988).

Pellegrin (1936) and Ladiges (1964) reported the presence of *C. dumerilii* (Steindachner 1866) in the Kunene River. The distribution of *C. dumerilii* is confined to the Zaire River System (Teugels 1982). Skelton and Teugels (1991) pointed out the similarities with *C. liocephalus* (Boulenger 1898).Whether *C. dumerilii* collected by Pellegrin (1936) and Ladiges (1964) is *C. liocephalus* still needs confirmation. The distribution of the latter species as indicated by Skelton and Teugels (1991), however, does not include the Kunene River.

Mochokidae

Bell-Cross (1966, 1982) and Jubb (1967) listed *Chiloglanis neumanni* (Boulenger 1911) from the Kunene River. *Chiloglanis angolensis* (Poll 1967), which is probably a synonym for *C. neumanni*, was reported from the Angolan coastal basin by Poll (1967). The presence of this species should be further investigated. It appears to prefer rapids and was also collected in isolated pools.

Synodontis macrostoma (Skelton and White 1990) is restricted to rocky environments and is present above the Ruacana Falls and *Synodontis thamalakanensis* (Fowler 1935) is present between the Ruacana and Epupa Falls.

Cyprinodontidae

Aplocheilichthys katangae has been collected below the Epupa Falls and above the Ruacana Falls (Namibian State Museum collection). The habitat appears to be swamps as well as clear pools and slow flowing water with abundant vegetation (Gaigher 1973).

Cichlidae

Chetia welwitschi (Boulenger 1898) was collected by Welwitch (Boulenger 1898) at Huila and by Pellegrin (1936) from the Cusso River, a tributary of the Kunene River. Ladiges (1964) and Poll (1967) reported it from the Angolan basin, but not from the Kunene. It appears to prefer swampy areas.

Orthochromis machadoi (Poll 1967) has been collected throughout the system. It is endemic to the Kunene River System (Greenwood 1984).

Pharyngochromis darlingi (Boulenger 1911) has been re-assigned to *Ph. acuticeps* (Regan 1922) by Greenwood (1992). It was collected by Poll (1967).

Sargochromis greenwoodi (Bell-Cross 1975) was not found below the Epupa Falls. Bell-Cross (1975) reported it to have a preference for slow water covered with aquatic vegetation.

Serranochromis altus (Winemiller and Kelso-Winemiller 1991) was described by Winemiller and Kelso-Winemiller (1991) from the Upper Zambezi River. It has been confused with *S. angusticeps*. *Serranochromis altus* is distinguished from *S. angusticeps* on morphometric characters and colour patterns especially the absence of distinct speckles on the face and chest and eye stripes that are characteristic of *S. angusticeps*. *Serranochromis altus* is likely to be present in the Kunene River, but further investigation is necessary. This species is a main stream dweller.

Serranochromis robustus jallae (Boulenger 1896) has not been recorded below the Epupa Falls (Namibian State Museum and Bell-Cross 1966). Larger specimens are mainly present in open waters with a slow current. Aquatic vegetation is also preferred.

Material submitted by Van der Waal to the J.L.B. Smith Institute of Ichthyology, Grahamstown, (Rusi no. 35354) has tentatively been identified as *Sargochromis gracilis*. However further investigation and specimens are needed to confirm the identification. This species is known only from the Cutato River in Angola which forms part of the Okavango drainage basin (Greenwood 1984).

Serranochromis thumbergi (Castelnau 1861) has not yet been collected below the Epupa Falls (Namibian State Museum collection). This species prefers flowing waters.

Representatives of the families Anguillidae, Anabantidae, Aplocheilidae and Mastacembelidae are all absent from the Kunene River. These are present from the neighbouring Okavango/Upper Zambezi River System. Species from the families Anabantidae and Mastacembelidae have been recorded by Bell-Cross (1982) from the Quanza River which forms part of the same watershed as the Kunene River. These families are encountered mainly from floodplain areas which dominate the upper reaches of the Kunene River. Their absence could therefore be related to the few collections made in these areas in recent years. Neither Pellegrin (1936), Ladiges and Voelker (1961), Ladiges (1964) nor Poll (1967), who performed surveys in the upper reaches, reported these families from the Kunene River. In contrast the Kunene River has a high degree of endemism in the haplochromine species such as *Thoracochromis buysi*, *Th. albolabris*, *Orthochromis machadoi* and *S. coulteri*. A further three species, *Barbus breviceps*, *B. dorsolineatus* and *Labeo ansorgii* from the Kunene River are endemic to Angola.

The influx of sea water into the mouth depends on the flow in the river itself and a true estuary is not present. Penrith (1982) stated that the total dissolved solid concentration rarely exceeded 2000 mg/l but a total dissolved solid concentration of 34254 mg/l was recorded during the 1990 survey (Table 2). The salinity is likely to decrease during late summer with an increase in river flow. This would result in an influx of fresh water species, especially cichlids, as these fish are known to move to and from saline lagunes with fluctuating waterlevels (Day *et al.* 1981).

CONCLUSION

When considering species diversity several anomalies appear. *Hydrocynus vittatus* is absent from the Kunene River. On the other hand *B. mattozi* and *L. ruddi* are present in the Kunene River, skip the Okavango/Upper Zambezi River System and reappear in the Limpopo System. The genus *Chetia* exhibits a similar distribution with *Chetia flaviventris* being present in the Limpopo River System and *C. welwitschi* in the Kunene River. Both species are absent in the Okavango/Upper Zambezi System. In the family Cichlidae *S. carlottae*, *S. longimanus* and *T. ruweti* have been identified from the Okavango/ Upper Zambezi River System with no record from the Kunene River System. Bell-Cross (1982) suggested that these anomalies may be traced to an early diversion of the Kunene River from a western basin of internal drainage from which many tropical southern Africa fishes are associated.

The Epupa and Ruacana Falls form formidable barriers to upstream migration. Despite these barriers no faunal separation appears to be present. The absence of several species from some river sections is probably due to their not being collected rather than them not being present. Habitat preferences and especially the large difference between the nature of the upper reaches and the middle and lower reaches seems to be the major factor limiting the distribution of the species.

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Bias in aerial censuses of Elephants in Etosha National Park, Namibia

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ABSTRACT

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Experimental counts of elephants in Etosha National Park were used to estimate the bias associated with low intensity counting methods developed for this species. Repeated counting of the same area showed that precise population estimates can be obtained from the method used, and that elephants react to survey aircraft by breaking up into smaller groups.Transect width in the range 1-4 km and altitude in the range 90-120 m could not be shown to affect population estimates within the ranges tested and applied in low-intensity elephant censuses. Photographic counts were less accurate than direct counts and could not be used to quantify counting bias.Counting bias proved to be difficult to estimate, but gross inaccuracies could not be detected and population estimates of elephants in Etosha are probably valid.

INTRODUCTION

Elephants are by virtue of their size, aggregation into groups and colour, regarded as the easiest terrestrial African mammal to count from aircraft in savanna regions.Only Eltringham (1972) attempted to determine the confidence that can be placed in aerial censuses of elephants. Caughley (1974), however, shows that results which appear satisfactory could be interpreted differently, and identified counting biases in Eltringham's (1972) data. Elephant censuses thus appear to be as subject to errors resulting from imprecise and from inaccurate counts, as censuses of other large mammals (Norton-Griffiths 1978).

Estimates of elephant population size have been derived for Etosha National Park (= Etosha) from aerial surveys since 1967, but logistical constraints have resulted in the use of widely varying counting techniques and census designs.Low-intensity censuses of elephants in Etosha were done since 1983 in addition to routine multi-species censuses based on narrow aerial transects and larger aircraft.The low-intensity elephant censuses yielded generally lower estimates of population size, which could be interpreted as the result of the less intensive census method used.The elephant population in Etosha occurs at a relatively low density and is unevenly distributed, with both factors typically resulting in a biased aerial census estimate (Norton-Griffiths 1978).

It was therefore necessary to estimate the bias in elephant counts in Etosha, at least for the recent censuses.Verification of the validity of population estimates from less-intensive counting methods was obtained from experimental counts of elephants, and this paper describes the approach followed.

METHODS

Basic elephant counting technique

A twin-seater fixed-wing aircraft (Piper Supercub) was used to obtain estimates of elephant numbers in Etosha in six censuses done from 1983-1985.The park was divided in two broad strata (shrubland and woodland), based on the structure and density of woody vegetation.Predetermined transects plotted on a 1:100 000 topographical map were used, but the starting points for transects were also determined from the time of flight since the end of previous transects.Transect widths used were 2 km and 4 km in woodland and shrubland respectively, double the widths used in previous censuses.Transect widths were demarcated by strut markers and streamers, as described by Pennycuick & Western (1972).Woodland and shrubland were flown over at an altitude of 90 m and 120 m respectively, conforming to previous censuses in Etosha and as used in East Africa (Norton-Griffiths 1978). Altitude was measured at the start of each transect, using a calibrated barometric aircraft altimeter and Pennycuick's (1973) shadowmeter.

Elephants not in line with the predetermined flight path, but within the limits of the transect, were counted by flying towards them and circling overhead for as long as necessary.Transect lines were interrupted when such a group was perpendicular to the transect line, and after the pilot had located a ground feature on which to re-align his flight path.This approach ensured that all groups sighted were counted accurately.Total group sizes, numbers of adult bulls, adult cows, and calves less than approximately two years old were recorded.The position of each group was plotted on a 1:100 000 map. Each family unit was photographed vertically at the designated transect altitude.

Transect design

Censuses in December 1983 and May and December 1984 were undertaken in approximately 100-700km^2 blocks demarcated by distinct ground features. Transects were flown across the long axis of a block, parallel to a conveniently straight side, usually more or less North-South (Design 1). In order to investigate census bias and a sample instead of a total census, the flight pattern was modified in subsequent censuses.Two sets of North-South transects were flown throughout the park in three elephant censuses in 1985 (Design 2).

Experimental counting

Design 3: As an estimate of precision, six arbitrary census blocks totalling 2 600 km^2 were counted twice in succession in the woodland stratum at a time when most trees had produced new leaves, and represented the worst conditions for visibility during the year in Etosha.The basic counting technique was followed with transects arranged as in Design 1. Repeated counts were compared with the Wilcoxon Signed Rank test (Zar 1984).

Design 4: A series of experimental transects of variable width and altitude were used in the August 1985 elephant censuses to determine the effect of these variables on apparent elephant density.The approach followed a model describing some major sources of variance in an aerial census (Caughley 1974; Caughley *et al.* 1976; Bayliss & Giles 1985). A woodland area with a relatively high density of elephants was chosen, and six treatment combinations of strip width (1 km, 2 km, 4 km) and altitude (90 m, 120 m) were randomly allocated to a series of North-South transects covering the whole area.The number of elephants counted was expressed as a density ($Y=N/km^2$). Areas of transects were calculated using designated strip width and lengths measured from a 1:100 000 map. Partial regressions of apparent density (Y) on strip width (X_1) and altitude (X_2) were calculated, using a polynomial multivariate regression method following Caughley (1974) and Steel & Torrie (1980).

Mark-resighting

A total of 30 elephants were marked with radio-collars and temporary painted numbers in 1984 and 1985, as part of a study of elephant movements in Etosha. Resightings of marked elephants during aerial censuses were used to roughly estimate census bias.

Photographic and direct counts

Elephants were counted from transparencies taken of family units during aerial censuses for photogrammetrical age estimation, and photographic counts were compared to direct counts of individual groups of elephants in the woodland stratum of the August 1985 census. Direct counts were made from the centre of the counting strip and at close range while circling over groups. As small calves are the most likely class to be counted inaccurately, the number of calves younger than approximately one year was used as an indication of accuracy.

RESULTS

Precision of census estimates

Table 1 presents estimates of precision in counting elephants in Etosha using the basic counting technique described in Design 3.The number of groups varied significantly between the first and second counts of census blocks, with more groups recorded in second than in first counts (Wilcoxon Signed Rank $T_- < T_{0.01(2),6}$).The total number of elephants in each block remained similar ($T_- > T_{0.01(2),6}$), indicating that disturbance by the aircraft caused herds to split into smaller groups.

TABLE 1: Mean (± Standard Error) percentage change in the number of groups of elephants and the number of individuals in first and second counts in six census blocks in Etosha National Park.

Number of groups in: First count	Second count	Time lapse between counts (min)	% change
12	20	30	+ 66.7
7	9	25	+ 28.6
17	22	45	+ 29.4
9	12	60	+ 33.3
2	2	15	0
5	6	20	+ 20.0
S: $T_- = 1 < T_{0.01(2),6}$*		x (±SE)	29.7 (±8.9)

Number of elephants in: First count	Second count	Time lapse between counts (min)	% change
139	145	30	+ 4.1
89	94	25	+ 5.6
121	118	45	- 2.5
93	90	60	+ 3.3
17	17	15	0
9	9	20	0
NS: $T_- = 7 > T_{0.01(2),6}$**		x (±SE)	1.8 (±1.3)

* Significant (Wilcoxon Signed Rank test)
** Not Significant (Wilcoxon Signed Rank test)

Accuracy of census estimates

The analysis of variance in apparent elephant density due to the individual and combined effects of changes in transect width and altitude is presented in Table 2. Elephant density was not significantly related to changes in both altitude or transect width, within the limits of those variables tested and thesub-optimal visibility in woodland.

Elephants marked during July 1984 and July 1985 were resighted in later censuses (Table 3). All those marked in July 1984 were present in the park and resighted in September 1984 and still showed the conspicuous painted numbers on their backs. By December 1984, most painted numbers were no longer conspicuous, but this is also the time when herds leave the park (Lindeque &

Lindeque 1991), which may account for the one herd missed.If only those censuses are used where marked elephants could definitely be recognized and were likely to have been in the census area, namely September 1984 and August 1985, the fractions not resighted were 0% and 11.5% respectively.

TABLE 2: Summary of analysis of variance in apparent elephant density (Y) in an experimental census of elephants in a 788km² section of Etosha National Park, using 15 transects with random combinations of altitude and transect width.

Source of variance	SS	df	MS	F
Main effect*:				
Transect width X_1	0.382	1	0.382	2.913 NS **
Altitude X_2	0.012	1	0.012	0.092 NS
Interaction:				
$Y/X_1;X_2$	0.370	1	0.370	2.822 NS
$Y/X_2;X_1$	0.001	1	0.001	0.001 NS
Residual	1.572	12	0.131	
Total	1.953	14		

* Random combinations of 1000m, 2000m and 4000m transect widths (X_1) with randomly allocated altitudes of 90m or 120m (X_2)

** Not Significant, F < p 0.05

TABLE 3: Radio-collared elephants resighted during censuses of elephants in Etosha National Park.

Resightings in Census					
Marked:	July 1984:	Sept 1984	Dec 1984	May 1985	Aug 1985
Family unit members	12	12	11; 1M/A	12	10; 2M/A
Bulls	1	1	1	1 A	1 A
Marked:	July 1985:				
Family unit members	3	-	-	-	2; 1A
Bulls	14	-	-	-	11;2A;1M
no. (%) present		13 (100)	13(92.3)	12(92.3)	26 (86.7)
no. (%) seen of those present		13 (100)	12(91.7)	12 (100)	23 (88.5)
no. (% of total) known to be absent		-	-	1 (7.7)	4 (13.3)
no. (%) possibly absent or missed		-	1 (8.3)	-	3 (11.5)

M: missed

A : absent from Etosha

An attempt to count elephants from transparencies taken during censuses in Etosha resulted in lower counts when compared to direct observations. In the woodland stratum of the August 1985 census, 95 calves younger than approximately one year were counted directly, but only 85 could be counted from vertical aerial photographs. In the same census, only 71 calves were counted from the centre of the counting strip as compared to 95 counted at close range.

DISCUSSION

Caughley (1974) used the difference in the number of groups of elephants in a series of counts of elephants in Eltringham (1972) to estimate the true population size using a binomial model.The estimate thus obtained was larger than the total number of elephants counted in any one survey done by Eltringham (1972), which Caughley (1974) ascribed to counting bias.This may be unfounded if elephants elsewhere react to aircraft in a similar way as in Etosha (Table 1). Experimental designs including repeated counting to assess the eg. the efficiency of different procedures, aircraft and observers, may be compromised as a result of behavioural responses to disturbance. Estimates of elephant numbers can be precise, however, as long as methods are standardized, environmental conditions do not vary significantly between censuses, and all possible measures are taken to reduce the variation in possible sources of error from one census to the next.

The accuracy of estimates of population size is dependent on two types of errors. Some animals seen will not be counted accurately (type A), and some will never be seen at all (type B). Measuring and compensating for inaccuracies in counting individuals spotted are relatively easy compared to type B errors. The design of a census is usually aimed at minimizing the probability of not seeing a significant proportion of the population, usually by defining transect widths which ensures effective coverage of the area and adequate sightability of elephants. Transect widths were designed to ensure that most if not all groups were sighted (Lindeque & Lindeque 1997a), but actual counting has to be done at close range.Trial counts of herds on the outer edge of the counting strip were up to 25% higher than the real number recorded at close range (pers. obs.). Small calves are underestimated when counted from far away, but the number of adults is overestimated, the same type of error as in the classification of elephants into age groups from the ground at long range (pers. obs.).

Counting animals from photographs taken during an aerial census has been used successfully to counteract type A errors (Sinclair1973; Watson *et al.* 1969; Norton-Griffiths 1973, 1974, 1978). This technique appears to be most useful when counting large aggregations of species like wildebeest or buffalo. Photographs nevertheless introduce a new set of biases different from observer bias. Elephant calves were less easily seen on photographs than counting at close range. Circling over each group and observing its members from all angles ensured that groups were counted accurately, unlike the single view of a group captured on a photograph.

Various methods have been proposed to estimate the other cause of inaccurate estimates, namely the proportion of the population not seen and thus not counted. An analysis of the effect of major census variables did not reveal that estimates of elephant density were biased due to variation in altitude and transect width within the range tested (Table 2). Should such bias have been detected the model proposed by Caughley (1974) would have allowed the correction of population estimates to compensate for the fraction not recorded due to variation in the parameters investigated.

The number of known individuals in an area or population has been used to estimate bias in aerial surveys (Rice & Harder 1977; Gasaway *et al.* 1985; Packard *et al.* 1985; Crete *et al.* 1986).This is done by radio-telemetry or the use of conspicuously marked individuals.The proportion of known individuals to unknown ones is, however, an important consideration, and can be determined for specific sampling intensities following the Peterson estimation procedures, as described by Rice & Harder (1977).Where marked or known animals are present, the proportion of those seen during a total count may therefore be used to estimate bias in counting.One proviso is that marked individuals should not be more visible than unmarked ones, which may complicate the use of this method, as also in this study due to method of marking elephants.Conspicuous numbers painted on the backs of elephants might have rendered groups containing a marked individual more visible.The data presented here may serve only as an indication of the efficiency of the census in recording a number of known individuals, and not to estimate population size using mark-resighting theory.

Other methods based on double counts, binomial and parabolic estimates, have been used to estimate the number of animals missed or counting bias and thus to correct census results (Caughley 1974; Caughley & Goddard 1972; Magnusson *et al.* 1978). Routledge (1981) and Pollock & Kendall (1987) regard these methods as flawed by invalid assumptions. All methods using mark-resighting or replicate counts are fraught with technical problems, and may be more useful with stationary objects or larger samples. The utility of these methods lies in the ability to detect gross inaccuracy but does not extend to the calculation of the number of individuals missed. It is also possible that estimations of bias are more effective the greater the variance is between surveys or within a multiple sampling method.

Estimations of population size of elephants and other large mammals in Etosha since 1973 were derived from total count procedures using narrow transects (1-2 km), a helicopter and 4-6 seater fixed-wing aircraft, and done over a 4-6 week period. These censuses were expensive (approx. N$10.50/km^2 at 1992 rates) and could not be done frequently enough to provide adequate estimates of population trend. The method used to count elephants in this study could not be shown to be grossly inaccurate compared to previous and more intensive methods used in Etosha. By using wider transects, and eventually a standard orientation of transect lines, flying time and costs could be reduced to 10 days and about N$1.30/km^2 (1992 rate) without affecting the quality of estimates of population size. Low intensity counting techniques described in this paper could be useful in future when frequent counts of elephants are required, such as in a culling programme. Further reductions in the intensity of surveys were achieved by doing a sample count instead of a total count (Lindeque & Lindeque 1997b) but this reduced the precision of population estimates. Alternative approaches to counting elephants are nevertheless available to allow monitoring to continue despite a reduction in resources available for censusing.

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The assessed parapatric species pairs and combinations of the Southern African Avifauna

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ABSTRACT

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At the present time, resurgence in interest on the part of the ornithological community in conservation issues in general has included, *inter alia*, a welcome re-awakening in the necessity for the re-appraisal of parapatric pairs and assemblages of species in an avifauna as potentially harbouring currently unrecognised and even undescribed full species. The Afrotropics have been determined as singularly rich in world terms in such groupings of closely related taxa, many of which are centred on the South African Subregion (Afrotropics south of *ca* 16 S.) alone. Locally, this awakened interest has already culminated in the recognition of additional full species previously treated as subspecies of polytypic species with extensive ranges, as for instance the southern African Black Korhaan and the Whitebrowed Coucal, both now accepted as composite and comprising elements of two discrete species.

From an assessment of pertinent literature and of available empirical evidence it has been concluded that if this concept is to realise its full potential a more rigorous interpretation of it as formulated by H.M.Smith (1965) is required, as the recent list of African cases drawn up by Dr Jürgen Haffer (1992) seemingly embraces complexes which, *prima facie*, are debatable instances of parapatry, the constituent taxa not now meeting in a readily definable secondary contact, without intergradation and reproductively isolated, and, in effect, recently evolved species of birds. In the South African list of parapatric species as here identified, some fifty-five pairs and groupings are recognised and discussed as a contribution to still further research in this fundamental field of systematic enquiry. Attention is drawn to forms which are seen as probably currently unrecognised species, while a short list of equivocal cases is appended to the main text.

INTRODUCTION

With the current widespread interest in the conservation of biodiversity, increasing attention is being paid by avian systematists to parapatric pairs and groups of closely related forms as possibly comprising both forms overlooked and of undescribed cryptic species. In a recent important preliminary study of parapatric species in different parts of the world, Haffer (1992) has shown that a large number is to be found in the Afrotropics. Earlier, Hall & Moreau (1970) dealt with many cases of parapatry in Africa in terms of straight-forward superspecies in course of their speciation research into the continent's passerines, and before the adoption of H.M.Smith's formulation, in 1965, of the parapatric species concept by the scientific community. This was seemingly first regularly employed by Prigogine (1984 and earlier) during his in-depth taxonomic researches in eastern Zairese montane birds, and is now an integral part of investigative avifaunal research. While Dr Haffer's list of parapatric species, based as it is on the maps in the *Atlas of Speciation* of Hall and Moreau (1970), is an important preliminary assessment of such taxa in the Afrotropics, scanning of the listed African cases reveals numerous spatially remote allopatric pairs which do not satisfy the criteria for treatment as instances of parapatry. Admittedly, some of the cited cases may well have been parapatric at some stage in their evolutionart history, but verification on this score is probably not possible.

With the South African Subregion better known and researched than any other major sector of the African continent, and with little likelihood of further readily determinable new species being discovered within its limits, critical re-appraisal of parapatric units already identified as possible sources of still unrecognised full, but usually cryptic, species taxa is called for. This has recently been highlighted by the taxonomic splitting of the single small bustard species *Eupodotis afra* into two species: *E. afra* and *E. afraoides* subspp (see Clancey (1989) & Crowe *et al.* (1994), the admitting of the coucals *Centropus superciliosus loandae* and *C. burchellii fasciipygialis* as representatives of two and not a single species (Clancey (1989), and the recognition from southern Namibia of Cave's Lark *Certhilauda cavei* (*vide* Crowe *et al.* 1994). In the list presented below I recognise over fifty cases of parapatry as here adopted, supplying in addition to the names of the taxa involved, the locations of the contact zones, major references in the standard literature, and further relevant taxonomic comment in complex cases.

RESEARCH BACKGROUND

In preparing the following list of parapatric species of birds for southern Africa, the maps covering both the non-passerine and passerine species of the Afrotropics appearing in Hall & Moreau (1970) and Snow (Ed.) (1978), as published by the British Museum (Nat.Hist.) London, both of which are essentially based on preserved material in the larger museums, were studied in close detail. This was later supplemented by an evaluation of the large data base provided by *S.A.O.S.Checklist of Southern African Birds* (Clancey (Ed.) 1980) and its two updates of 1987 and 1991, and the extensive series of 67 parts published by P.A.Clancey under the title "Miscellaneous Taxonomic Notes on African Birds" in the *Durban Museum Novitates* between 1952 and 1986; and like contributions published during the same time span in other series, such as *Arnoldia (Rhodesia)* and the *Bulletin of the British Ornithologists' Club* to the year 1993. Dr Jürgen Haffer's eminently useful contribution was also carefully scrutinised in so far as it affected the southern African list as determined by me.

Before enumerating the southern parapatric species so far determined, it is desirable to first ascertain the speciation stage involved in the concept. Just what is parapatry and what is served by recognising so-called parapatric species in the first place? Parapatry as initially defined by H.M. Smith (1965) is essentially a taxonomic concept designed to facilitate identification and the nature of the structures and mechanisms of such species units, which at some stage in their history had seen integral elements spatially sundered from other (probably mainly core) populations in a state of allopatry. These detached birds later spread to re-unite with their parental conspecifics in distributional contiguity and virtual sympatry in secondary or even tertial contacts. The re-unification was probably activated by a comparable set of biogeographical factors to those which had initiated the cleavage in the species population cotinuum in the first place. The secondary contact event has far reaching taxonomic implications for the forms concerned, and the present list of parapatric cases in southern Africa should go some way in stimulating still further research into this important field of scientific enquiry.

In order to limit recondite and currently unrecognised species continuing to be overlooked, parapatric pairs and complexes need to be identified, re-assessed and the points of secondary contact established by both field research and the critical examination of adequate series of specimens in museum collections. Such incipient species are seemingly in the main the outcome of both expansionary and contractive phases involving major biomes, such as the Lower Guinea rainforest during the Pleistocene and perhaps earlier in the case of the eastern and southern African fauna, which, periodically, either facilitated or inhibited distributional extensions of forms generated in centres of radial speciation to both the north and south of the equatorial rainforest belt of the continent.

At this point a cautionary note is, however, required as many species pairs identified in the austral African avifauna speciated via allopatry, enhanced in the early formative stages by distributional and ecological shifts, and are now spatially segregated often quite widely from one another. The well-known southern African species pairs grouped in superspecies in the sugarbirds *Promerops cafer* and *P. gurneyi*, the rockjumpers *Chaetops frenatus* and *C. aurantius* and the siskins *Pseudochloroptila totta* and *P. symonsi* are cases in point. Many parapatric combinations enumerated in Haffer's list are in effect species pairs, and like those just mentioned now pursue independent evolutionary courses, these usually aligned with spread into a new environment. It would be taxo-nomically acceptable to view such species pairs as derived from close ancestral analogues and to have evolved through parapatry and subsequent distributional divergence and allopatry into the geminal (paired) combinations present today.

The composition of simple parapatric pairs calls for little additional comment to that given for such species in the formal list, but complexes are of necessity composite and may vary widely in both nature and complexity. The main parapatric paradigm (as a pattern or model), which is repeatedly to be found in the southern African avifauna, is exemplified by that furnished by the southern aggregation of medium-sized parrots of the genus *Poicephalus*, as given in (a) below, *et seq.* -

a) Three congeneric species in state of west - east parapatry, one monotypic in the west, the others polytypic and hybridizing in the secondary contact interface: *Poicephalus rueppellii / P. meyeri / P. cryptoxanthus*. See Clancey (1977), Clancey (Ed.), *Checklist*, 1980, p.95 (Map 1).

b) A single polytypic species, four races of which are distributed west-east, this sequence present to the north of a second species of an earlier ancestral lineage with two races, the two species meeting without hybridization in the south-east of the range: Goldentailed and Knysna Woodpeckers *Campethera abingoni / C. notata*. See Clancey 1988, Clancey (Ed.), *Checklist*, 1980, p.135 (Map 2).

c) Three species, two polytypic, meet in a compact mosaic centred on a major arid zone, all evincing minor instances of hybridization. The monotypic species is a remnant of an earlier radiation than in the case of the polytypic ones: bulbuls of the genus *Pycnonotus: Pycnonotus capensis / P. nigricans / P. barbatus*. See Clancey (Ed.), *Checklist*, 1980, p.171; also Lawson (1962) (Map 3).

d) Two polytypic warblers disposed in a west - east sequence, with a complex of stabilized subspecies derived from both parental forms interposed between them. This southern group intergrades to the north of its range with a further complex of forms (*C. simplex*), and is detachedly represented to the south-west by an isospecies (see Amadon & Short 1992). Barred Bush Warblers *Calamonastes fasciolatus / C. stierlingi*, the isospecies *Euryptila subcinnamomea*. See Clancey (Ed.), *Checklist*, 1980, p. 209 (Map 4)

A quantitative study of the southern African instances of both pair and multiple parapatry reveals that most occur in the eastern sector of the Subregion, particularly in association with the Malawi Rift, south along the eastern continental escarpment to South Africa, south to the mid-Limpopo R., as demonstrated in the following:

Lower Malawi Rift - Limpopo R.	10	20%	} 42%
Limpopo R. - Umtamvuna R., Natal/Transkei	11	22%	
N.Botswana/W.Zimbabwe	8	16%	
Namibia	7	14%	
Transvaal plateau	6	12%	
Western Cape Province	4	8%	
Eastern Cape Province	4	8%	
TOTAL	50:	100%	

This disposition correlates closely with the conclusion reached earlier that the mesic eastern constituents of the avifauna stem largely from eastern African centres of speciation, their subsequent distributional history much influenced by oscillations in the extent of the equatorial rainforest belt and concomitant spread and contraction of the woodland savanna biomes lying both to the south and north of the Equator.

SOUTHERN AFRICAN PARAPATRIC PAIRS AND COMPLEXES

The English and scientific names of the forms involved are followed by a brief outline of the zone or zones of secondary contract, and indication if hybridization occurs or not. Reference is also made to major relevant statements in the literature. Additional taxonomic comment is given as and when required.

The present research project has highlighted the possible need to recognise several additional bird species, as defined in cases 14, 21, 31 and 39 in the following list. In addition, in case 50, it is suggested that a restructuring of the current arrangement of the southern African Zosteropidae is perhaps desirable. Such a restructuring would result in the recognition of four species in the South African Subregion.

1. **Reed and Crowned Cormorants**
   Phalacrocorax africanus / P. coronatus
   Contact: Western Cape coast. See Snow, in Snow (Ed.), *Atlas*, 1978.
   Note: Both species formerly widely viewed as conspecific, as *P. africanus* is additionally maritime in north-west of continental range.

2. **Jackal and Augur Buzzards**
   Buteo rufofuscus / B. augur
   Contact: South-central Namibia to Zimbabwe. See Snow, in Snow (Ed.), *Atlas*, 1978.

3. **Pale and Dark Chanting Goshawks**
   Melierax canorus / M. metabates
   Contact: Northern and eastern Botswana (see Snow, in Snow (Ed.), *Atlas*, 1978.
   Note: *M. metabates* is linked parapatrically with *M. poliopterus* in eastern Africa.

4. **Cape, Natal, Redbilled and Hildebrandt's Francolins**
   Pternistis capensis / P. natalensis / P. adspersus / P. hildebrandti
   Contact: *P. natalensis / P. adspersus:* south-western Zambia - north-western Zimbabwe; *P. natalensis / P. hildebrandti:* south-eastern Zambia - Zambezi valley west of Shiré R. confluence (see Snow, in Snow (Ed.), *Atlas*, 1978.

5. **Crested Guineafowl**
   Guttera pucherani / G. edouardi
   Contact: Southern Tanzania on the Rufiji R. See Crowe & Snow, in Snow (Ed.), *Atlas*, 1978.
   Note: Crowe, in his definitive study of guineafowl, united *edouardi* and *pucherani*, but qualified opinion clearly favours their treatment as allospecies, which view is supported here.

6. **Karoo and Rüppell's Korhaans**
   Eupodotis vigorsii / E. rueppellii
   Contact: Southern Namibia *ca* 15 S. See Clancey & Snow, in Snow (Ed.), *Atlas*, 1978.
   Note: *E.v. barlowi* (Roberts), 1937, now seen as an interspecific hybrid between the two species cited.

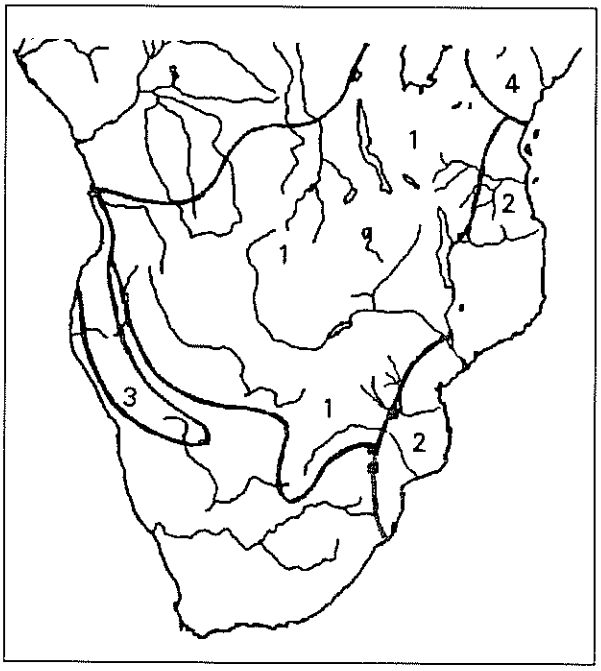
7. **Black Korhaans**
   Eupodotis afra / E. afraoides
   Contact: Cradock district, eastern Cape (see Crowe *et al*, 1994); Clancey (1989); Clancey & Snow, in Snow (Ed.), *Atlas*, 1978, and also Clancey (Ed.), *Checklist*, Second Update, 1991.

8. **Greyheaded and Hartlaub's Gulls**
   Larus cirrocephalus / L. hartlaubii
   Contact: South-western Cape coasts, where hybridizing (*vide* Maclean, *Roberts' Birds*, 1985.

9. **Rüppell's, Meyer's and Brownheaded Parrots (Map 1)**
   Poicephalus rueppellii / P. meyeri / P. cryptoxanthus
   Contacts: *P. rueppellii / P. meyeri:* north-east of Etosha Pan, Namibia; *P. meyeri / P. cryptoxanthus:* south-eastern Zimbabwe to north-eastern Transvaal, where hybridizing. See Clancey (1977); also Clancey (Ed.), *Checklist*, 1980.

10. **Liliau's and Blackcheeked Lovebirds**
    Agapornis lilianae / A. nigrigenis
    Contact: Mid-Zambezi R. from Victoria Falls downstream. No established hybridization. See Irwin, *Birds of Zimbabwe*, 1981.

11. **Knysna, Livingstone's and Schalow's Louries**
    Tauraco corythaix / T. livingstonii / T. schalowi
    Contacts: *T. corythaix / T. livingstonii:* Northern Zululand and Lebombo Mtns; *T. livingstonii / T. schalowi:* Shiré R. valley and southern Malawi Rift. No interspecific hybridization. See Clancey (1989); also Clancey (Ed.), *Checklist*, 1980.



MAP 1: Complex of three west-east parrot paraspecies with limited hybridization between two taxa: *Poicephalus meyeri* and *P. cryptoxanthus* marked thus: ■

1 = *P. meyeri*, 2 = *P. cryptoxanthus*, 3 = *P. rueppellii*, 4 = *P. rufiventris*.

12. Whitebrowed and Burchell's Coucals

Centropus superciliosus / C. burchellii

Contact: East of Malawi Rift and south-eastern Zambia. See Clancey (1989); also Snow & Clancey, in Snow (Ed.), *Atlas*, 1978.

13. Black and Bradfield's Swifts

Apus barbatus / A. bradfieldi

Contact: Northern Cape on the lower Vaal R. and mid-Orange R. drainage. See Brooke, in Snow (Ed.), *Atlas*, 1978.

14. Speckled and Whitecheeked Mousebirds

Colius striatus simulans / C. leucotis berlepschi

Contact: Shiré R. valley and Rift of Malawi. See Schifter (1985).

Note: The sharpness of the point of secondary contact and distinctiveness of the character suites justify the recognition of the *leucotis* group of Speckled Mousebird forms as specifically discrete from the southern *C.striatus* differentiates.

15. Redfaced and Bluenaped Mousebirds

Urocolius indicus / U. macrourus

Contact: South-western Tanzania from Lake Rukwa to northern end of Lake Malawi. See Schifter (1985).

16. Redbilled and Violet Woodhoopoes

Phoeniculus purpureus / P. damarensis

Contact: Centred from interior of Namibia north to Angola.

Note: Status uncertain as some populations show general intergradation between the two forms (see Clancey, *Rare Birds*, 1985). Perhaps a localised remnant of an earlier evolutionary radiation, as a somewhat similar population of *damarensis*-type *(P. granti)* is present in East Africa. In an Angolan and Namibian context, *P. damarensis* is generally accorded full species status.

17. Crowned and Bradfield's Hornbills

Tockus alboterminatus / T. bradfieldi

Contact: Mid-Zambezi R. above Victoria Falls. See Kemp & Fry, in Snow (Ed.), *Atlas*, 1978.

Note: *T. bradfieldi* is more ecologically xeric than *T. alboterminatus*.

18. Acacia and Miombo Pied Barbets

Tricholaema leucomelas / T. frontatus

Contact: Mid-Zambezi drainage, south-western Zambia. See Goodwin & Clancey, in Snow (Ed.), *Atlas*, 1978.

19. Anchieta's, Sowerby's and Whyte's Barbets

Stactolaema anchietae / S. sowerbyi / S. whytii

Contacts: *S. anchietae / S. sowerbyi:* Copper Belt, Zambia; *S. sowerbyi / S. whytii:* Shiré R. valley and lower Malawi Rift. See Goodwin & Clancey, in Snow (Ed.), *Atlas*, 1978.

Note: The splitting of *sowerbyi* and *whytii* is adumbrated in Goodwin & Clancey, *loc.cit.*

20. Redfronted and Yellowfronted Tinkerbirds

Pogoniulus pusillus / P. chrysoconus

Contact: South-eastern Transvaal, east to the Maputo district, Mozambique. See Goodwin & Clancey, in Snow (Ed.), *Atlas*, 1978.

Note: The two species are again in secondary contact in east-central Africa.

21. Bennett's and Specklethroated Woodpeckers

Campethera bennettii / C. scriptoricauda

Contact: Shiré R. valley and lower Malawi Rift. See Short & Tarboton, in Snow (Ed.), *Atlas*, 1978.

Note: *C. nubica* is not a constituent form of the present complex. *C.b. buysi*, described from the Kaokoveld, has characters probably meriting specific status.

22. Goldentailed and Knysna Woodpeckers (Map 2)

Campethera abingoni / C. notata

Contact: South-western Natal-Transkei border. No recorded instances of hybridization. See Clancey (1988); also Short & Tarboton, in Snow (Ed.), *Atlas*, 1978.

23. Clapper and Flappet Larks

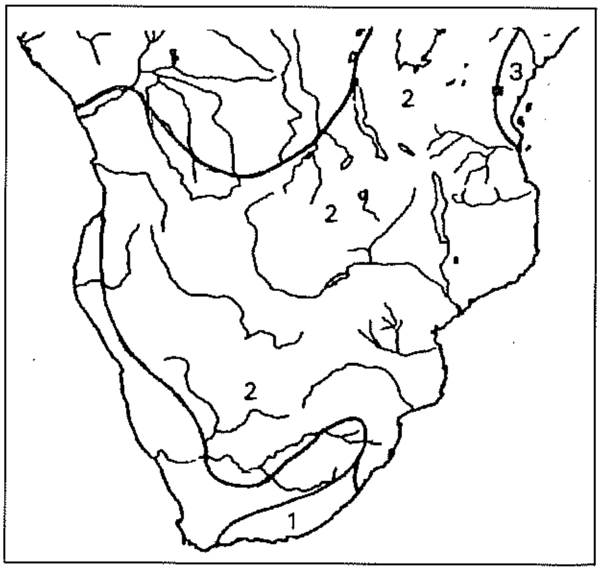
Mirafra apiata / M. rufocinnamomea

Contact: Barotseland, south-western Zambia, and north- eastern Botswana. See Hall & Moreau. *Atlas*, 1970.

24. Karoo, Red and Dune Larks

Certhilauda albescens / C. burra / C. erythrochlamys

Contacts: *C.a. karruensis:* hybridizes freely with *C. burra* at Brandvlei and elsewhere in north-western Cape; *C.a. cavei* is seemingly of stabilized hybrid origin, being distributionally interposed between *C.e. barlowi* and *C.a. guttata.* See Clancey,(1989), but for revised taxonomy see Crowe *et al.* 1994.



MAP 2: A case in which a widely distributed savanna woodpecker *Campethera abingoni* abuts parapatrically and interdigitates with a deep southern forestal taxon *C. notata*, without hybridization, but which hybridizes (■) with a contiguous savanna woodland taxon *C. mombassica* in East Africa.

1 = *C. notata*, 2 = *C. abingoni*, 3 = *C. mombassica*.

25. Pinkbilled and Botha's Larks

Spizocorys conirostris / S. fringillaris

Contact: East-central southern Transvaal plateau, but precise disposition not established.

Note: Hall & Moreau, *Atlas*, 1970, link the Pinkbilled and Sclater's Larks *S. sclateri*, but the latter's bill-shape, dusky tear-drop lower orbital mark, single egg clutch and nest among stone fragments, negate any close association. These workers also associate Botha's with Stark's Lark *Eremalauda starki*, which is again unacceptable, as Stark's is a highly gregarious and nomadic xeric species. Contiguous grassland plateau -ranges, bill and plumage colour features compared with *S.c. griseovinacea* favour the arrangement adopted here.

26. Southern and Acacia Grey Tits

Parus afer / P. cinerascens

Contact: South-western Great Namaqualand, Namibia, and mid-Orange R., Cape. See Clancey (1958). No verified hybridization.

27. Whitewinged, Carp's and Southern Black Tits

Parus leucomelas / P. carpi / P. niger

Contacts: The first two taxa are in contact on the south-western periphery of the Miombo biome in western and southern Angola, where this abuts on the arid bushveld which *P. carpi* inhabits. See Clancey (1972); also Clancey (Ed.), *Checklist*, 1980. Furthermore, *P. niger* is a melanistic species related to the *P. major*, *P. afer* and *P. cinerascens* clade and not to *P. leucomelas*. *P. niger* and *P. leucomelas* intertigitate ecologically in the south of the core range of the latter, while in the case of *P. niger* this has been found to occur sympatrically in the Waterberg of north-central Namibia and on the mid-Kunene R. alongside *P. carpi* (C J Brown pers. comm.), confirming that three full species of these tits are involved (Clancey in press).

28. Cape and Grey Penduline Tits

Anthoscopus minutus / A. caroli

Contact: Extends narrowly from northern Namibia, Caprivi and northern Botswana to north-western Zimbabwe. See Clancey (Ed.), *Checklist*, 1980.

29. Cape, Blackeyed and Redeyed Bulbuls (Map 3)

Pycnonotus capensis / P. barbatus / P. nigricans

Contacts: *P. capensis / P. barbatus:* Sundays R. region of eastern Cape; *P. barbatus / P. nigricans:* western Transvaal and western Zimbabwe. Hybridizing at both stated points of secondary contact. See Lawson (1962); also Clancey (Ed.), *Checklist*, 1980.

30. Sentinel and Short-toed Rockthrushes

Monticola explorator / M. brevipes

Contact: East-central plateau of Transvaal. See Kemp *et al.*, 1985.

31. Olive and Karoo Thrushes

Turdus olivaceus / T. smithi

Contact: Localised occurrences of *T. olivaceus* subspp. within karroid range of *T. smithi* in interior of eastern Cape and O.F.S. through anthropogenic habitat alteration. No direct evidence of hybridization. P.F.I.A.O. & author in prep. The specific status of *T. swynnertoni* of Zimbabwe has yet to be determined. Described initially by Bannerman as a full species.

32. Chorister and Natal Robins (Figure 1)

Cossypha dichroa / C. natalensis

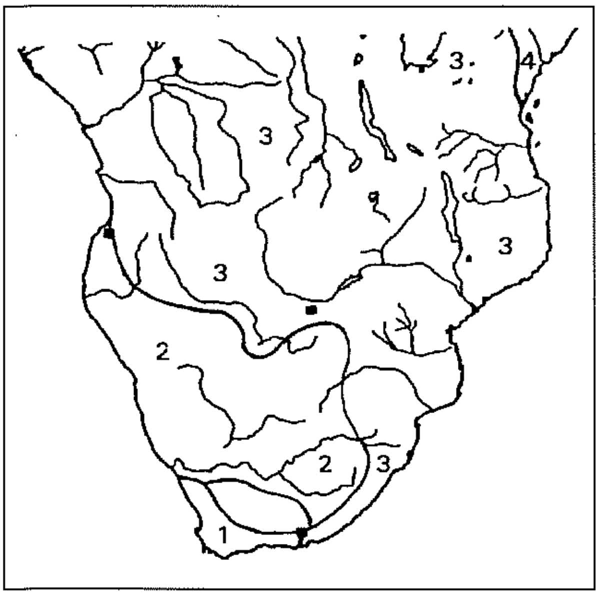
Contact: Coastal forests of Transkei. Limited hybridization. See Clancey (1982); also Hall & Moreau, *Atlas*, 1970.

33. Collared and Rufoustailed Palm Thrushes (Morning Warblers)

Cichladusa arquata / C. ruficauda

Contact: No evidence that these two species are now in contact.

Note: Haffer (1992) groups *C. arquata* and *C. guttata* as comprising a parapatric pair, but the forms concerned are sympatric in East Africa. *C. ruficauda* and *C. arquata* are a better match and of immediate common evolutionary origin, their plumage pattern and ecology closely congruent.



MAP 3: The *Pycnonotus* bulbul complex in southern Africa with limited instances of hybridization at points along the contact interfaces (marked thus ■), between the extensively polytypic *P. barbatus* and the austral endemics of earlier evolutionary events, *P. capensis* and *P. nigricans*.

1 = *P. capensis*, 2 = *P. nigricans*, 3 = *P. barbatus*, 4 = *P. barbatus dodsoni* group.

34. Brown, Bearded and Eastern Bearded Scrub Robins

Erythropygia signata / E. barbata / E. quadrivirgata

Contacts: *E. signata / E. quadrivirgata:* Maputo Bay, southern Mozambique, west to eastern Transvaal; *E. barbata / E. quadrivirgata*: Zambia south of the mid-Kafue R. and the Muchinga escarpment. One verified case of hybridization between the first two species at Lake St. Lucia, Zululand. See Clancey (Ed.), *Checklist*, 1980; also Benson *et al.*, 1971, appendix 4, Map 6.

35. African and Cinnamon Reed Warblers

Acrocephalus baeticatus / A. cinnamomeus

Contact: *A. cinnamomeus fraterculus* ranges to the Natal coast to the south of Durban and some interior localities, as well as the Transvaal plateau, while *A. baeticatus* is present at others in the high eastern interior (west to Johannesburg). Status of the case is still unresolved, but seemingly represents one of incipient secondary contact without consolidation. See Clancey, 1994a.

36. Blackheaded and Chirinda Apalises

Apalis melanocephala / A. chirindensis

Contact: Recorded seasonally alongside one another in the Makurupini Forest, Haroni-Lusitu confluence, eastern Zimbabwe, but *A. chirindensis* breeds at

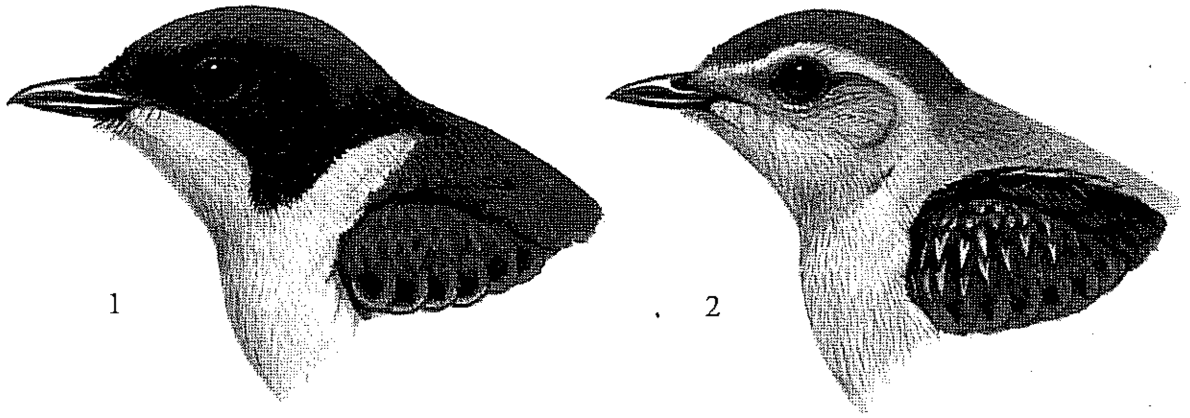


FIGURE 1: Heads of two southern African *Cossypha* species, showing the striking differences in plumage pattern, with *C. dichroa* (no. 1) derived from an early expansionary event and endemic to South Africa, and *C. natalensis* (no. 2) an Afrotropical element which has marginally invaded part of the Transkei and eastern Cape at sea level in secondary contact, where the two robins now hybridize to a moderate degree.

higher elevations than *A. melanocephala*, so that the two are altitudinally segregated. Hybrids not recorded in the literature. See Irwin, 1981.

37. Green- and Greybacked Bleating Bush Warblers

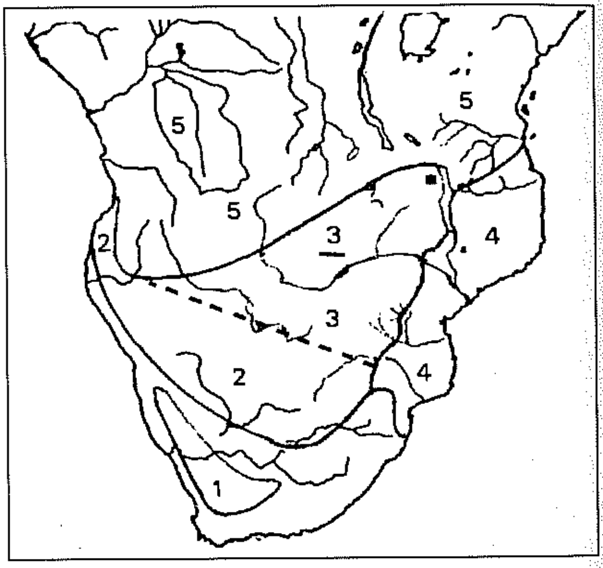
Camaroptera brachyura / C. brevicaudata

Contact: Well-defined zone of secondary contact hybridization between these two species is centred on the frontier highlands of Zimbabwe and southern Mozambique, and a less sharply marked one along the course of the Save R. in the Mozambique lowlands. A narrow tongue of introgression by *C. brevicaudata* genes also extends through *C.b. constans* from the eastern Transvaal to Zululand (see Clancey (1970); also Clancey (Ed.), *Checklist*, 1980.

38. Barred Bush and Stierling's Barred Bush Warblers (Map 4)

Calamonastes fasciolatus / C. stierlingi / Euryptila subcinnamomea

Contact: Two subspecies of *C. stierlingi* are phenotypically intermediate between *C. stierlingi* and *C. fasciolatus*, these being *C.s. pintoi* and *C.s. irwini*, with *C.s. olivascens* and nominate *stierlingi* disposed both to the east and north, resulting in three southern groupings. In Zambia *stierlingi* hybridizes in depth with *C. simplex*, while *E. subcinnamomea* is a karroid isospecies present to the south-west of the *fasciolatus/stierlingi* group. See Hall & Moreau, *Atlas*, 1970.



MAP 4: The austral African Barred Bush Warbler complex evinces little direct evidence of hybridization (■), but intergrades through a broad secondary contact in Zambia in the case of *Calamonastes stierlingi / C. fasciolatus* with *C. simplex*. Populations "3̲" north of the Zambezi R. comprise ecophenotypes of both *C. fasciolatus* and *C. stierlingi*; populations "3" south of the Zambezi consist largely of *C. fasciolatus*. *Euryptila subcinnamomea* is an isospecies.

1 = *E. subcinnamomea*, 2 = *C. fasciolata*, 3 = *C. fasciolata & stierlingi*, 4 = *C. stierlingi*, 5 = *C. simplex*.

39. Palecrowned Cloud Cisticola and Sibling (Wetland Cisticola) (Figure 2)

Cisticola brunnescens / C. taciturnus

Contact: On the breeding grounds, *C.b. egregius* affects the moist interior grasslands of Natal and the Transvaal, generally above 1525 m a.s.l., with *C. taciturnus* replacing it along the coast from Transkei and Natal and Zululand to the Limpopo R. floodplain in Mozambique. While some elements of *C.b. egregius* reach the coastlands as winterers, the two near contiguous cisticolas do not intergrade or hybridize and two species are apparently involved, but further work on their vocalizations, phenology and mtDNA is required to resolve their status. The vernacular Wetland Cisticola is here introduced for *C. taciturnus* as the two forms occur alongside one another in the southern winter months, when both affect comparable littoral estuarine wetland habitat (see Clancey 1992).

40. Lazy and Rockloving Cisticolas

Cisticola aberrans / C. emini

Contact: Shiré R. valley of Malawi Rift. See Hall & Moreau, *Atlas*, 1970.

41. Spotted (or Karoo) and Saffronbreasted Prinias

Prinia maculosa / P. hypoxantha

Contact: Interior of eastern Cape to west of East London. See Clancey (1982a, 1989), also Clancey (Ed.), *Checklist*, 1980.

Note: *P. maculosa* and *P. flavicans* also meet and interbreed in north-western Cape (*vide* Brooke (1993).

42. Pririt, Chinspot and Mozambique Batises

Batis pririt / B. molitor / B. soror

Contacts: *B. pririt* conjoins in interior of eastern

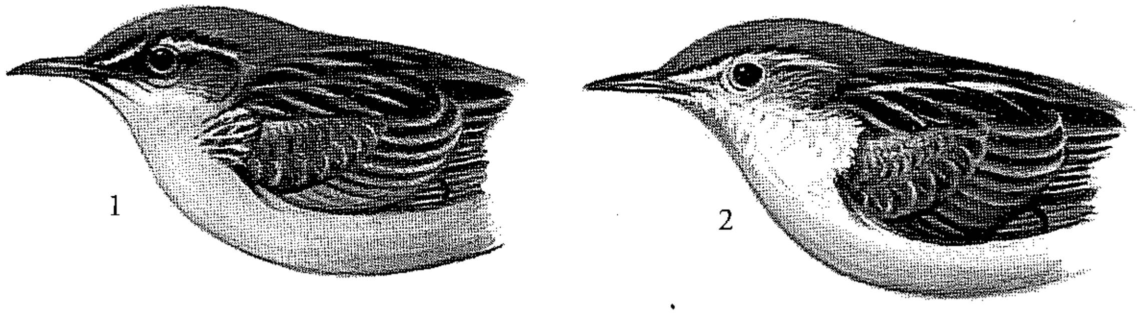


FIGURE 2: Heads and partial dorsal and lateral plumage patterns of two sibling cisticola species, *Cisticola brunnescens egregius* (no. 1) and *C. tacitumus* (no. 2), showing assumption of breeding characters in the former taxon and lack of a similar development in the latter species. The two cisticolas are assessed as representing an early post-parapatric stage of evolutionary development in which one species has either retained or lost the assumption of a breeding dress in association with the breeding cycle. Species 1 *C.b. egregius* is part of a wide-ranging Afrotropical species, while species 2 *C. tacitumus* is confined to the south-eastern African coastlands.

Cape with *B. molitor*, which species pair is widely distributed throughout the *Acacia* country of the southern African plateau and arid west, while *B. soror* replaces *B. molitor* to the north of the lower Limpopo R. valley. The three allospecies are not recorded as hybridizing. See Clancey (Ed.), *Checklist* 1980.

43. Bluemantled Flycatcher

Trochocercus cyanomelas segregus / T.c. megalolophus

Contact: *T.c. segregus*, with short crest, is confined to interior evergreen forests south of the Limpopo R., with *T.c. megalolophus* replacing it in Zimbabwe forests and along the Mozambique coast as far south on the littoral as Mtunzini, Zululand, this with an elongated crest. No recorded instances of hybridization between the two phenotypes. See Clancey (Ed.), *Checklist*, 1980.

44. Grassveld and Mountain Pipits

Anthus cinnamomeus / A. hoeschi

Contact: Drakensberg massif, with *A. hoeschi* replacing *A.c. rufuloides* on the alpine summit grasslands, down to *ca* 1250 m a.s.l. with marginal overlap, but not hybridizing; see Mendelsohn (1984). *A. hoeschi* spends off-season in the grasslands of the Zambezi/Zaire watershed. Strongly migratory with northbound passage through Namibia, the return one *via* eastern Botswana. It is noteworthy that the local races of *A. cinnamomeus* breeding adjacent to the wintering grounds of *A. hoeschi* in south-central Africa show loss of most of the white on the penultimate rectrices, suggesting *A. hoeschi's* ancestors originated in that sector of the Afrotropics. See Clancey, *Rare Birds*, 1985.

45. Yellowthroated and Fülleborn's Longclaws

Macronyx croceus / M. fuelleborni

Contract: Luangwa R. valley region of eastern Zambia. Not hybridizing. See Hall & Moreau, *Atlas*, 1970; also Benson *et al.*, 1971.

46. Southern, Tropical and Swamp Boubous

Laniarius ferrugineus / L. aethiopicus / L. bicolor

Contacts: *L. ferrugineus / L. aethiopicus:* Mid-Limpopo R. valley and Save R. of Mozambique; hybridizing; *L. aethiopicus / L. bicolor:* northern Botswana, Caprivi Strip and mid-Zambezi R.,and in parts of southern Angola; also hybridizing. See Hall (1954), Quickelberge (1966), Hall & Moreau, *Atlas*, 1970 and Irwin (1987).

Note: Irwin (1987) argues for the recognition of *L.f. savensis* as a full species, but the said taxon intergrades to the south of its range with *L.f. tongensis*, and is an integral part of *L. ferrugineus*.

47. Southern and Threestreaked Tchagras

Tchagra tchagra / T. australis

Contact: Lebombo Mtns and lowlands of Transvaal, Swaziland, Sul do Save, Mozambique, and Zululand. For discussion on *T. australis* races see Clancey (1969).

48. Brubru

Nilaus afer solivagus / N.a. miombensis

Contact: Southern Mozambique/northern Zululand border. No established intergradation or hybridization established. See Clancey (Ed.), *Checklist*, 1980.

49. Eastern and Guinean Olive Sunbirds

Nectarinia olivacea / N. obscura

Contacts: *N. olivacea* essentially eastern, and *N. obscura* central and western African in range, with *N. obscura granti* interposed insularly alongside elements of *N. olivacea changamwensis*, and further south in highlands of Zimbabwe-Mozambique frontier by *N. obscura sclateri*. Small hybrid *olivacea/obscura* population remotely placed in south-eastern Zambia, at Marble Hill, south-east of Lusaka. See Clancey (1994).

Note: *N. violacea / N. olivacea* are not related, *contra* Hall & Moreau, *Atlas*, 1970, and Haffer (1992), the former sunbird seemingly a relict.

50. Cape and Yellow White-eyes

Zosterops pallidus / Z. senegalensis

Contact: Lebombo Mtns and adjacent lowlands of sou-thern Mozambique and northern Zululand.

Note: A case for the restructuring of the *Z. pallidus* mosaic is perhaps worthwhile reconsidering, splitting it into three allospecies: *Z. pallidus*, *Z. capensis* and *Z. virens*, along with *Z. senegalensis* subspecies. See Clancey (1968); Clancey (Ed.), *Checklist*, 1980.

51. Whitebrowed Sparrow Weavers

Plocepasser mahali terricolor / P.(m.) pectoralis

Contact: Hwange National Park, Zimbabwe (see Irwin, 1981).

52. Northern and Southern Greyheaded Sparrows

Passer griseus / P. diffusus

Contact: The extralimital subspecies of *P. diffusus* - *P.d. luangwae* is ecologically segregated but otherwise sympatric with *P. griseus ugandae* in the Luangwa R. valley of south-eastern Zambia (*vide* Benson *et al.*, 1971).

53. Pink and Redthroated Twinspots

Hypargos margaritatus / H. niveoguttatus

Contact: Ranges interdigitate in region of lower Limpopo R. floodplain, Mozambique, that of *H. margaritatus* seemingly under pressure from *H. niveoguttatus*, which is now well-established south of the Limpopo at Macia and Chimonzo.

54. Blackfaced and East African Swees

Estrilda melanotis / E. quartinia

Contact: Southern Zimbabwe, but not currently in immediate secondary contact. See Irwin (1981).

55. Blackthroated and Lemonbreasted Canaries

Serinus atrogularis / S. citrinipectus

Contact: Sabi-Lundi confluence region, south-eastern Zimbabwe. See Irwin (1981), also Clancey (Ed.), Checklist, 1980.

ADDITIONAL EQUIVOCAL INSTANCES OF PARAPATRY INVOLVING SOUTHERN AFRICAN SPECIES PAIRS, MOST OF WHICH ARE ALLUDED TO BY HAFFER (1992), ARE BRIEFLY COMMENTED ON IN THE FOLLOWING LIST.

a. Fasciated and Banded Snake Eagles

Circaetus fasciolatus, Circaetus cinerascens

Not in parapatric contact. Morphological differences deemed too great to warrant close association.

b. Grey and Dickinson's Kestrels

Falco ardosiaceus, Falco dickinsoni

Sympatric over western and north-western parts of joint range.

c. Rednecked and Swainson's Francolins

Pternistis afer, Pternistis swainsonii

Widely sympatric over eastern southern Africa from Natal north to Zimbabwe and parts of Zambia.

d. Cape Parrot

Poicephalus robustus, P. (robustus) suahelicus

Both parrot taxa meet without intergradation in the region of the mid-Limpopo R. drainage. They differ is size, bill-length and the colour of the head and neck, and are viewed by some workers as being attributable to two species, but the case requires further study on the basis of a larger panel of material than is available at the present time. Should a second species be recognised, it would take the binomen *P. suahelicus*, as the West African *P. fuscicollis* is closely associated with marine mangroves according to Bannerman (1931), and probably represents a third nominal parrot species.

e. Barred Owl

Glaucidium capense, P. (capense) scheffleri

Prigogine (1985) proposed the treatment of *G. capense* as a monotypic species and the grouping of the subspecies to the north of its southern African range as elements of another closely allied form, *G. scheffleri* Neumann, 1911. The case awaits critical re-evaluation. Prigogine listed both *G. capense* and *G. scheffleri* in close taxonomic association with two other *Glaucidium* spp., *G. castaneum* and *G. albertinum*.

f. Woodland and Mangrove Kingfishers

Halcyon senegalensis, Halcyon senegaloides

Do not form a superspecies, differing widely in biology, phenology, and bill-mass and colouration. Bill uniform and dull crimson in *H. senegaloides*, bicoloured scarlet and black in *H. senegalensis*. Vocalisation also widely different.

g. Blackeared and Chestnutbacked Finchlarks

Eremopterix australis, Eremopterix leucotis

Not obviously closely allied, *E. australis* being ecologically karroid, *E. leucotis* inhabiting lightly wooded savanna. Colour patterns of adult males widely different.

h. Greater and Lesser Striped Swallows

Hirundo cucullata, Hirundo abyssinica

Sympatric over eastern parts of joint southern African range, with *H. abyssinica* affecting lower altitudes and a somewhat moister climatic regime.

i. Cloud Cisticola

Cisticola textrix major, Cisticola (textrix) marleyi

Range disposition suggests *C. marleyi* is not conspecific with *C.t. major*. The case has similarities to that of the Palecrowned and Wetland Cisticolas dealt with earlier under No. 39 in the previous list.

j. Arrowmarked and Barecheeked Babblers

Turdoides jardineii, Turdoides gymnogenys

Not allied. Ranges misleadingly shown as abutting in Hall & Moreau, *Atlas*, 1970. *T. gymnogenys* more xeric than *T. jardineii*.

k. Striped and Yellowtufted Pipits

Anthus lineiventris, Anthus crenatus

Differing from one another in plumage pattern and ecology, only revealing convergence in the yellowish edging to remiges, rectrices and wing-coverts. Doubtfully parapatric. *A. lineiventris* closely associated with rocks under trees. See Hall & Moreau, *Atlas*, 1970.

l. Lesser Doublecollared and Neergaard's Sunbirds

Nectarinia chalybea, Nectarinia neergaardi

Not associated parapatrically at any point, with

N. chalybea an inhabitant of interior evergreen forest, *N. neergaardi* being restricted to humid savanna woodland on the Mozambique coast and eastern Zululand. Also, note that *N. chalybea* terminates its range to the south of the Limpopo R., and is replaced to the north on the plateau by *N. manoensis*.

m. Redheaded and Cut-throat Finches
Amadina erythrocephala, Amadina fasciata
Sympatric in Transvaal on the plateau. Often breeding in *Bubalornis* nests in the same tree.

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Mass-Length relationships of Namib Tenebrionids

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Understanding ecological relationships, ecosystem dynamics and energetics and energy flow often require biomass data on a large scale. In a desert environment, large-scale collection of individuals from the sparse biota is not desirable. On the other hand, capture and release of organisms, particularly the common tenebrionid beetles, is feasible. This note presents a general mass-vs-length equation for deriving biomass from length measurements of Namib Desert tenebrionid beetles.

We derived such a relationship from forty species found in the dunes, gravel plains and riverbed near Gobabeb, Namibia (23°32'E, 15°02'S) during a long-term population study of tenebrionids (Table 1). We used voucher specimens (n = 280) that have been kept air-dried for at least 10 years in the collection of the Desert Ecological Research Unit at Gobabeb. Total head-and-body length was measured with callipers (± 0.1mm). Air-dried individuals were weighed (electronic balance ± 0.1mg). One

TABLE 1: Tenebrionid species measured for the present study. Mean dry mass and length of each are indicated.

TRIBE	SPECIES	LENGTH (mm)	MASS (mg)
Adesmiini	Cauricara eburnea (Pascoe)	9.7	44
Adesmiini	Epiphysa arenicola Penrith	18.0	384
Adesmiini	Eustolopus octoseriatus Gebien	13.1	105
Adesmiini	Metriopus depressus (Haag)	11.1	54
Adesmiini	Onymacris plana (Péringuey)	18.7	328
Adesmiini	Onymacris rugatipennis r. (Haag)	17.7	235
Adesmiini	Onymacris unguicularis (Haag)	17.4	252
Adesmiini	Physadesmia globosa (Haag)	15.4	236
Adesmiini	Physosterna cribripes (Haag)	18.4	402
Adesmiini	Stenocara gracilipes Solier	12.5	110
Adesmiini	Stenocara (Cauricara) phalangium (Gebien)	9.8	34
Adesmiini	Stenocara (Cauricara) velox (Péringuey)	9.4	35
Cryptochilini	Pachynotelus albonotatus Haag	13.2	71
Cryptochilini	Pachynotelus lineatus Haag	8.0	13
Eurychorini	Eurychora sp.	14.5	70
Eurychorini	Lepidochora discoidalis (Gebien)	10.7	35
Eurychorini	Lepidorchora kahani Koch	15.3	68
Eurychorini	Lepidochora porti Koch	12.1	47
Eurychorini	Stips dohrni (Haag)	11.6	47
Eurychorini	Stips stali (Haag)	11.9	56
Molurini	Namibomodes muculicollis Koch	12.1	37
Molurini	Namibomodes serrimargo (Gebien)	12.7	33
Molurini	Namibomodes zarcoi Koch	10.6	21
Molurini	Psammodes sp.	27.7	501
Opatrini	Gonocephalum sp.	11.7	37
Opatrini	Parastizopus armaticeps (Péringuey)	16.7	160
Opatrini	Psammogaster malani Koch	5.1	6
Platynotini	Gonopus tibialis Fabricius	18.9	321
Scaurini	Carchares macer Pascoe	11.9	34
Tentyriini	Rhammatodes subcostatus Koch	7.3	7
Zophosini	Zophosis (Calosis) amabilis Deyrolle	11.0	36
Zophosini	Zophosis (Occidentophosis) cerea Penrith	10.8	27
Zophosini	Zophosis (Occidentophosis) damarina Pér.	11.6	32
Zophosini	Zophosis (Gyrosis) devexa Péringuey	7.3	12
Zophosini	Zophosis dorsata Péringuey	13.6	56
Zophosini	Zophosis (Cardiosis) fairmairei Péringue	5.5	3
Zophosini	Zophosis (Cardiosis) hamiltonuli Koch	4.2	2
Zophosini	Zophosis (Cerosis) hereroensis Gebien	8.9	16
Zophosini	Zophosis (Gyrosis) moralesi (Koch)	9.6	33
Zophosini	Zophosis (Gyrosis) orbicularis Deyrolle	11.2	62

beetle of each species was oven-dried at 65°C and reweighed to determine its mass loss due to moisture. The difference between air-dried and oven-dried specimens ($2.9 \pm 2.0\%$) was used to calibrate all mass data to the oven-dried standard. We calculated linear regressions on logarithmically transformed data and applied a modified t-test to compare slopes of regression equations, following Zar (1984).

The general mass-vs-length equation for Namib tenebrionids is: Mass = 0.0186 x Length $^{3.201}$ ($r^2 = 0.89$; $n = 280$).

The regression equations derived for each species were not significantly different between tribes (t-test; $P>0.1$).

Namib tenebrionids were heavier than expected from Rogers *et al.*'s (1976) general curve (mass = 0.0305 x length $^{2.62}$) by $3.0 \pm$ SD 1.4 times (range: 1.0 – 7.8 times). This may be because Namib beetles are more heavily chitinized than the average insect in North America.

Our mass-vs-length relationship can be used to improve previous estimates. To illustrate this, we applied the equation to Henschel's (1994) data on the diet and consumption rates of the spider *Leucorchestris arenicola*. We found that these spiders consume 7 times their own mass per annum. An average-sized 1.7g spider thus consumes 33mg prey.spider^{-1}.day^{-1}, or 1.9% of its body weight per day. This is two-thirds of the consumption rate of an equivalent-sized Australian lycosid (Humphreys 1975), instead of one-quarter, as Henschel (1994) had estimated.

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A review of *Hemirhagerrhis viperina* (Bocage) (Serpentes: Colubridae), a rupicolous Psammophine snake

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ABSTRACT

Most of the recorded specimens of *Hemirhagerrhis viperina* (Bocage) have been examined and compared with abundant material of *H. nototaenia* from central Africa. *H. viperina* can be most readily distinguished by its relatively short tail and colour pattern, but there are also average differences in several head shield characters. Although sympatry or parapatry has not been recorded, *H. viperina* is a rupicolous species, whereas *H. nototaenia* is an arboreal form in dry savanna, so the two forms are considered to be specifically distinct.

INTRODUCTION

The genus *Hemirhagerrhis* was erected by Boettger in 1893, with *H. kelleri* Boettger as type species by monotypy. In the same year Stejneger proposed that *Ablabes hildebrandtii* Peters 1878 and *Coronella nototaenia* Günther 1864 should be included in *Hemirhagerrhis*, but Boulenger (1896) included *nototaenia* in the genus *Amplorhinus* A. Smith, with *Psammophylax viperinus* Bocage 1873 and *A. hildebrandtii* Peters 1878 as synonyms. Bogert (1940) pointed out that *nototaenia* has a typical Psammophine hemipenis and is obviously congeneric with *H. kelleri*, leaving *Amplorhinus* as a monotypic genus of uncertain affinities. Bogert also revived *viperinus* as a subspecies of *H. nototaenia*, although he subsequently had doubts about this status: "I wonder whether you may not eventually find that snakes as different in pattern as well as tail-length, with rather extensive mean differences in ventrals and subcaudals, may not prove to be separate species, unless intergrades turn up in samples of *Hemirhagerrhis*" (pers comm., 11 April 1986).

Bogert (1940) tabulated the differences in ventral and caudal counts between *nototaenia* and *viperina*, with an overlap in caudal counts (68-98 vs. 52-75). The highest subdaudal count for *H. viperina* was based on Bocage (1895), who recorded 177 ventrals and 75 subcaudals for a snake from Humbe, Angola. In this work he mentions six specimens, the type specimen of *P. viperinus* from Dombe, two from Maconjo, one from Capangombe and two from Humbe. In a footnote (p. 109), he provides ventral and subcaudal counts for one individual each from Capangombe, Humbe and Maconjo. However, when I examined the material in the Museu Bocage in 1968, I found only five specimens: one from Dombe and two each from Maconjo and Capangombe. The missing specimens from Humbe may have been typical *H. nototaenia*. The Museu Bocage collection was subsequently destroyed by fire.

Since Bogert (1940), additional material of *H. viperina* from southern Angola and northern Namibia has accumulated, mostly in the Transvaal Museum and the National Museum of Namibia. Although there is still no evidence of either sympatry or intergradation between typical *H. nototaenia* and *viperina*, I decided to analyse the available data in an attempt to determine the status of *viperina*.

MATERIAL AND METHODS

I have examined most of the available material of *H. viperina* (29 specimens) and most of the material of *H. nototaenia* (151 specimens) from areas between 8° and 23°S to the east of Angola and Namibia, i.e. Botswana, Zambia, Zimbabwe, Malawi, Mozambique and southern Tanzania.

The following characters were recorded for each specimen: colour pattern; number of supralabials and those entering orbit; number of infralabials and those in contact with the anterior sublinguals; number of preoculars, postoculars and temporals (anterior + posterior); dorsal scale rows anteriorly, at midbody and posteriorly (17-17-13 in all specimens); number of ventrals by the Dowling (1951b) method; number of subcaudals, excluding the terminal spine (the anal shield was divided in all specimens examined); length from snout to vent, plus tail, in mm measured against a white-face tape.

Dorsal scale reduction formulae were recorded for a sample of each species, using the Dowling (1951a) method, the collated data being presented in the modified form previously used (Broadley, 1977).

Maxillary tooth formulae appear with the number of solid anterior teeth in arabic numerals separated by a + sign from the number of grooved fangs indicated by roman numerals, e.g. 9+II.

Institutional abbreviations follow Leviton *et al.*(1985), with the addition of AJL = A.J. Lambiris collection, JPT = J.P. Tello collection and SPQ = Sable Park collection (Kwekwe, Zimbabwe).

A figure in parentheses after a catalogue number indicates the number of specimens bearing that number.

CHARACTER ANALYSIS

1. Ventral shields

The variation in number of ventrals is shown in Table 1. There is no sexual dimorphism, so the data for both sexes are combined. There is no significant difference between the two species.

TABLE 1: *Hemirhagerrhis viperina* and *H. nototaenia*: variation in ventral and subcaudal counts and Tail/total length ratio.

SPECIES	*VIPERINA*	*NOTOTAENIA*
Ventrals		
Range	156-183	153-179
Mean	164,67 (n = 28)	168,93 (n = 141)
S.D.	7,26	4,61
C.V.	4,41	2,73
Subcaudals		
Range	52-66	68-90
Mean	58,73 (n=27)	76,63 (n = 133)
S.D.	3,80	4,00
C.V.	6,47	5,22
Tail/total length ratio		
Range	.17-.21	.22-.29
Mean	.195 (n = 22)	.2483 (n = 128)
S.D.	.0090	.0153
C.V.	.0005	.0006

2. Subcaudal shields

The variation in number of subcaudals is shown in Table 1, there is again no sexual dimorphism. The two species are clearly separated on this character, with no overlap in range of counts, the Coefficient of Difference being 2,24. Hoevers & Johnson (1982) have recorded higher counts for *H. nototaenia* in southern Somalia (85-103).

3. Dorsal scale row reduction formulae

The dorsal scale row reduction formulae can be summarised as follows:

H. viperina **17** 2+3, 3+4, 4+5 or 5+6 (102-118) **15** 2+3, 3+4, 4+5 or 5+6 (109-126) **13** n=5.

H. nototaenia **17** 3+4, rarely 4+5 or 5+6 (84-108) **15** 3+4, rarely 2+3 or 4+5 (104-119) **13** n=10.

H. viperina is more variable and the reductions tend to take place closer together and more caudad than in *H. nototaenia*.

4. Infralabial formula

In *H. viperina* the usual formula is 10, the first five in contact with the anterior sublinguals, whereas the normal formula in *H. nototaenia* is 9(4). Variation in number of infralabials is shown in Table 2.

TABLE 2: *Hemirhagerrhis viperina* and *H. nototaenia*: variation in number of infralabials and temporal formula (anterior + posterior).

SPECIES	*VIPERINA*		*NOTOTAENIA*	
Infralabials	**sides**	**%**	**sides**	**%**
7	–	–	1	0.3
8	–	–	10	3,4
9	2	3,8	242	81,2
10	46	88,5	42	14,1
11	4	7,7	3	1,0
Temporals	**sides**	**%**	**sides**	**%**
1+2	5	8,6	287	93,2
1+3	10	17,2	10	3,2
2+2	3	5,2	4	1,3
2+3	40	69,0	7	2,3

5. Temporal formula

In *H. viperina* the most common formula is 2+3, followed by 1+3. In contrast the usual formula in *H. nototaenia* is 1+2, although Hoevers & Johnson (1982) reported 2+3 as normal in southern Somalia. Variation in temporal formula is shown in Table 2.

6. Position of nostril

In *H. viperina* the nostril is pierced nearly vertically in the nasal, whereas in *H. nototaenia* it is pierced dorsolaterally.

7. Maxillary dentition

Bogert (1940) recorded 9+11 maxillary teeth for two Angolan specimens of *H. viperina* and a Tanzanian specimen of *H. nototaenia*, Stejneger (1893) also recorded 9 anterior maxillary teeth in a Kenyan specimen of *H. nototaenia*. However, two specimens of this species from Botswana and Zimbabwe have 10+11 maxillary teeth, and Bourgeois (1968, Fig. 63) illustrates the same arrangement in a Zaire specimen. Dr. Garth Underwood (*in litt.*) examined the dentition of another *H. viperina* (BM 1906.8.24.75) and recorded 8+11 maxillary teeth.

8. Ratio tail length/total length

This character was used by Bogert (1940) and it clearly separates the short-tailed *H. viperina* (.17 to .21) from *H. nototaenia* (.22 to .29). See Table 1.

9. Colour pattern

The two species differ considerably in colour pattern. *H. viperina* is very variable in pattern. The ground colour varies from cream to dark grey, the tail bright orange posteriorly and the ventrum always paler than the dorsum. The head is pale with sparse dark speckling and usually two dark streaks extending diagonally from the eye to the posterior supralabials (Fig. 1). The dorsal markings are usually brown and may consist of staggered rows of spots (Fig. 3), a zigzag line which led Bocage (1873) to apply the name *viperinus* to this snake (Fig. 7) or paired synchronised blotches more like the markings of *H. nototaenia* (Fig. 5).

H. nototaenia is grey above and below. The top of the head is dark speckled, with a pale stripe that passes through the upper part of the iris of the eye, while a black lateral stripe passes through the rest of the eye (Figs. 2, 8, 9). A darker vertebral stripe is bordered by paired black triangles with their apexes pointing outwards (Fig. 3) these may be synchronised to form short cross bars. There is usually a tinge of orange on the neck and the tail tip. The base of the tongue is red.

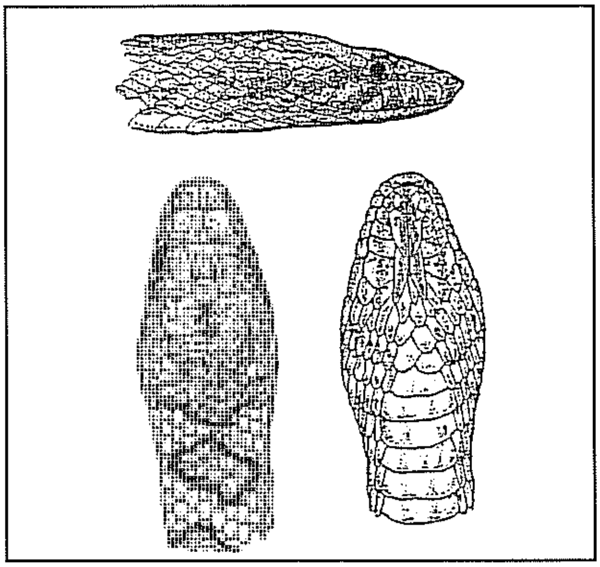

FIGURE 1: *Hemirhagerrhis viperina*: AMNH 50506 - Huambo, Angola. Lateral, dorsal and ventral views of head (x 4) (after Bogert, 1940).

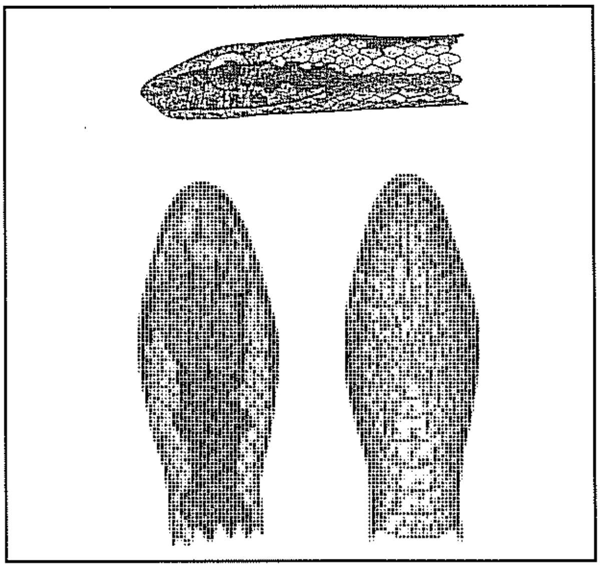

FIGURE 2: *Hemirhagerrhis nototaenia*: MRAC 9325 - N'gayu, Shaba Province, Zaire. Lateral, dorsal and ventral views of head (x 4) (after Witte, 1953).

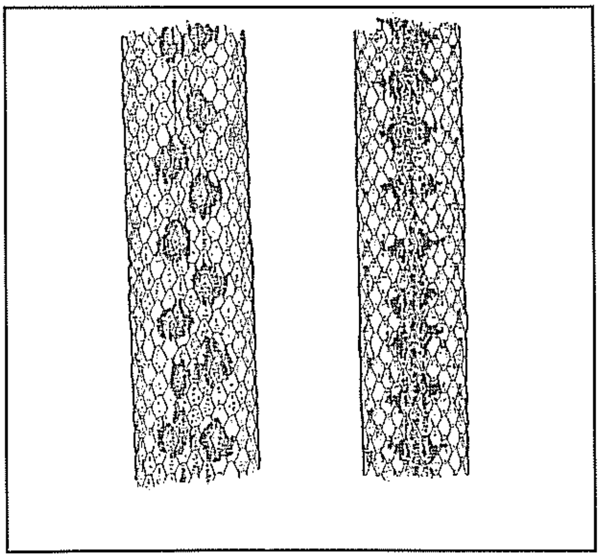

FIGURE 3: Comparison of patterns at midbody (x 3).
A – *Hemirhagerrhis viperina* AMNH 50506 – Huambo, Angola.
B – *Hemirhagerrhis nototaenia* AMNH 50505 – Tindi, Tanzania.

SYSTEMATIC ACCOUNT

HEMIRHAGERRHIS VIPERINA (Bocage 1873)
viperine rock snake (Figures 1, 3A, 4, 5, 6 & 7)
Psammophylax rhombeatus? Bocage, 1867: 224.
Psammophylax viperinus Bocage, 1873: 222. Type locality: "Dombe" = Dombe Grande, Benguela, Angola.
Psammophylax nototaenia Bocage, 1895: 109.
Amplorhinus nototaenia Boulenger, 1896: 125 (part); Sternfeld, 1910a, 23 and 1910b: 55; Werner 1925: 131 (part); Lawrence, 1929: 26; Monard, 1937: 126, 128; FitzSimons, V., 1938: 157.
Hemirhagerrhis nototaenia viperinus Bogert, 1940: 75, Fig. 12A, 13 & 15E; FitzSimons, V. 1962: 208; Laurent, 1964: 112; FitzSimons, V., 1966: 63 & 1970/74: 125/126; Broadley, 1983: 120; Bauer *et al.*, 1993: 135.
Hemirhagerrhis nototaenia viperina Mertens, 1955: 92 & 1971: 85; Elzen, 1980: 399, Fig. 2.

Description: Snout blunt; rostral much broader than deep, just visible from above; internasals much shorter than prefrontals; frontal narrowed mesially, about twice as long as broad, longer than its distance from end of snout, subequal to a parietal; loreal longer than deep; nostril pierced vertically in a semi-divided nasal; preocular just reaching or failing to reach frontal; postoculars 2 (rarely 3); temporals usually 2+3, sometimes 1+3, rarely 1+2 or 2+2 (Table 2); supralabials 8, the fourth and fifth entering the orbit; infralabials usually 10, rarely 11 or 9 (Table 2), the first 5 (rarely 4) in contact with the anterior sublinguals, which are subequal in length to the posterior. Dorsal scale rows smooth in 17-17-13 rows, reducing by loss of lateral rows only; ventrals 154-177; anal divided; subcaudals 52-66 (Table 1), without sexual dimorphism.

Colouration: The ground colour varies from pale buff (Fig. 4, 6) to dark grey (Fig. 5) and the dorsal markings vary from brown to black. These may consist of two rows of staggered blotches Fig. 3A, a zig-zag line bisected by a thin yellow vertebral line (Fig. 7) or the blotches more or less synchronised to form crossbands as in *H. nototaenia* (Fig. 5). The head is pale above except for some sparse darker stippling, there is no dark stripe through the eye, only some dark blotches and streaks on the supralabials (Fig. 1). The ventrum is always paler than the dorsum, with sparse stippling.

Size: Largest ♂ (TMP 45175 – Tundavala to Sa da Bandeira, Angola) 337+77 = 414 mm. Largest ♀ (CAS 175097 – Farm Franken, northern Damaraland, Namibia) 407+85 = 492 mm. Tail .17-.21 per cent of total length.

Ecology: This is a rupicolous species. Wulf Haacke supplied habitat data for three Angolan specimens: TM 40101 amongst rocks on overgrown black amphibolite outcrop, associated lizards were *Agama planiceps*, *Rhoptropus barnardi* and *Cordylus vittifer machadoi*; TM 45175 found under flake of granite on boulder on a wooded slope; TM 46736 collected at ca. 16h00 in the sun on top of a granite boulder. The association of this species with rocky habitats is confirmed by FitzSimons (1938), Elzen (1980) and Bauer *et al.* 1993. Bogert (1940) recorded a small *Mabuya quinquetaeniata* in the stomach of a Hanha specimen, but as this skink does not occur in Angola, it is more likely to have been another blue-tailed rupicolous species *Mabuya laevis*.

Distribution: Southwestern Angola and northwestern Namibia (Fig. 10, 11).

LOCALITIES

Angola: Capangombe (Bocage, 1895) MB 1716 (2); 5 km S of Chibemba TMP 40101; Caraculo TMP 22517, 46736; Dombe Grande (Bocage, 1867, 1873, 1895) MB 1715 (type); Hanha (Bogert, 1940); Huambo (Bogert 1940) AMNH 50506; Humpata (Laurent, 1964); Huxe BMNH 1906.8.24.75; Lungo TMP 24420; Maconjo (Bocage, 1895) MB 1714 (2); Munhino (Bogert, 1940) AMNH 50509-10; 8 km from Tundavala to Sa da Bandeira TMP 45175.
Namibia: no locality (Mertens, 1955) TMP 38234; Brandberg SMWN 3195, 8047; Epupa Falls TMP 47720; Erongo Mts SMWN 2364; Etemba TMP 66779; Fran-ken (Bauer *et al.*, 1993) CAS 175094, 175097; Gobabis (Sternfeld, 1910b); Kamanjab (Bauer *et al.*, 1993) SMWN 2365 & 62 km ESE CAS 193659; Karossfontein NMZB 12220; SMWN 8048; Lichtenau TMP 57937; Omandumba West (Elzen, 1980); Omaruru (Mert., 1955a); Paderborn (Bauer *et al.*, 1993); Ruacana Falls SMWN 2670.
Unknown origin: ("Griffin Mine, Leydsdorp, Transvaal") TMP 5316.

HEMIRHAGERRHIS NOTOTAENIA (Günther)

bark snake (figure 2, 3B, 8 & 9)

Coronella nototaenia Günther, 1864: 309, pl. xxvi, fig. 1. Type locality: "Rios de Sena, Zambezi", Mozambique.
Ablabes Hildebrandii Peters, 1878: 205, pl. ii, fig. 6. Type locality: Kitui, Kenya.
Amphiophis nototaenia Boulenger, 1891: 307.
Hemirhagerrhis nototaenia Stejneger, 1893: 730.
Psammophylax nototaenia Bocage, 1895: 109.
Amplorhinus nototaenia Boulenger, 1896: 125 (part) and 1897: 801; Boettger, 1898: 99; Hewitt, 1913: 481; Boulenger, 1915: 629; Werner, 1925: 131 (part); Loveridge, 1933: 250; Pitman 1934: 296; FitzSimons, 1935: 314.
Amplorhinus Güntheri Mocquard, 1906: 251. Type locality: "Environs du lac Ugami, l'Afrique australe". (error for Ugami, east Africa, vide NMHN catalogue).
Hemirhagerrhis nototaenia nototaenia Bogert, 1940: 73; Loveridge, 1951: 192, 1953: 269 and 1955: 185; Witte, 1953: 226, Fig. 74; Vesey-FitzGerald, 1958: 57; Broadley, 1959: 41; Broadley & Pitman, 1960: 443; Broadley, 1962: 832; FitzSimons, 1962: 206, fig. 56, pl. xxxiv; Johnsen, 1962: 123; Wilson, 1965: 161; FitzSimons, V., 1966: 63; Visser, 1966: 22, pl. 54; Bourgeois, 1968: 149, Fig. 62-64; FitzSimons, V., 1970/74, pl. 125; Broadley, 1971: 83, pl. x; Broadley & Cock,, 1975: 75, pl. 33; Broadley & Blake, 1979: 11; Broadley, 1983: 118, fig. 71, pl. xxiii; Auerbach, 1987: 161, pl. 15/4; Broadley, 1988: 392; Broadley & Howell, 1991: 27.

Description: Snout blunt; rostral much broader than deep, just visible from above; internasals much smaller than prefrontals; frontal narrowed mesially, about twice as long as broad, longer than its distance from the end of the snout, subequal to a parietal; loreal longer than deep; nostril pierced dorsolaterally in a semi-divided nasal; preocular not in contact with frontal; postoculars 2; temporals 1+2, very rarely 1+3, 2+3 or 2+2 (Table 2); supralabials 8, very rarely 7 or 9, the fourth and fifth (very rarely third and fourth or fifth and sixth) entering the orbit; infralabials 9, rarely 10, very rarely 8 or 11 (Table 2), the first 4 (rarely 5) in contact with the anterior sublinguals, which are subequal in length to the posterior. Dorsal scale rows smooth in 17-17-13 rows, reducing by loss of lateral rows only; ventrals 153-179; anal divided; subcaudals 68-90 (Table 1), without sexual dimorphism.

Colouration: Ash-grey to grey-brown above and below; top of head blackish, continuing as a vertebral stripe about three scales wide, jet black on the neck but fading posteriorly, a row of black spots merges with the vertebral stripe on either side, usually opposed to form crossbars, rarely alternating to form a zigzag. A dark lateral streak on the head passes through the lower two-thirds of the eye and fades out on the neck, being replaced by a row of grey lateral spots (Figs. 2, 8 & 9), usually a tinge of orange on the nape and tail tip.

Size: Largest ♂ (JPT Coll. – Morera, Mozambique) 300+95 = 395 mm. Largest ♀ (JPT 1346 – Matchova, Mozambique) 335+97 = 432 mm (tail tip missing). Tail .22-.29 percent of total length.

Ecology: This is a semi-arboreal species which inhabits dry savanna at altitudes up to ± 1 200 metres. It is sometimes found under loose bark or in hollow trees, especially Mopane (*Colophospermum mopane*). The diet consists largely of small geckos (including *Lygodactylus capensis*, *Pachydactylus punctatus* and *Hemidactylus mabouia*), but skinks (*Mabuya striata*) are also taken. Hoevers & Johnson (1982) recorded predation on the eggs of *Hemidactylus platycephalus* by a population of *H. nototaenia* living on Acacia trees at Chisimaio on the Somali coast.

Predation by *Agama atricollis* has been recorded in Zambia. Four to eight eggs are laid at a time.

Distribution: Tropical East Africa from southern Sudan and Somalia southwards to Mozambique and the eastern Transvaal, west to southern Zaire, Zambia, eastern Namibia (Caprivi) and Botswana, it probably occurs in

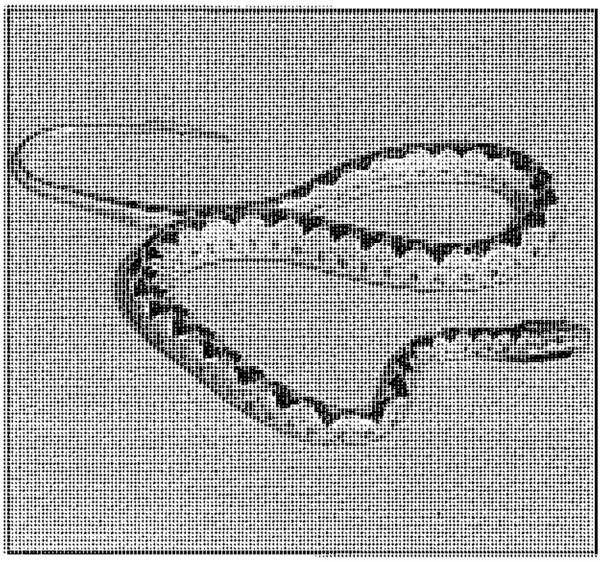

FIGURE 4: *Hemirhagerrhis viperina*, TMP 46736 – Caraculo, Angola.

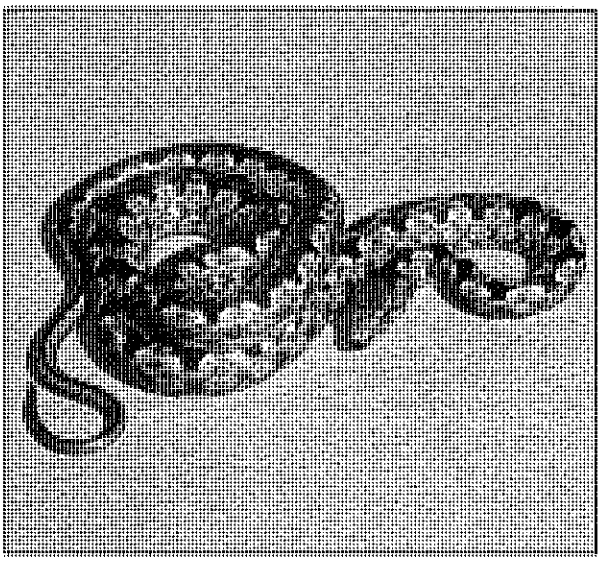

FIGURE 5: *Hemirhagerrhis viperina*, TMP 40101 – 5 km S of Chibemba.

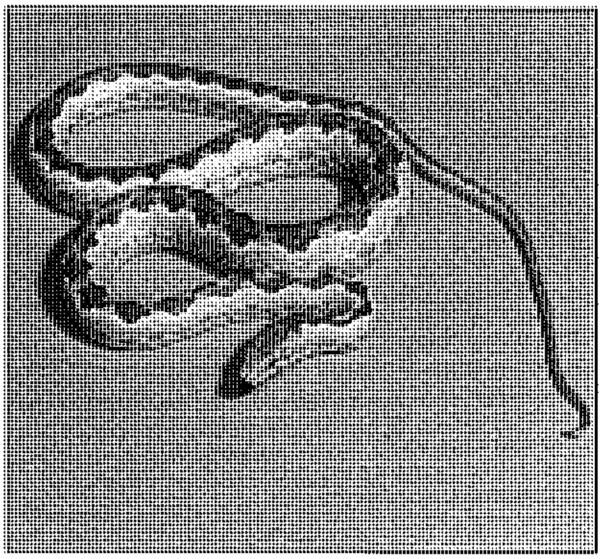

FIGURE 6: *Hemirhagerrhis viperina*, TMP 47720, Epupa Falls, Kaokoveld, Namibia.

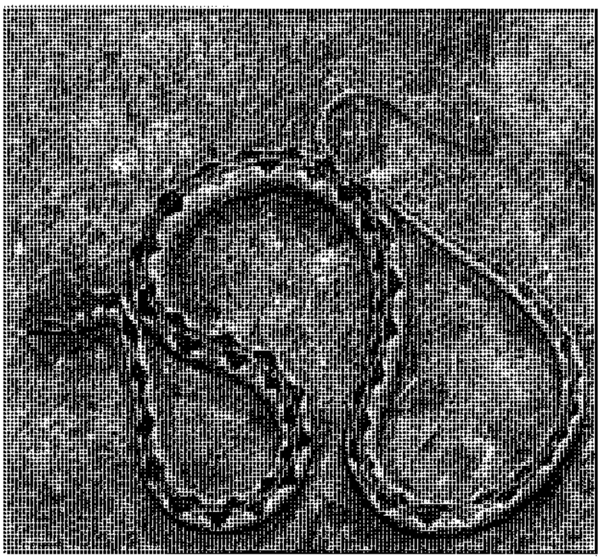

FIGURE 7: *Hemirhagerrhis viperina*, SMWN 8048 – Karossfontein, Namibia.

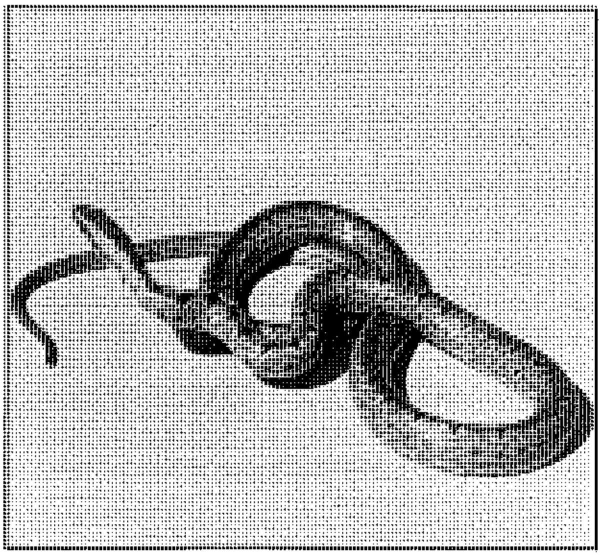

FIGURE 8: *Hemirhagerrhis nototaenia*, eastern Transvaal.

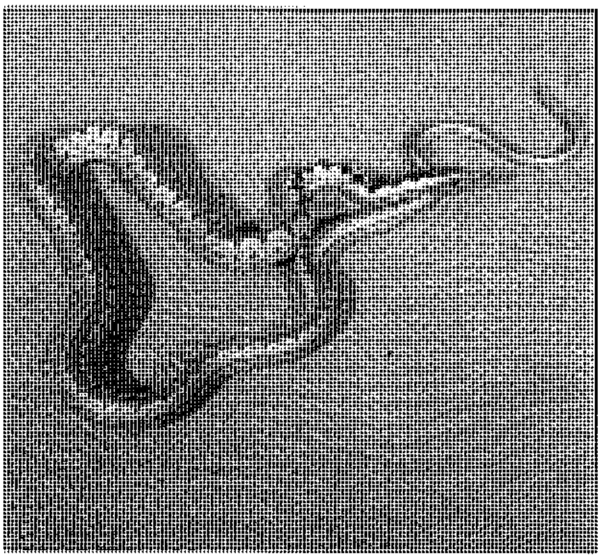

FIGURE 9: *Hemirhagerrhis nototaenia*, Zimbabwe.

south-eastern Angola (Figs. 10 & 11). Roman (1980: 75) recorded a *Hemirhagerrhis* from Diapaga in south-east Burkina Faso with 155 ventrals and 55 subcaudals and noted that he had also examined a live specimen from near Kandi in northern Benin. These records are separated from the nearest records of *H. nototaenia* in southern Sudan by 2 400 km and may represent an undescribed short-tailed species. These localities are indicated by question marks in Fig. 11.

LOCALITIES

Namibia (Caprivi): Katima Mulilo SMWN 6846, 8092 and 15 km WSW NMZB-UM 21301; Lianshulu SMWN 7811.

Botswana: Francistown NMZB-UM 10481; Kabulabula (FitzSimons, 1935) TMP 14696; Kasane NMZB-UM 13354; Makalamabedi NMZB-UM 16181; Selebi-Pikwe (?) SAM 45485; Tsodilo Hills NMZB-UM 16198; SAM 43882; Tsotsoroga Pan (FitzSimons, 1935) FMNH 17723.

Zimbabwe: Beitbridge NMZB 358; Birchenough Bridge NMZB-UM 4705, 7499, 23871, 28351-2, 32942; Chiredzi FMNH 205870; NMZB-UM 8519, 13411, 19752, 29399; Chimanimani Hot Springs NMZB-UM 19167; Chinhoyi Caves AJL 171; Chipangayi Bridge NMZB-UM 27416; Chipinda Pools NMZB-UM 31625; 65 km NE of Chirundu NMZB 377; Chitora River NMZB-UM 28634; Condo NMZB 4168; Devon, Odzi River NMZB 675; Dorowa NMZB-QVM 390; Fishan, Gonarezhou Nat. Park NMZB-UM 4936; Gwanda NMZB 7102, 8908; Humani Ranch NMZB-UM 29209; Hwange National Park NMZB-UM 29627; Inyokene NMZB 9719, 11332; Kapami NMZB-UM 853; Kariba NMZB 3224; NMZB-UM 2744, 5167, 11629, 11744-5, 11893, 23684, 24151, 32624; Kariba Lake – Charara Confluence NMZB-UM 5166, 5343 & Sinamwenda NMZB 9349; Karoi NMZB-UM 21415; Kazuma Pan NMZB 11059; Kwekwe SPQ 111; Lupane NMZB 31849; Majoda NMZB 8979; Malapati Drift NMZB-QVM 167; Mana Pools NMZB-UM 5560; Marhumbeni NMZB 2303; Mashumbi Pools NMZB 10435; Matetsi (Hewitt, 1913) NMZB 1170; Mount Darwin NMZB-UM 32; Mzarabani West NMZB 8830; Nyanyadzi NMZB-UM 23070, 23785; Rupisi Hot Springs NMZB-UM 27871; Ruware NMZB-UM 5834; Sanyati Gorge NMZB 3586, 3603-4; Sengwa Research Station NMZB-UM 22791; Shashe–Limpopo Confluence NMZB-UM 13140; Shashe – Shashani Confluence NMZB-UM 5707; Siakobvu, Bumi River NMZB-UM 18298; Tivuli Spring, Binga NMZB-UM 10576; Tuli NMZB 3225; Victoria Falls NMZB 13365; Whitewaters NMZB-UM 17866.

Zambia: Chipangali NMZB-UM 17315-6; Chunga NMZB-UM 30038, 30053; Kabompo NMZB 1308; Kalichero NMZB-UM 2763; Kaniki NMZB-UM 682-3, 685; Kasuru NMZB 3273, 4259; Lochinvar NMZB-UM 693; Lubungu Pontoon NMZB-UM 4520; Lundazi NMZB-UM 2762; Lusaka East NMZB-UM 1694; Mbala (Vesey-FitzGerald, 1958) NMZB 1548; Mpika District (Pitman, 1934); Mporokoso NMZB 1549; Mufuwe Lagoon NMZB-UM 5991; Mukupa IRSNB 2561; Mweru-Wantipa (Vesey-FitzGerald, 1958); Namwala Dist. (Pitman, 1934); Ndola (Johnsen, 1962); Ngoma NMZB-UM 18059; Nyamkolo (Loveridge, 1933); Rukuzi Dam NMZB-UM 3104; Siantamba NMZB 3452, 3778; Simamba NMZB 3450-1.

Malawi: Cape McLear (Boulenger, 1891); Lake Malawi (Boulenger, 1891); Chitipa = Fort Hill (Boulenger, 1897).

Mozambique: Alves de Lima NMZB-UM 27001; Boroma (Boettger, 1898); Canganetole CM 40444-8; NMZB-UM 29120; Maforga NMZB-UM 7110; Malanguene NMZB 29094; Matchova JPT 1346; 1376; NMZB-UM 28917; Metambanhe NMZB-UM 9314; Miquia NMZB-UM 30663-4; Morera JPT –; Muabsa JPT –; Rios de Sena (Günther, 1864); Tec-Tec NMZB-UM 29130; Xiluvo NMZB-UM 7151, 7244; Zinave NMZB-UM 30662; JPT 1092-3, 1193.

Tanzania: Kitungulu (Loveridge, 1933); Liwale FMNH 81672-4; NMZB 151, 186, 206-7, 539(2); Mahenge NMZB-UM 6564-5; Nachingwea FMNH 78238-42; Rukwa Valley (Vesey-FitzGerald, 1958).

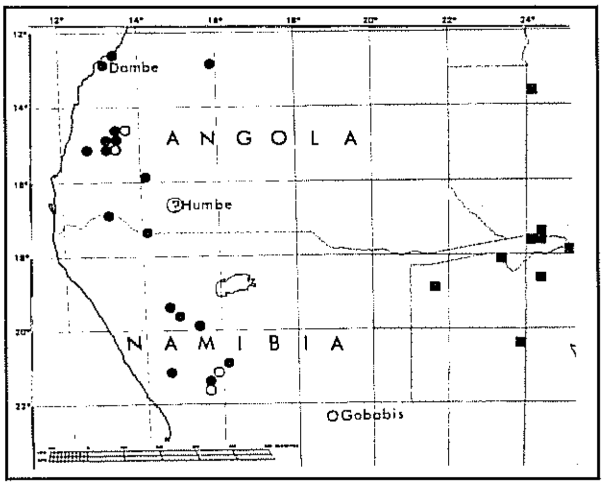

FIGURE 10: Distribution of *Hemirha-gerrhis viperina* (circles) and adjacent records of *Hermirhagerrhis nototaenia* (squares), by quarter degree squares.

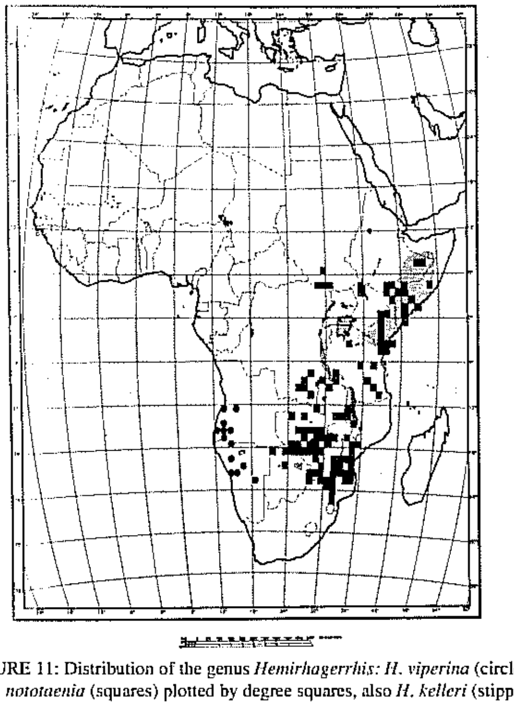

FIGURE 11: Distribution of the genus *Hemirhagerrhis*: *H. viperina* (circles) and *H. nototaenia* (squares) plotted by degree squares, also *H. kelleri* (stippled).

KEY TO THE GENUS *HEMIRHAGERRHIS*

1a. Dorsum with a broad black-bordered vertebral band; ventrum with paired brown longitudinal lines; ventrals 144-155 .... *H. kelleri*

1b. Dorsum without a broad black-bordered vertebral band; ventrum with dark speckling; ventrals 153-183 2

2a. Ventrum paler than dorsum; subcaudals 52-66; rupicolous .... *H. viperina*

2b. Ventrum dark grey like dorsum; subcaudals 68-105; semi-arboreal .... *H. nototaenia*

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I am grateful to Prof. G. Sacarrão for granting facilities to study material in the Museu Bocage in 1968, and to the following for ready assistance with loan material: W.D. Haacke and Ms S. Ritter (TMP), Ms E. Griffin (SMWN), C. McCarthy (BMNH), A.E. Zammit (AMNH), R.C. Drewes (CAS), M.I. Cherry (SAM). For providing the excellent colour photographs I am indebted to Wulf Haacke (Figs 4-6), Mike Griffin (Fig. 7), John Visser (Fig. 8) and the late Paul Coates Palgrave (Fig. 9). Garth Underwood provided tooth counts for a *Hemirhagerrhis viperina* during an earlier study of Psammophine dentition. I also thank Mike Griffin for donating a specimen of *Hemirhagerrhis viperina* to the Bulawayo collection.

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A new species of *Coluber* from northern Namibia (Reptilia: Serpentes)

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ABSTRACT

A new species of *Coluber* (*sensu lato*) is described from near the Cunene River in northern Namibia. The genus has not previously been recorded south of Kenya. This snake appears to be most closely related to *C. florulentus*, which occurs 3 000 km to the north, but it differs in its strongly-banded pattern, suggesting mimicry of the Zebra Spitting Cobra *Naja nigricollis nigricincta*.

INTRODUCTION

The polyphyletic genus *Coluber* (s.l.) presently comprises about 34 species (Schätti & Lanza, 1989) distributed throughout the Nearctic, Palearctic and northern Afrotropical regions. The Old World taxa will probably have to be assigned to several genera, but phyletic analyses of these groups have not yet been completed (Schätti 1986). A single representative *Coluber smithi* (Boulenger), is found south of the equator in southernmost Kenya and probably adjacent Tanzania (Schätti 1988).

A single damaged male *Coluber* found in northern Namibia in 1991 is described below as a new species. Its discovery provides further evidence for the transient arid corridor linking the Horn of Africa with the South-West Arid (Balinsky 1962: Fig. 1). The dik-dik (*Madoqua kirkii*) and gemsbok (*Oryx gazella*) show this disjunct distribution particularly well (Smithers 1983).

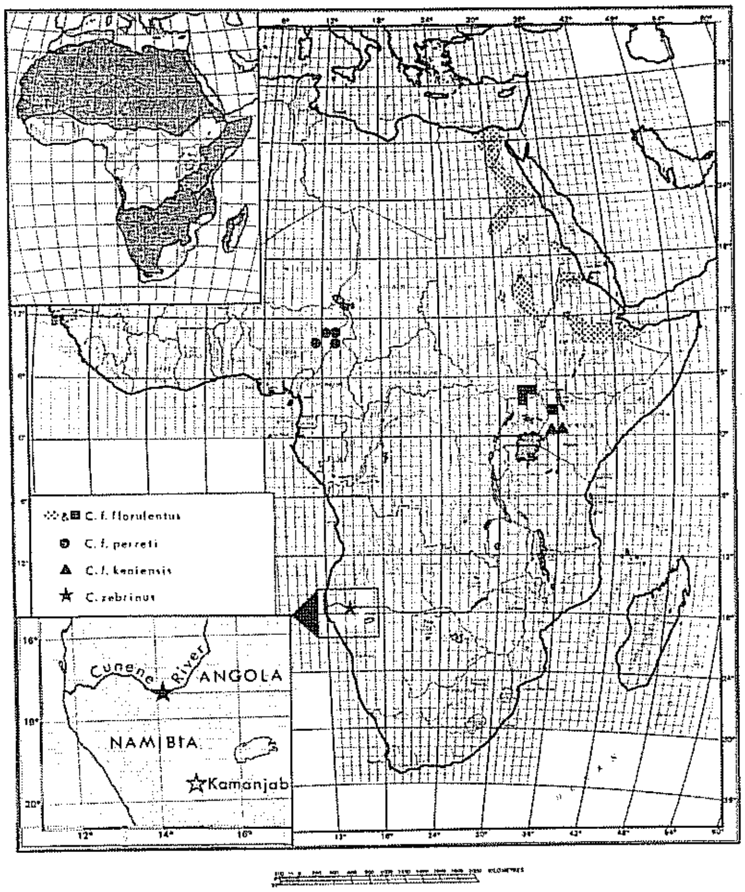


FIGURE 1: Distribution of *Coluber zebrinus* in relation to that of *C. florulentus*. Upper insert (shaded): The 'arid corridor', the areas in which the rainfall is less than 10 mm per month in at least three consecutive months (from Balinsky 1962).

COLUBER ZEBRINUS sp. nov. (Figs 2 & 3)

Holotype: a male, SMWN (= National Museum of Namibia, Windhoek) R. 8046, from near the Cunene River, at Ruacana, western Owamboland, Namibia (17°25'S, 14°10'E). Collected dead on road by M. Lindeque and M. Griffin, 10 April 1991.

Etymology: Named for the zebra striping on the dorsum.

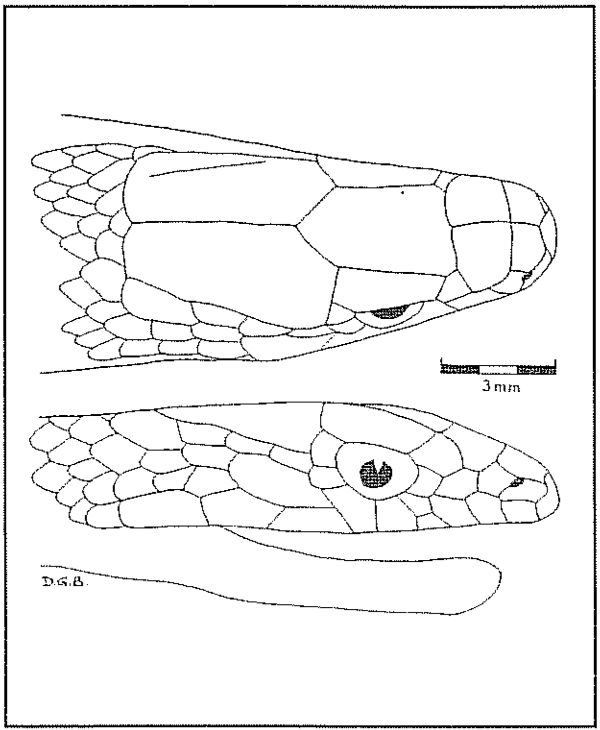


FIGURE 2: *Coluber zebrinus* sp. nov. (holotype). Dorsal and lateral views of head.

Diagnosis: A species of Coluber with 21 scale rows on the neck, 23 at midbody and 17 before the vent, the increase and reductions all lateral; ventrals approx. 195, subcaudals 90.

Description of the holotype: Ventrals approx. 195 (neck region damaged), paired subcaudals 90; anal scute divided. Nine supralabials, fifth and sixth entering orbit, one anterior subocular above fourth and anterior part of fifth supralabials, smaller than loreal shield. Two preoculars and two postoculars, upper one larger. A single large lower anterior temporal shield above 7th and 8th supralabials, two upper anterior temporals, three posterior temporals (Fig. 2). Dorsal scales with two apical pits, in 21 rows anteriorly (but neck damaged), increasing to 23 rows at the level of the 37th (right) and 39th (left) ventral by the division of row 5, reducing caudad to 17 rows by means of three lateral reductions including rows 5 + 6 = 5 at the level of the 119th ventral, 3 + 4 = 3 (126) and 4 + 5 = 4 (174/175). Maxillary with 17 + 2 teeth separated by a diastema. Snout-vent length 290 mm, tail 95 mm.

Pale grey above, becoming white laterally and ventrally, with irregular broad, dark crossbands which seem to be derived from the fusion of paravertebral rows of black blotches, which have in some cases fused again with lateral series of irregular black vertical bars or two rows of lateral spots; both anteriorly and posteriorly the dorsal crossbars are not aligned with the lateral vertical bars (Fig. 3). These dorsal markings fade out at the base of the tail. Snout yellowish, top of head uniform grey-brown, labials yellowish, with a black patch on the fifth supralabial just below the eye. Ventrum uniform white, except for irregular black spots laterally, in some cases these are linked to the lateral black bars; subcaudals white with some fine grey stippling laterally.

DISCUSSION

This new species may be most closely related to *C. florulentus* Geoffroy, the nearest populations being *C. f. perreti* in north-western Nigeria and northern Cameroon, *C. f. florulentus* in southern Sudan and north-western Kenya and *C. f. keniensis* in western Kenya

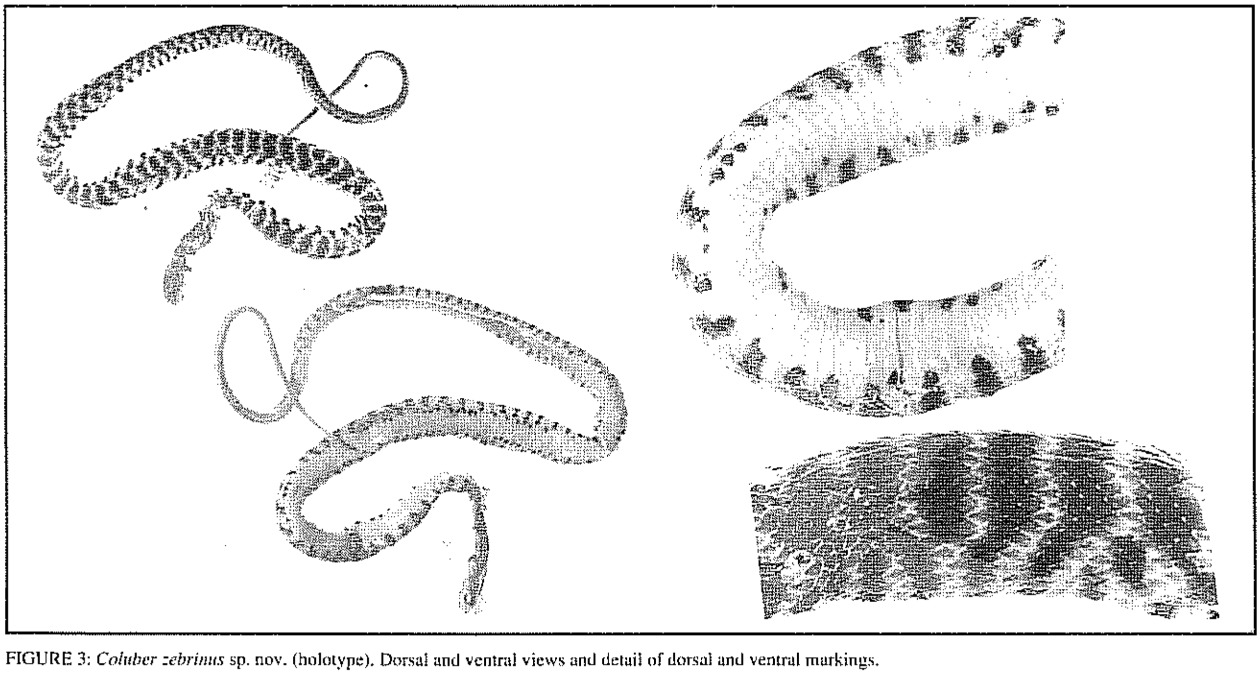


FIGURE 3: *Coluber zebrinus* sp. nov. (holotype). Dorsal and ventral views and detail of dorsal and ventral markings.

(Schätti 1988). A single large lower temporal shield and a divided preocular are found in *C. zebrinus* and *C. florulentus*. However, the latter species has one lateral and at least two paravertebral reductions, whereas in *C. zebrinus* all fusions are lateral (rows 3 to 6). *C. florulentus* differs from *C. zebrinus* in having dark head markings and the dorsal and lateral rows of dark spots are discrete and usually staggered, so that there is no fusion. Parker (1949) noted that in "[African] mainland species of *Coluber* a pattern of distinct crossbars is associated with immaturity, the crossbands tending to be broken up or to become indistinct with increasing age. In the absence of any evidence that such a distinctive livery is a special adaption for the young, it is reasonable to regard the presence of the pattern as primitive and its loss as secondary". The banded pattern of *C. zebrinus* suggests that it is a Batesian mimic of the sympatric Zebra Spitting Cobra (*Naja nigricollis nigricincta* Bogert), which is a relatively slim cobra and is often active by day.

HABITAT

The type specimen was killed at 09h00 on stony ground (dolomite) with ,thick scrub *Colophospermum* and *Terminalia*, several kilometres from the Cunene River at Ruacana (Fig. 4).

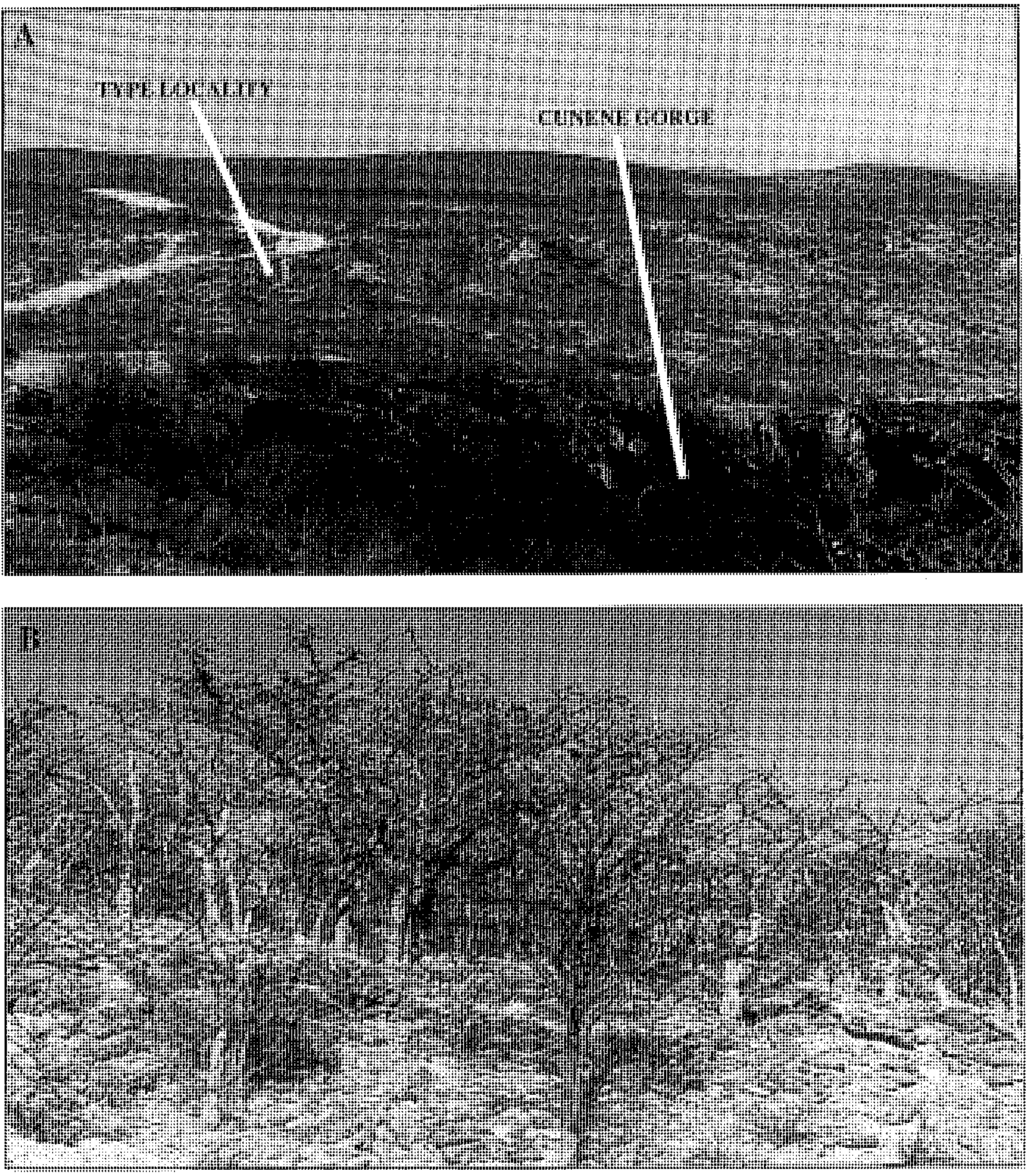
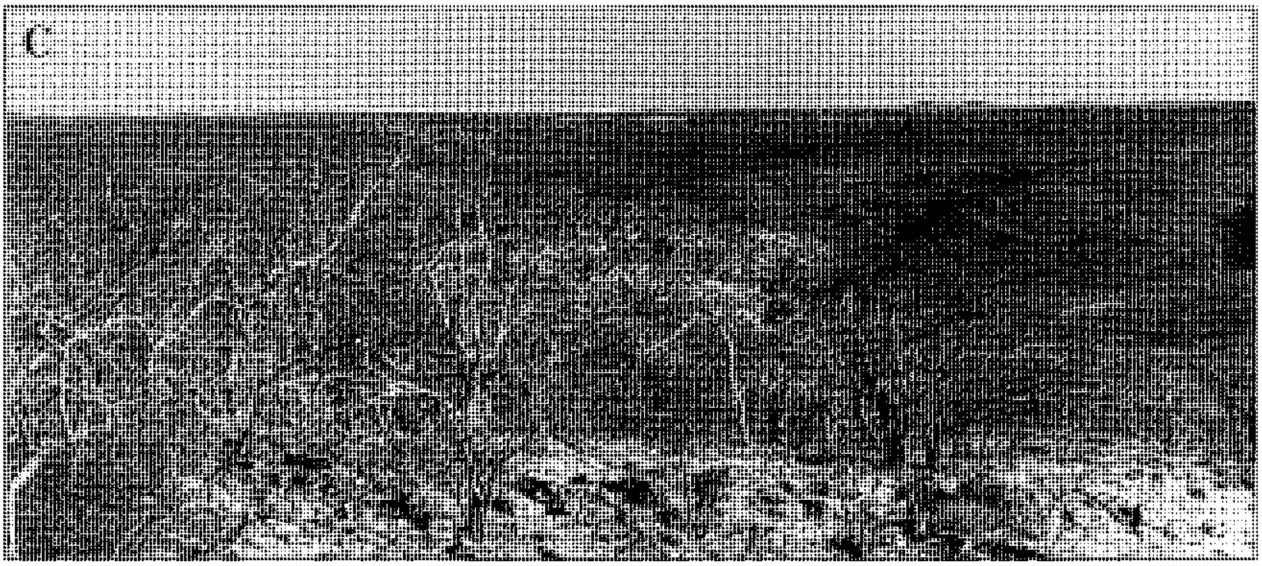


FIGURE 4: Habitat of *Coluber zebrinus* just south of the Cunene Gorge.

FIGURE 4: *continued*



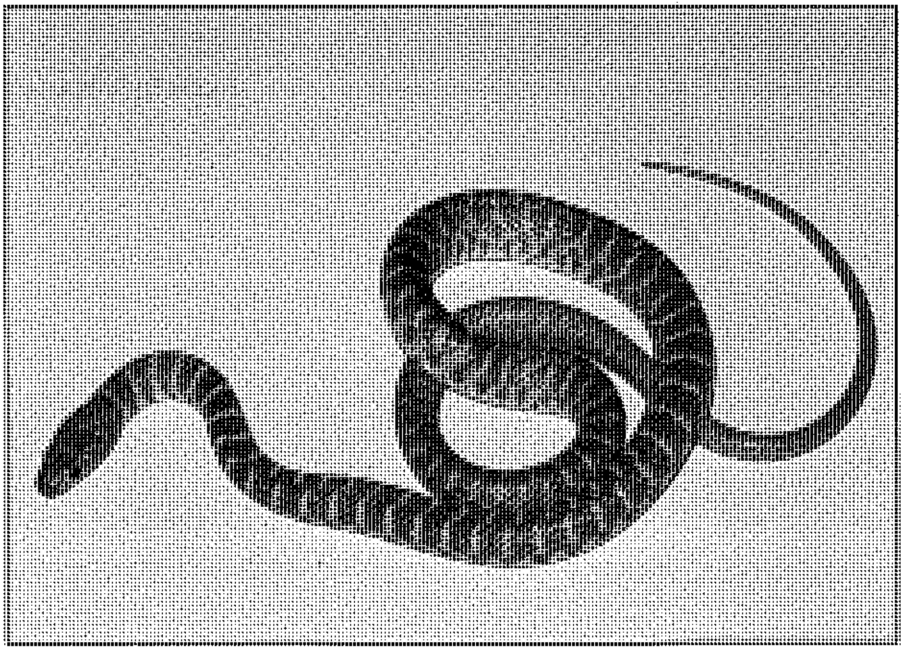


FIGURE 5: A 65 cm live specimen of *Coluber zebrinus* from near Kamanjab, Namibia

ACKNOWLEDGEMENTS

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