

# A preliminary investigation of patterns of distribution and species richness of southern African waterbirds

A. Guillet and T.M. Crowe

FitzPatrick Institute, University of Cape Town, Cape Town

Uni- and multivariate numerical techniques are employed to describe and explain patterns of distribution and species richness for waterbirds in southern Africa south of the Cunene and Zambezi Rivers and results are compared with those found for Afrotropical and South American waterbirds. Waterbirds partition southern Africa into two avifaunal zones. Zone 1 in the east and north has a relatively high species richness, and is subdivided, roughly along the Limpopo River valley, into a northern and a southern province. Zone 2 in the drier west, has a much lower species richness. Waterbird species richness also exhibits a general east-west longitudinal gradient. The species richness is correlated with measures of geographical variation in climate and the availability of both natural and man-modified aquatic biotopes. The relatively high waterbird species richness in certain areas, which cannot be explained in terms of present-day environmental variation, might be a consequence of the areas acting as refugia during dry climatic phases. Difficulties encountered in broad-scale biogeographical syntheses are discussed, and possible approaches to overcome them are outlined.

*S. Afr. J. Wildl. Res.* 1986, 16: 65–81

Enkelvoudige en meervoudige numeriese tegnieke word gebruik om verspreidings- en spesierikheidspatrone vir watervoëls in suidelike Afrika, suid van die Kunene- en Zambezi-riviere te beskryf en te verduidelik en resultate word vergelyk met dié gevind vir Afrotropiese en Suid-Amerikaanse watervoëls. Watervoëls verdeel suidelike Afrika in twee voëlsones. Sone 1, in die ooste en noorde het 'n betreklik hoë spesierikheid en word ongeveer langs die Limpoporiviervallei in 'n noordelike en suidelike provinsie verdeel. Sone 2, in die droër weste, het 'n veel kleiner spesierikheid. Die spesierikheid van watervoëls vertoon ook 'n algemene oos-wes longitudinale gradiënt. Die spesierikheid word gekorreleer met geografiese variasies van klimaat en die beskikbaarheid van beide natuurlike en mens-gewysigde waterbiotope. Die betreklik hoë spesierikheid van watervoëls van sekere gebiede, wat nie in terme van huidige omgewingsvariasie verduidelik kan word nie, kan miskien 'n gevolg wees van die gebruik van die gebiede as toevlugoorde tydens droë klimaatfasies. Moeilikhede ondervind met omvattende biogeografiese samevattinge word bespreek en moontlike benaderings om hulle te bowe te kom word uitgewys.

*S.-Afr. Tydskr. Natuurnav.* 1986, 16: 65–81

This paper constitutes part of the 25th anniversary commemoration of the Percy FitzPatrick Institute of African Ornithology and is dedicated to the memory of the late Dr J.M. Winterbottom, the Institute's first director.

A. Guillet\* and T.M. Crowe

FitzPatrick Institute, University of Cape Town, Rondebosch, 7700 Republic of South Africa

Received 23 September 1985; accepted 1 March 1986

## Introduction

With relatively few noteworthy exceptions (Moreau 1966; Winterbottom 1967, 1972; Reichholf 1975; Siegfried 1981), studies of continental and subcontinental patterns of avian distribution and/or species richness in Africa (e.g. Chapin 1923; Rabinovich & Rapoport 1975; Rapoport & Ezcurra 1979; Diamond & Hamilton 1980; Crowe & Crowe 1982) have focused on birds from non-aquatic habitats. In another paper (Guillet & Crowe 1985), we have investigated broad distribution/diversity patterns for waterbirds on an Afrotropical scale. The primary differences between African aquatic and non-aquatic birds are that the aquatic bird fauna partitions Africa into fewer zoogeographic zones (Figure 1), and waterbird species richness (number of species) exhibits a longitudinal, not a latitudinal, gradient (Figure 2).

In this paper we examine patterns of waterbird distribution and species richness in southern Africa south of the Cunene-Zambezi Rivers (Figure 3) in more detail. In comparison with our Afrotropical study, we use a much denser grid (250 quadrats, Figure 3) and include more varied and recent distributional information. Relative abundance of species is also estimated more accurately, and Palearctic migrants, which form an important component of the southern African aquatic bird fauna (Winterbottom 1972) are included. As in Guillet & Crowe (1985), we analyse taxonomic, morphological, ecological and ethological guilds to determine whether species richness patterns, exhibited by these subsets, parallel those found for the total waterbird fauna. We employ a liberal definition of the term guild: an assemblage of species whose taxonomic, morphological, ecological or behavioural affinities require (or may have required) them to deal with similar selective pressures. We also relate geographical variation in total and guild species richness to variation in measures of natural environmental conditions. For quadrats which fall within South Africa, correlations between waterbird species richness and various measures of the availability of man-made and/or modified impoundments are analysed.

## Data base and Methods

### Data base and extraction methods

For the purpose of this study, a waterbird is taken to be any species which is dependent on non-marine aquatic biotopes for feeding and/or breeding. Waterbird distributional and natural history data were extracted from published (James 1921, 1925, 1929; Frade 1953a,b; Smithers 1964; Skead 1965; Winterbottom 1968a, 1970, 1971; Clancey 1971; Mills 1976; Penzhorn & Badenhorst 1976) and unpublished sources. The choice of species to include in our analyses was very

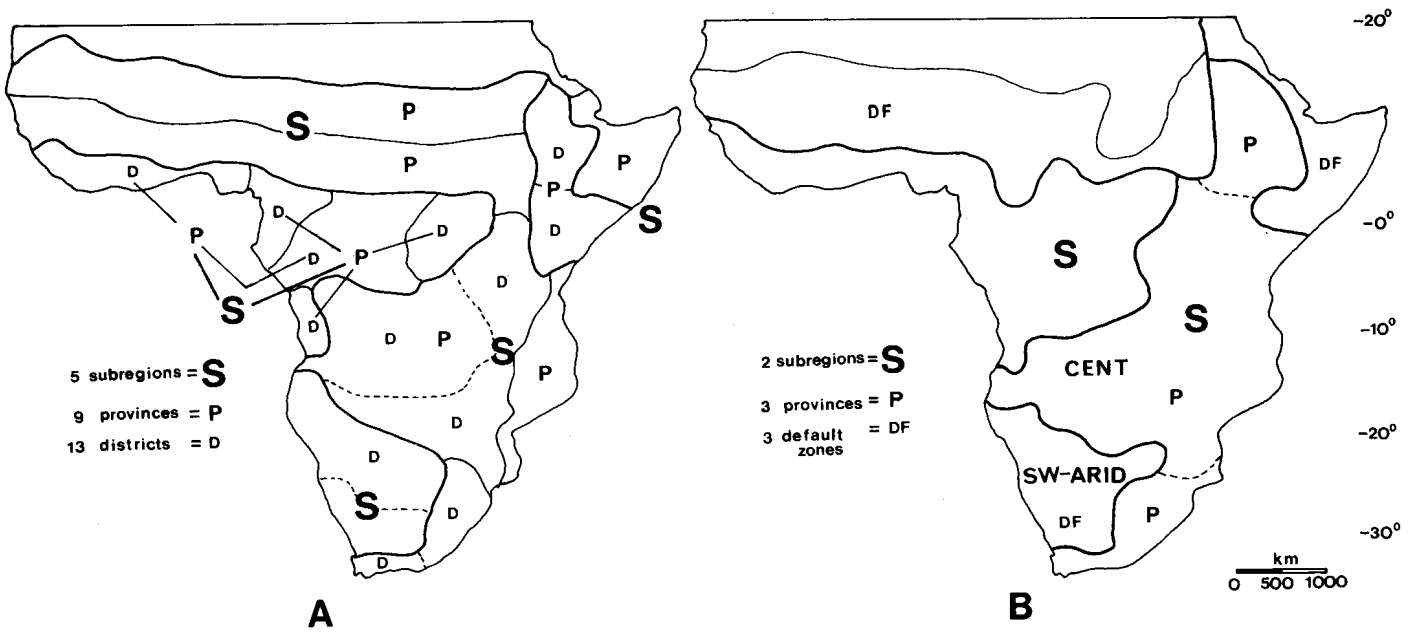


Figure 1 African avifaunal zones recognized by (A) Crowe & Crowe (1982) for passerine birds, and (B) Guillet & Crowe (1985) for waterbirds.

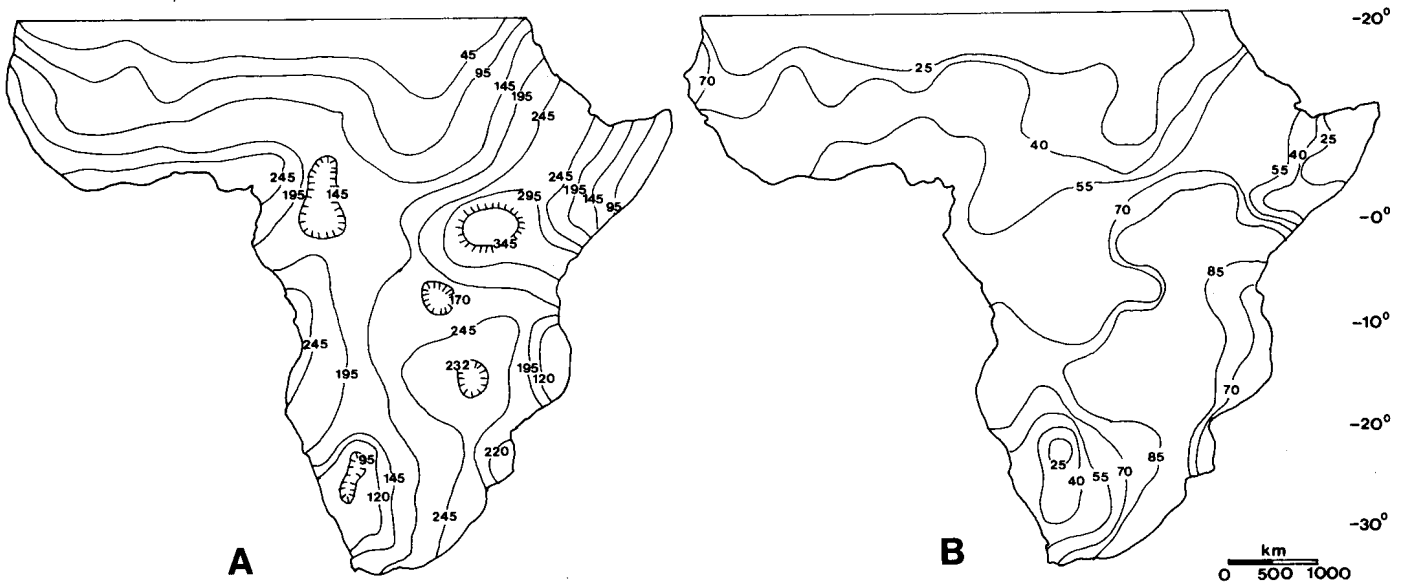


Figure 2 Geographical variation in species richness of African (A) passerine birds (after Crowe & Crowe 1982), and (B) waterbirds (after Guillet & Crowe 1985).

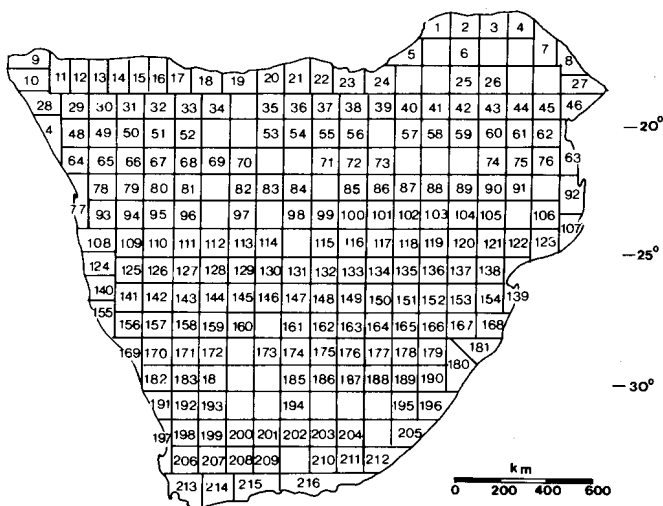


Figure 3 The grid system used to extract distribution and species richness data for southern African waterbirds. Unnumbered quadrats were not analysed.

difficult, and was ultimately a consensus of advice and information available. Nevertheless, separate analysis of 'hard core' (e.g. storks, herons and ducks) and 'borderline' guilds (e.g. weavers and warblers) should allow interpretation of our results at various levels, depending on the reader's personal criteria. Moreover, in the results and discussion sections which follow, we have refrained from identifying and explaining distribution/diversity 'patterns' which are based primarily on information from 'borderline' species.

In order to estimate both the distribution and relative abundance of the waterbird species within each of the 250 quadrats (Figure 3), each species was scored on a scale from 0 to 5: 0 = absent; 1 = rare or sparsely distributed; 2 = uncommon, but potentially widespread; 3 = common, but only in certain seasons or poorly represented habitats; 4 = common year-round, but not widespread; 5 = common and widespread year-round. For some relatively poorly studied areas, e.g. in Namibia and Botswana, we relied chiefly on reports from local ornithologists. Thus, our scoring system

**Table 1** Species richness values, codes, abbreviations, mobility percentages, and definitions for southern African waterbird taxonomic, morphological, ethological and ecological guilds. See Appendix 1 for more information on individual species

Guild types	No. of species	Codes in Appendix 1	Guild abbreviations	% in mobility classes 2-3	Guild names/ definitions	
Taxonomic (TAX)	18	1	T-AN	78	Ardeidae	
	7	2	T-CI	100	Ciconiidae	
	18	3	T-AN	89	Anatidae	
	4	4	T-AC	50	Accipitridae	
	14	5	T-RA	57	Rallidae	
	9	6	T-CH	55	Charadriidae	
	16	7	T-SC	94	Scolopacidae	
	7	8	T-LA	85	Laridae	
	5	9	T-AL	60	Alcedinidae	
	13	10	T-SY	23	Sylviidae	
	6	11	T-MO	49	Motacillidae	
	16	12	T-PL	44	Ploceidae	
	Body mass (BMS)	59	1	M-1	49	< 80 g
		53	2	M-2	70	> 80 < 400 g
43		3	M-3	79	> 400 < 2000 g	
15		4	M-4	86	> 2000 g	
Trophic (TPH)	43	1	D-V	67	Predominantly vertebrates	
	93	2	D-I	66	Prevalently invertebrates	
	34	3	D-H	67	Mixed feeders with substantial vegetable component	
Migratory status (MST)	137	1	S-R	59	Residents	
	33	2	S-M	100	Migrants	
Foraging mode (FOR)	17	1	F-S	94	Surface swimmers	
	12	2	F-D	83	Divers	
	78	3	F-TP	78	Peckers	
	13	4	F-DH	54	Plunge divers	
					Species using a water induced habitat without necessarily 'getting feet wet':	
	20	5	F-P	40	- Predominantly plant eaters	
30	6	F-A	37	- Predominantly animal eaters		
All species	170			67		

can be criticized as being subjective. However, we feel that it is superior to a scheme based only on the presence or absence of species, since it takes into account our present knowledge of the dynamic nature of waterbird dispersion (e.g. Gentilli & Bekle 1983). To minimize bias owing to quadrats with inadequate information, after careful scrutiny of preliminary analyses, we discarded data for 34 quadrats (those unnumbered in Figure 3) which appeared to have been very poorly sampled (i.e. few sources of data and low species richness when compared with adjacent quadrats with similar aquatic biotopes). We analysed resident and migrant waterbird guilds separately. The remaining guilds were divided in much the same manner as in Guillet & Crowe (1985), although we

**Table 2** Measures of quadrat environmental conditions (and their abbreviations) used in correlation and regression analyses of waterbird species diversity and environmental variation

Measurements	Abbreviations	Definitions and source
Mean annual rainfall	RF	mean of 10 approximately uniformly spaced measurements (Thorntwaite 1962)
Mean maximum temperature	TMAX	mean of 10 approximately uniformly spaced measurements (Jackson 1961)
Mean elevation	XALT	mean of 10 approximately uniformly spaced measurements (Clark 1967)
Elevation range	RALT	the largest minus the smallest elevation (Clark 1967)
Permanent river number	PRN	digitized from Bartholomew (1973)
Permanent river length	PRL	digitized from Bartholomew (1973)
Non-permanent rivers/wadis number	NNPR	digitized from Bartholomew (1973)
Non-permanent rivers/wadis length	LNPR	digitized from Bartholomew (1973)
Lakes number	LN	digitized from Bartholomew (1973)
Lakes perimeter	LP	digitized from Bartholomew (1973)
Lakes area	LA	digitized from Bartholomew (1973)
Swamps/marshes number	MN	digitized from Bartholomew (1973)
Swamps/marshes perimeter	MP	digitized from Bartholomew (1973)
Swamps/marshes area	MA	digitized from Bartholomew (1973)
Mud flats number	NMF	digitized from Bartholomew (1973)
Mud flats perimeter	PMF	digitized from Bartholomew (1973)
Mud flats area	AMF	digitized from Bartholomew (1973)

tend to have more guilds per guild type in this paper (Table 1). The waterbird species considered, their migrant/resident status, and guild membership are listed in Appendix 1.

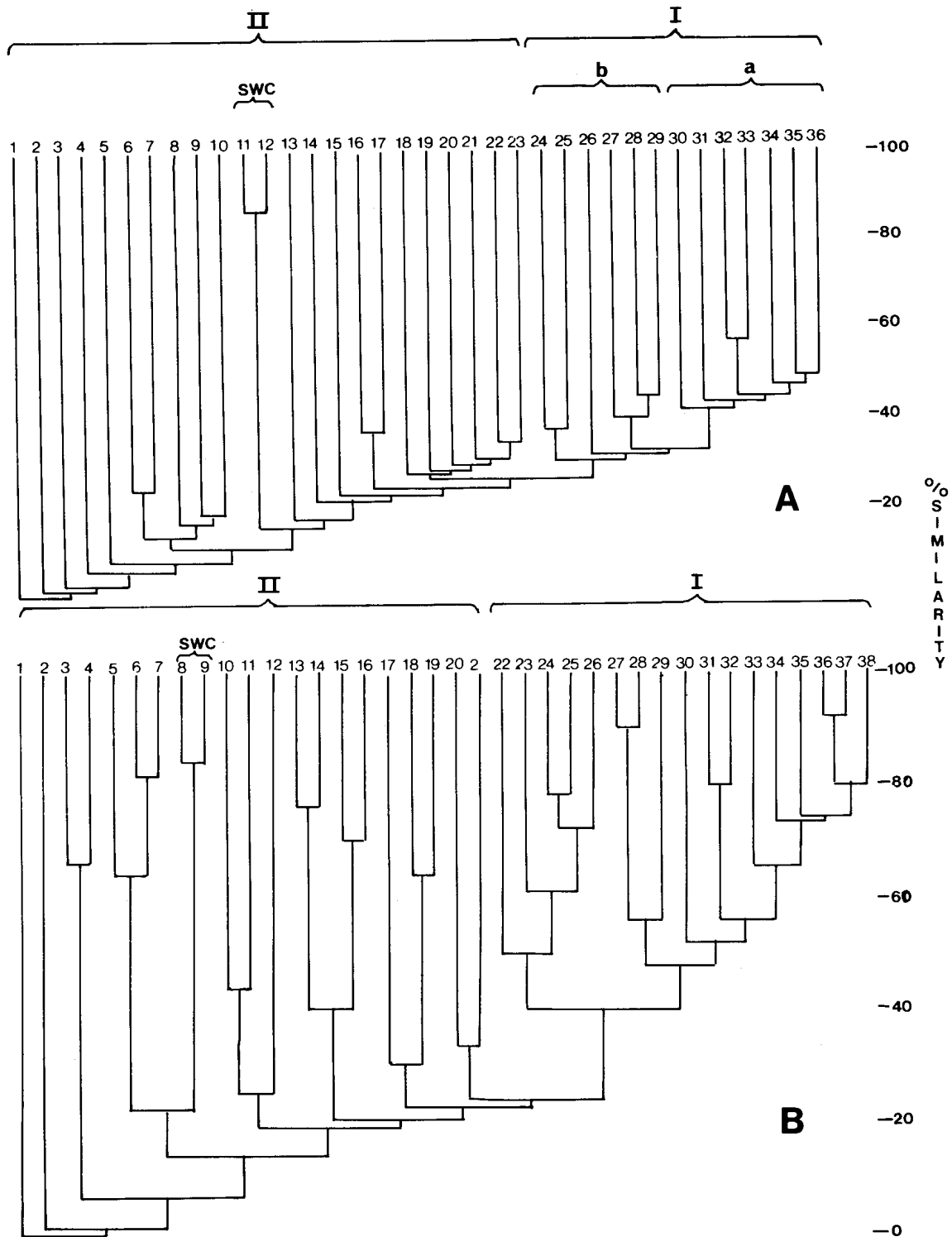
### Numerical methods

Patterns of waterbird distribution were identified by means of cluster analysis (Anderberg 1973; Field & McFarlane 1968), using the Bray & Curtis (1957) similarity measure and a group-average sorting method (Lance & Williams 1967). Species which characterize the waterbird faunal zones indicated by cluster analysis were identified by means of information statistic tests (Field 1969). We define a characteristic species as one generally confined to (at least two-thirds of its recorded occurrences), and widespread within, an avifaunal zone, and the limits of whose range help to delineate the boundaries of the zone. The results of the cluster analysis and information statistic tests were then combined into a cartographic representation, using the distributional limits of characteristic species

to delineate the boundaries of waterbird avifaunal zones.

Geographical variation in resident and migrant waterbird species richness per quadrat was depicted as contour maps drawn with the aid of SACLANT (Diederiks 1979), a computer program which fits an approximate contour surface to a grid of data points (in this case, quadrat species richness values), using least squares polynomial analysis. Correlation, regression and stepwise multiple regression programs in the BMDP Series (Dixon 1981) were used to identify environmental factors which may influence waterbird guild species richness. The environmental variables included in these analyses are listed in Table 2. Length of rivers, and the perimeter and surface

areas of lakes, swamps and mud flats within each quadrat were estimated from equal area projection maps (1:5 000 000 scale) employing the digitization methods described in detail in Guillet & Crowe (1985). If waterbird species richness is largely a function of the environment, paleo-ecological events (e.g. wet-dry climatic cycles and attendant shifts in the dispersion of biotopes) may not have influenced southern African waterbird species richness to the same degree that they appear to have influenced terrestrial and waterbird species richness on an Afrotropical scale (Diamond & Hamilton 1980; Crowe & Crowe 1982; Guillet & Crowe 1985). If, however, regression analysis fails to explain most of the variance in waterbird



**Figure 4** Southern African avifaunal zones as suggested by cluster analyses of 216 quadrats according to (A) 136 resident and (B) 33 migrant waterbird species. See Appendix 2 for list of quadrats which comprise dendrogram terminal points. Codes as in Figure 5; SWC = south-western Cape quadrats.

species richness, we feel that consequences of geographically localized ecological synergies of ancient, and/or recent origin (e.g. habitat modifications by modern man), may have influenced southern African waterbird species richness in addition to the effects of present-day 'natural' environment.

In our studies of the possible effects of impoundments (ranging in size from small farm dams to large man-made lakes) on waterbird species richness, a series of correlation and bivariate regression analyses were done for quadrats which fall within South Africa (ca. 50% of the total study area). Impoundment information was extracted from a register of dams compiled by the South African Department of Water Affairs. Variables studied included impoundment density (number per quadrat), and quadrat mean, range and/or total values for: impoundment catchment area, depth, volume and surface area. Multiple regression analysis could not be employed in this aspect of our research, because some of the quadrats had missing data for at least one of the 'impoundment' variables. Since impoundment density in quadrats 206 and 213 in the south-western Cape Province was much higher than that for the remaining quadrats, thereby potentially biasing regression results, we excluded information from these quadrats from subsequent analyses. A preliminary regression analysis of total waterbird species richness against impoundment density indicated that the relatively xeric quadrats (with less than 400 mm of annual rainfall) which occur mainly in western South Africa have disproportionately lower waterbird species richness than those with relatively high rainfall for a given number of dams. Therefore, we analysed the relatively xeric (< 400 mm rainfall) and mesic (> 400 mm rainfall) quadrats separately in correlation and regression analyses.

## Results

### Distribution

As in our Afrotropical-scale study (Guillet & Crowe 1985), the cluster analysis and information statistic test results (Figure 4 and Appendixes 1 and 2) suggest that waterbirds partition southern Africa into two avifaunal zones, one in the east and north, the other in the west (Figures 1b and 5). The western zone is a 'default' zone, delimited mainly by the range limits of species which do not occur within its boundaries. In fact, the southern African waterbird fauna, with only two endemic species (the South African shelduck *Tadorna cana* and the Cape shoveller *Anas smithii*), is essentially a depauperate version of that found to the north.

Despite their broad correspondence, there are several interesting differences between the distributional results of this study and those of Guillet & Crowe (1985). First, in the analysis of resident birds (the guild most comparable to the results of our Afrotropical waterbird study), certain quadrats which are geographically in the western zone, appear to be 'enclaves' of the east-north zone (Figure 5a). Moreover, this east-north zone is partitioned, roughly along the Limpopo River valley, into two contiguous subzones. The boundary between these subzones corresponds to the southern boundary of the Central Province in our Afrotropical-scale analysis (CENT in Figure 1b), although it falls somewhat farther south. In the analysis of migrants (Figure 5b), the east-north zone is bisected by a 'corridor' of west zone quadrats which extends along the Limpopo valley. Despite its fragmentation, the east-north zone in the migrant analysis also appears to penetrate farther west than in the resident analysis. Lastly, in both resident and migrant cluster analyses (Figures 4a and b), quadrats from the south-western Cape Province (Nos. 197, 206, 207, 213, 214; labelled SWC in Figure 4) form a well-

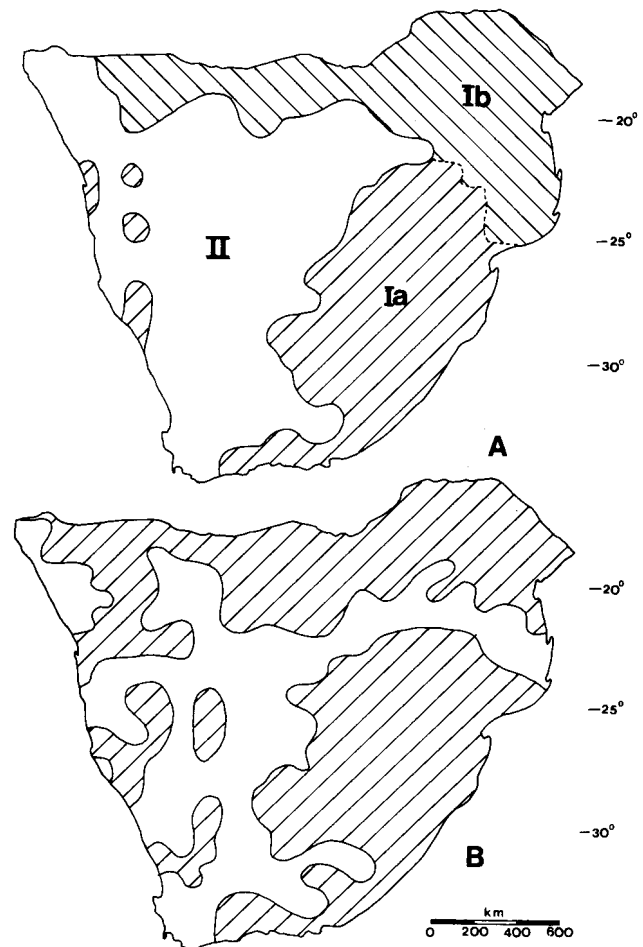


Figure 5 Southern African avifaunal zones for (A) resident and (B) migrant waterbirds as suggested by results of the cluster analyses and the distributions of characteristic species as listed in Appendix 1.

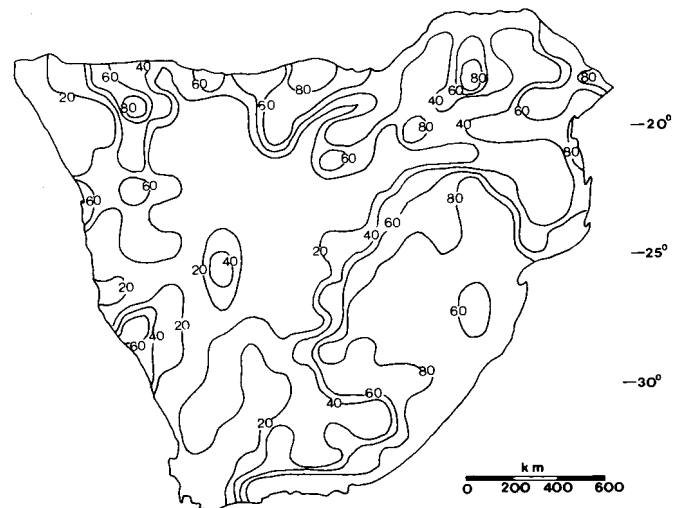


Figure 6 Geographical variation in southern African waterbird species richness.

defined cluster apparently imbedded in the west zone portion of the dendrograms.

### Species richness

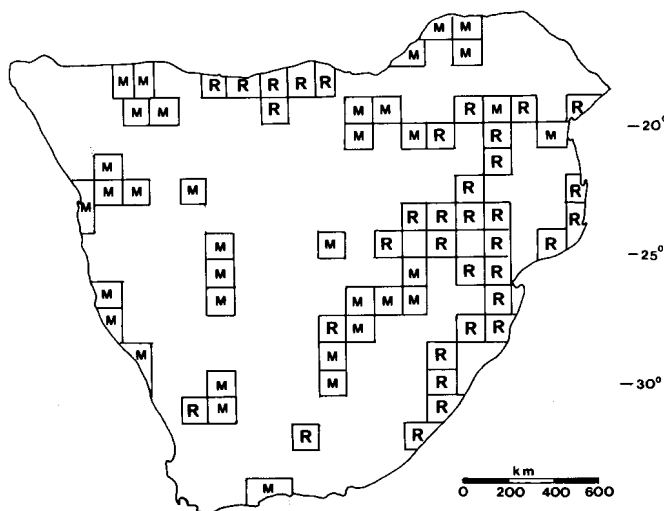
Patterns of resident and migrant waterbird species richness in southern Africa exhibit an essentially longitudinal north/east-west gradient, higher in the eastern and northern areas (Figure 6). All waterbird guild species richness measures show

significant positive correlations with longitude. Only Anatidae species richness and the species richness of some guilds dominated by Anatidae is significantly correlated with latitude (Table 3), a result consistent with our Afrotropical-scale study. Although migrant and resident species richness are strongly positively correlated ( $r=0,88$ ;  $P < 0,001$ ), reciprocal regressions of migrant and resident species richness for all quadrats, and regressions of migrant and resident species richness vs longitude for a band of quadrats between 20 and 27°30'S, reveal several subtle patterns. In the first two analyses, quadrats in which migrant species richness is over-represented, i.e. large positive residuals at least one standard deviation above the regression line, are largely confined to western southern Africa (quadrats marked with an 'M' in Figure 7), whereas those in which residents are over-represented are mainly in the east (quadrats marked with 'R' in Figure 7). Results of regression analyses of residents and migrants vs longitude, are summarized in Figures 8a and b, and show that the resident species richness curve is much steeper than the migrant species richness curve. This suggests that the species 'subtraction' effect for resident birds, as one moves west, is more severe. Indeed, the negative slope of a similar regression of the resident/migrant ratio (Figure 8c) supports this interpretation.

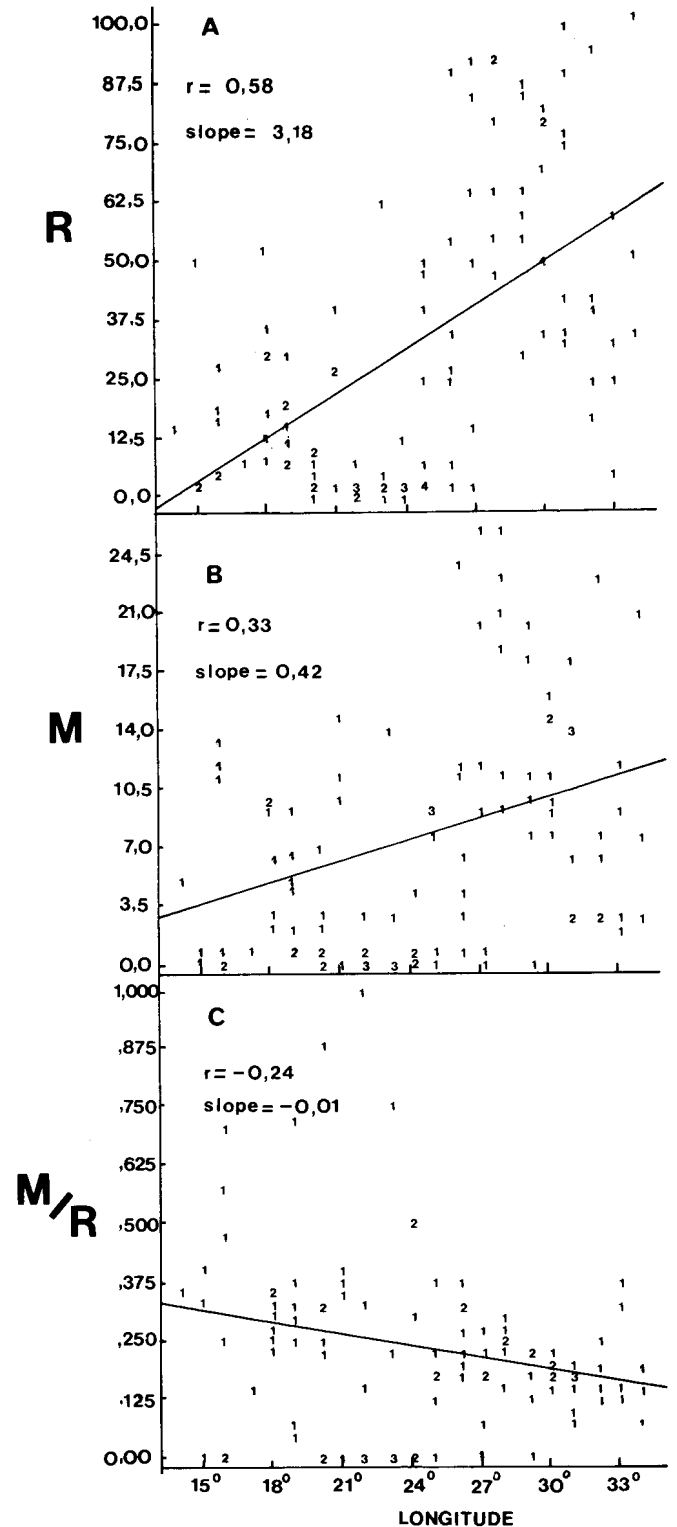
Results of the correlation and multiple regression analyses of resident, migrant and guild species richness for waterbirds against measures of environmental variation are summarized in Tables 3 and 4. The dominant environmental variables in these analyses are mean annual rainfall (RF) and the availability of aquatic habitat, especially the length (LPR) and number (NPR) of permanent rivers. Moreover, among the regression analyses, there are trends in total  $R^2$  which seem to be related to mobility, size and foraging mode. Resident (S-R), smaller body mass (M-1, M-2), herbivore (D-H) and 'dry-feet' foraging (F-P, F-A) guild species richness tends to be better predicted by environmental variation than that for the migrant (S-M), larger body mass (M-3, M-4), invertebrate feeder (D-I) and 'wet-feet' foraging (F-D, F-S) guilds.

**Impoundments**

The correlation and bivariate regression analyses of impoundment variables against measures of waterbird species richness



**Figure 7** Geographical distribution of quadrats 'overrepresented' (at least one standard deviation above the regression line) in resident (R) and migrant (M) waterbird species richness, as suggested by the residual plot of reciprocal resident-migrant regression analyses.



**Figure 8** Results of regression analyses of measures of southern African waterbird species richness versus longitude: (A) residents (R), (B) migrants (M), and (C) migrant/resident ratio (M/R).

(Table 5) show several consistent patterns. First, within the relatively xeric, western quadrats, impoundment density (ID) is the only impoundment variable significantly correlated with species richness. Second, within the mesic quadrats, ID is not correlated with the species richness of any guilds, and some guilds [e.g. Anatidae (T-AN), Scolopacidae (T-SC), Laridae (T-LA)], tend to be correlated with measures of impoundment area, and others [e.g. Accipitridae (T-AC), Charadriidae (T-CH)] with volume measures or volume plus area.



**Table 4** Significant ( $P < 0,05$ ) results of stepwise multiple regression analyses between waterbird guild species richness and environmental diversity measures. Guilds are ranked according to their total  $R^2$ , environmental variables in ascending step order followed by the contribution to total  $R^2$  in parentheses (see Tables 1 and 2 for abbreviations)

Total $R^2$	Guild	Entering variables and their contribution to total $R^2$
0,59	T-PL:	LPR (0,49); RF (0,07); NL (0,02); RALT (0,01)
0,51	T-AL:	LPR (0,49); RF (0,02)
0,48	T-SY:	NPR (0,40); RF (0,06); AS (0,02)
0,42	T-MO:	RF (0,33); LPR (0,07); RALT (0,02)
0,39	T-AR:	LPR (0,33); RF (0,06)
0,37	T-AC:	RF (0,31); NPR (0,04); PL (0,02)
0,33	T-RA:	RF (0,27); NPR (0,04); XALT (0,02)
0,31	T-AN:	NPR (0,27); XALT (0,04)
0,29	T-CH:	LPR (0,24); PL (0,03); PMF (0,02)
0,27	T-SC:	LPR (0,20); RF (0,04); NMF (0,03)
0,26	T-LA:	RF (0,16); PL (0,04); PS (0,92); LPR (0,03)
0,19	T-CI:	LPR (0,17); RF (0,02)
0,52	M-1:	LPR (0,49); RF (0,06); NL (0,01)
0,43	M-2:	RF (0,36); LPR (0,07)
0,38	M-3:	LPR (0,31); RF (0,04); XALT (0,01); NL (0,02)
0,35	M-4:	LPR (0,27); PMF (0,05); RF (0,03)
0,52	D-H:	LPR (0,42); RF (0,07); NL (0,01); XALT (0,01); AS (0,01)
0,42	D-V:	LPR (0,36); RF (0,06)
0,41	D-I:	LPR (0,35); RF (0,06)
0,58	F-P:	LPR (0,45); RF (0,09); NL (0,02); AS (0,01); RALT (0,01)
0,50	F-A:	RF (0,39); NPR (0,38); AS (0,03)
0,41	F-DH:	LPR (0,36); RF (0,04); PL (0,01)
0,40	F-TP:	LPR (0,33); RF (0,06); PMF (0,01)
0,33	F-D:	LPR (0,26); RF (0,03); XALT (0,02); NL (0,02)
0,31	F-S:	NPR (0,27); XALT (0,03); PMF (0,01)
0,48	S-R:	LPR (0,41); RF (0,07)
0,33	S-M:	LPR (0,25); RF (0,04); NMF (0,02); PL (0,02)

**Table 5** Summary of significant results of correlation analyses between quadrat guild species richness and measures of impoundment availability

Guilds <sup>a</sup>	Xeric quadrats			Mesic quadrats		
	Impoundment variable(s)	r	df	Impoundment variable(s)	r	df
Residents	* <sup>b</sup> ID	0,29	50	* ITVOL <sup>c</sup>	0,38	32
				* IXVOL	0,40	32
				* IRVOL	0,38	32
Migrants				** ITAR	0,45	35
				* IXAR	0,38	32
				* IRAR	0,40	32
Anatidae	* ID	0,36	50	* ITAR	0,36	35
				* IRAR	0,34	32
Rallidae	* ID	0,32	50	* ITAR	0,35	35
				* IXAR	0,35	32
				* IRAR	0,35	32
Charadriidae				* ITVOL	0,41	32
				** IXVOL	0,48	32
				* IRVOL	0,46	32
				** ITAR	0,44	35
Scolopacidae				** IXAR	0,53	32
				** IRAR	0,51	32

**Table 5** Continued

Guilds <sup>a</sup>	Xeric quadrats			Mesic quadrats		
	Impoundment variable(s)	r	df	Impoundment variable(s)	r	df
Alcedinidae	* ID	0,29	50			
Accipitridae				* ITVOL	0,37	32
				* IXVOL	0,34	32
				* ITAR	0,34	35
Laridae				** ITAR	0,45	35
				** IXAR	0,46	32
				** IRAR	0,47	32
Diet: vertebrates				* ITVOL	0,37	32
				* IXVOL	0,38	32
				* IRVOL	0,37	32
				* ITAR	0,34	35
Diet: invertebrates				* IXVOL	0,35	32
				* IRVOL	0,34	32
Diet: mixed with veg. component				* ITVOL	0,35	32
				* IXVOL	0,39	32
Body-mass 1				* IRVOL	0,36	32
				* ITVOL	0,41	32
				* IXVOL	0,43	32
Body-mass 3	* ID	0,33	50	* IRVOL	0,40	32
				** ITAR	0,45	35
				* IXAR	0,40	32
Body-mass 4				* IRAR	0,42	32
				* ITVOL	0,42	32
				* IXVOL	0,41	32
Surface swimmers				* IRVOL	0,39	32
	* ID	0,34	50	* IXAR	0,40	32
				* IRAR	0,41	32
Peckers				* IRVOL	0,35	32
				* ITAR	0,34	35
				* IXAR	0,34	32
Plunge divers	* ID	0,28	50	* ITVOL	0,41	32
				* IXVOL	0,41	32
				* IRVOL	0,41	32
				* ITAR	0,37	35
Plant eaters				* IXAR	0,36	32
				* IRAR	0,35	32
				* IXVOL	0,35	32

<sup>a</sup>See Table 1 for complete guild information.

<sup>b</sup>Significance level: \* =  $P < 0,01$ ; \*\* =  $P < 0,001$ .

<sup>c</sup>ITVOL = total impoundment volume, IXVOL = mean impoundment volume, IRVOL = range of impoundment volume, ITAR = impoundment total area, IXAR = mean impoundment area, IRAR = range of impoundment area, ID = impoundment density (number per quadrat).

Orange River estuary. These areas support populations of species whose distributions are largely confined to the east-north zone quadrats, e.g. the great crested grebe *Podiceps cristatus*, lesser flamingo *Phoeniconaias minor* and purple gallinule *Porphyrio porphyrio*.

The second difference, the southward extension to the Limpopo valley of the boundary between the two subzones which comprise the east-north zone, is, in part, due to differences in species which statistically best characterize the northern subzone as opposed to the Central District of Guillet & Crowe (1985), which emphasized the importance of species essentially endemic to the Central District. However, in the present study, species which are more widespread in Africa,



e.g. the streakybreasted flufftail *Sarothrura boehmi*, blackshouldered wattled plover *Vanellus albiceps*, and locust finch *Ortygospiza locustella*, characterize the northern subzone. Thus, this boundary shift could be an artifact of the geographical limits of our study area. However, the finer scale of this study draws attention to the importance of the Limpopo valley, as a zoogeographical barrier. Benson, Irwin & White (1962) long ago emphasized the significance of the Limpopo valley as an avian zoogeographical barrier, identifying it as a corridor of xeric habitat dominated by *Colophospermum mopane* woodland. The transition of this vegetation type into the equally xeric *Acacia* and *Commiphora* wooded steppe on the plateau of eastern Botswana is equally 'desertic' for waterbirds, and might explain the greater north-eastern penetration of the western zone in both this and our Afrotropical-scale study (SW-ARID in Figure 1b), relative to that identified by non-aquatic birds (Figure 1a).

Comparison of the distributional results for resident and migrant waterbirds, re-emphasizes the importance of the Limpopo valley. In the migrant analysis, the valley forms a west zone 'corridor' (Figure 5b), possibly an effect of the dry nature of the Limpopo valley during summer months (Harrison 1984). The geomorphology of the valley is also not conducive to the formation of large floodplains, favoured habitat of many migrant waterbirds. In fact, we suggest that the greater westward penetration of the east – north zone in the migrant analysis (compare Figures 5a & b) may be due to the seasonal availability of floodplains and extensive non-permanent water systems such as large mud flats (e.g. Quadrats 38, 54, 55, 56, 72 encompassing the Makarikari Pan), and major wadis (e.g. Quadrats 68 and 81 including the interfluvium between the Black and the White Nossob Rivers).

The biogeography of the south-western Cape quadrats, which unite to form 'long-tailed', discrete clusters in both resident and migrant cluster analyses (Figures 4a and b), is a matter of dispute. Moreau (1952) states that the south-western Cape avifauna is essentially a subset of that of eastern South Africa. However, Chapin (1932) and Winterbottom (1959) include the south-western Cape in a south-west arid zone. With particular regard to waterbirds, Winterbottom (1967, 1968b) reiterates his position, stressing that the avifaunas of the south-western Cape, and probably Namibia, differ significantly from his 'East African Tropical Aquatic Avifauna' which encompasses water systems from the Nile Sudd down to Lake St Lucia in Natal. In both our southern African resident and migrant cluster analyses, south-western Cape quadrats do not associate with the bulk of eastern quadrats (Figure 4). However, examination of the similarity matrices generated by the cluster analyses, reveals a different position. In the resident analysis, they are more similar to quadrats in the eastern zone, and, in the migrant analysis, to western zone quadrats. In our Afrotropical-scale study, which specifically excluded migrants, the south-western Cape also clustered with the east – north zone.

The reason why the south-western Cape behaves differently biogeographically for resident and migrant waterbirds remains obscure. One possible explanation of its west-zone affinities in the migrant analysis is that, historically, the avifauna of the area has karoo affinities (Winterbottom 1968c), and that its present migrant avifauna is relict in nature. Owing to the inherently mobile nature of many waterbirds (Appendix 1), we feel that this hypothesis is unlikely. Other ecological and geological explanations are that: (i) migrants visit the south-western Cape only during the relatively dry austral summer and therefore cannot utilize the fluctuating water habitat made

available by winter rainfall; (ii) the bulk of the south-western Cape which is potentially habitable by migrant waterbirds receives too little rain overall, with most of the areas with locally high rainfall being associated with mountain systems (Fuggie 1981); (iii) the Palaearctic migrant component of the south-western Cape is dominated by 'marine' waders (Siegfried 1981) which prefer the relatively mild ambient temperatures in that area; and (iv) the geomorphology of the south-western Cape does not favour the formation of highly productive, shallow water bodies. On the other hand, the high concentration of impoundments in the south-western Cape provides relatively deep-water aquatic habitat which favours resident waterbirds, hence the east – north zone affinities in the resident analysis.

### Species richness in general

The general longitudinal gradient of waterbird species richness in southern Africa is the result of a 'subtraction effect' from the relatively species-rich eastern parts of Africa. We attribute this subtraction effect to the combined influences of rainfall and geomorphology. Annual rainfall in southern Africa shows a marked east – west gradient (Clark 1967). Moreover, it also shows a general east – west trend in reliability (Onesta & Verhoef 1976). Even when and where there is adequate rain in the west, the porous, sandy soil which dominates that part of southern Africa (Clark 1967) does not favour the formation of durable water bodies which could sustain a waterbird fauna. Anatidae species richness (T – AN), the only real exception to this pattern, also has a significant positive correlation with latitude. This exception is possibly a consequence of the high mobility of many southern African Anatidae (Winterbottom 1972; Oatley & Prÿs-Jones 1986). In fact, their opportunistic mobility, often over long distances, enables them to reach even small, remote water bodies. Thus, the latitudinal gradient in Anatidae species richness is possibly the result of exploitation of ephemeral water bodies, especially impoundments, which abound in the southern part of the subcontinent (Noble & Hemens 1978).

The explanation we offer for the general longitudinal pattern of waterbird species richness in southern Africa also has bearing on the differences found between resident and migrant waterbird species richness, and between waterbird species richness in general and that of terrestrial birds. The extremely seasonal and unpredictable rains which fall on the relatively porous soils of western southern Africa favour the creation of ephemeral aquatic biotopes usually fed by wadis and other non-permanent rivers. These biotopes generate a short-term flush of resources, especially food, e.g. invertebrates and tadpoles (Weir 1969), which is readily exploited by migrants; hence, their less dramatic longitudinal subtraction effect (Figure 8). Thus, our results are consistent with the hypothesis that migrant birds use a periodical superabundance of food and/or habitat which cannot be utilized fully by resident birds (Morel & Bourliere 1962; Willis 1966). This ephemeral superabundance of aquatic resources in western southern Africa also explains the much sharper subtraction effect of terrestrial birds relative to waterbirds (Guillet & Crowe 1984).

In comparison with our Afrotropical-scale study, results of the waterbird vs environmental diversity correlation and stepwise multiple regression analyses show only one major difference. Mean annual rainfall (RF) is much better correlated ( $r = 0,57$  vs  $0,26$ ) with resident species richness (S – R). This is probably due to the generally lower rainfall ( $\bar{x} = 377$  mm vs 926 mm for Africa as a whole) and the strong east – west

rainfall gradient in southern Africa.

### Guild species richness: comparisons

The species richness of resident waterbirds in southern Africa is much better predicted by variation in the environment than that of migrant waterbirds. The most obvious explanation of this difference is that the environmental data used in the regressions reflect year-round conditions in the quadrats, i.e. the conditions under which resident waterbirds must exist. Migrant waterbirds, as we have said above, appear to exploit ephemeral and seasonally superabundant resources, thereby avoiding unsuitable conditions which may predominate in many quadrats through much of the year.

In addition to the differences between resident and migrant species richness, Table 4 shows that the number of small waterbird species which feed mainly on plant food in the vicinity of, but not in water [i.e. members of the 'dry feet' (F-P) guild dominated by ploceids] tend to be better predicted by year-round environmental conditions within quadrats. This 'tracking' of local conditions by these species, together with their ability to shift their feeding niches opportunistically, allows them to exploit what is locally available. Skead (1964) and Elliott (1973) demonstrate this clearly for ploceids. However, the species richness of guilds whose members forage in water and/or mud (e.g. Scolopacidae and Anatidae), especially those which are large (e.g. Ciconiidae), have relatively narrower foraging niches, and are dependent on animal food, tend to be poorly predicted. We attribute this low predictability to a lack of foraging flexibility, compensated for by relatively high mobility. In other words, these species are dependent on a relatively limited variety of foraging habitat and/or food types whose availability varies considerably spatially and temporally, requiring the birds to move, sometimes over large distances.

In this regard, it is necessary to draw attention to the distinction between mobility *sensu lato*, and migration. Appendix 1 shows that several 'resident' waterbirds are often highly mobile within southern Africa, even if not in any regular fashion (e.g. the yellowbilled duck *Anas undulata*, the redknobbed coot *Fulica cristata*, and the avocet *Recurvirostra avosetta*). In fact, relatively mobile, resident waterbirds are very well represented in highly aquatic guilds (F-S and F-D) and vertebrate-eaters (D-V), and are poorly represented in 'dry feet' (F-A) and invertebrate feeder (D-I) guilds (Table 1). The larger body-mass guilds, M-3 and M-4, which are characterized by vertebrate-eaters with more aquatic foraging modes, are the worst predicted by variation in the environment.

Finally, we focus on differences between Ardeidae and Anatidae species richness which figured importantly in our Afrotropical-scale study and in Reichholf's (1975) study of waterbird biogeography in South America. In South America, Ardeidae species richness is highest in the tropics and lowest in temperate areas, whereas the reverse pattern is found for Anatidae. For the Afrotropics, both Ardeidae and Anatidae species richness tends to be higher away from the tropics and we explained this in terms of geographical variation in habitat suitability.

Working on a much finer scale within southern Africa, we find somewhat more complex relationships between Ardeidae and Anatidae species richness. Ardeidae, and to a lesser extent, Anatidae species richness exhibits the same general geographical pattern as that found for the other waterbird taxonomic guilds. Each has an area of consistently high species richness centred on the upper reaches of the Vaal and Olifants

Rivers' drainage systems in the Transvaal, and from the Komati down to the Mzimvubu Rivers' drainage systems (on the Indian Ocean coast). However, Ardeidae species richness tends to decrease dramatically from this centre of high diversity towards the west and south, and relatively gradually to the north and east, in much the same way as does overall waterbird species richness (Figure 6). Anatidae species richness, on the other hand, shows an additional minor centre of high diversity in the south-western Cape Province, and decreases much more sharply to the north and east. This pattern is shown clearly in an examination of the residual plots of Ardeidae and Anatidae species richness vs resident species richness (Figure 9).

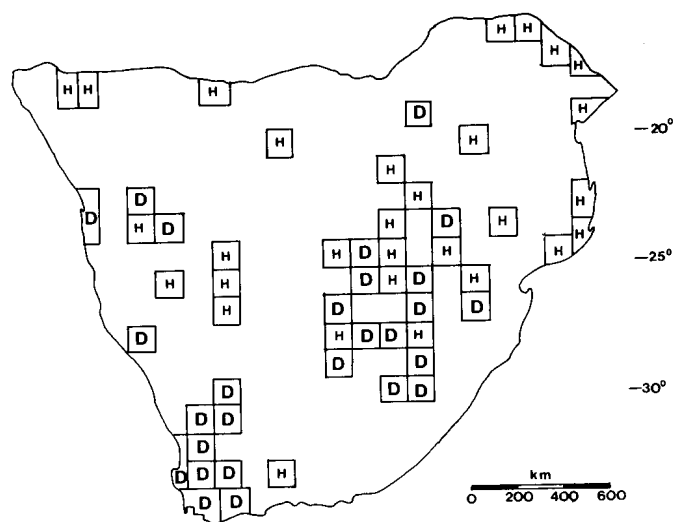


Figure 9 Geographical distribution of quadrats 'overrepresented' in heron (H) and duck (D) species richness, as suggested by the residual plots of reciprocal Ardeidae-Anatidae regression analyses.

We feel that these differences between Ardeidae and Anatidae species richness reflect the availability of aquatic habitat and certain abiotic conditions. Aquatic biotopes suitable for Anatidae (e.g. 'discrete' pond-like water bodies) abound in the south-western Cape; whereas shallow, protected stretches of vegetated water preferred by Ardeidae, are much more readily available in the eastern and north-eastern part of our study area. Supporting evidence for this 'habitat' suitability hypothesis is the positive correlation between Anatidae species richness and impoundment density in the quadrats of western South Africa and the lack of such correlation for Ardeidae (Table 5). We would also suggest that Anatidae make good use of the very high density of impoundments in the south-western Cape which, as we have said above, tends to be of an order of magnitude higher than elsewhere. Rowan (1963), Winterbottom (1969) and Siegfried (1970) have also drawn attention to the role of impoundments in extending the range of certain Anatidae (e.g. the South African shelduck and the spurwinged goose *Plectropterus gambensis*). Other studies (Rowan 1963; Siegfried 1965, 1976; Geldenhuys 1979) have invoked temperature as a potentially limiting factor for certain Anatidae species, but this hypothesis cannot be used to distinguish factors which differentiate Anatidae and Ardeidae, because both Ardeidae and Anatidae species richness are significantly negatively correlated with ambient temperature (Table 3). An additional, yet unexplored, reason for high Anatidae species richness in the south-western Cape is a possible pre-adaptation to salt water which enables

several Anatidae species (e.g. the South African shelduck, the Cape shoveller *Anas smithii*, the Maccoa duck *Oxyura maccoa*, the Cape teal *A. capensis*) which are adapted to inland saline biotopes, to utilize brackish water biotopes along the western Atlantic coast (W.R. Siegfried, pers. comm.). These same species may be excluded from north-eastern southern Africa by unfavourable regimes of ambient temperature (Rowan 1963; Siegfried 1965; Snow 1978; Geldenhuys 1979).

### Centres of high waterbird species richness

In the present study, as in our Afrotropical-scale research (Guillet & Crowe 1985), the species richness vs environment multiple regression analyses failed to predict the waterbird species richness of certain quadrats. In fact, the total  $R^2$  in our analysis of residents, is only 48% vs 69% for the Afrotropics as a whole. This low  $R^2$  might reflect the relative shortage and clumped nature of major, reliable, aquatic ecosystems in southern Africa (Siegfried 1970). Moreover, since southern Africa is not a centre of endemism for waterbirds, we suggest that quadrats or groups of quadrats whose waterbird species richness is much higher than predicted in the regressions, contain or comprise true refugia (*sensu* Crowe & Crowe 1982).

In other words, although these quadrats may not have acted as centres of speciation for waterbirds, they encompass reliable and diverse aquatic ecosystems and catchment systems which would withstand dry climatic cycles longest. Suggested refugia occur within the following quadrats (Figure 10): (i) Quadrat no. 16 (52 spp.) the origin of the major southern tributaries of the Cubango River, and the Ovambo River drainage into the Etosha Pan; (ii) Quadrat 18 (72 spp.) the confluence of the Kavango and Cuito Rivers; (iii) Quadrats 36 and 53 (76, 77 spp.) the Okavango system including Lake Ngami; (iv) Quadrats 21 and 22 (88, 91 spp.) the eastern Caprivi strip including the confluences of Cuando, Linyote and Zambezi Rivers; (v) Quadrats 31 and 32 (82, 101 spp.) the peak of Otavi including the origin of the Ugab and Ovambo River systems; (vi) Quadrats 45 and 63 (83, 123 spp.) Save and Revue Rivers including their origins; (vii) Quadrat 71 (60 spp.) Lake Dow which drains Makarikari pan; (viii) Quadrats 77 and 79 (68, 71 spp.) Windhoek highlands drainage into the Atlantic Ocean

in Walvis Bay area; (ix) Quadrat 89 (95 spp.) the central southern tributaries of the Limpopo River which drain the eastern Soutpansberg Mountains; (x) Quadrat 128 (54 spp.) Nossob and Auob interfluvium including the Kalahari Gemsbok National Park; (xi) Quadrats 118, 134–136, 149–152 and 163 (88–199 spp.) the Vaal drainage giving rise to a system of major dams and lakes including Nyl Lake and Hartebeespoort, Loskop, Barberspan, Potchefstroom, Vaal and Bloemhof Dams, in its upper part; and (xii) Quadrat 175 (84 spp.) sustaining in its lower part numerous small endorheic systems known locally as pans; (xiii) Quadrats 121, 139, 154, 168 and 181 (105–125 spp.) including the Kruger National Park and Usutu, Drakensberg and Lebombo Mountains, and their drainage into the Indian Ocean comprising major estuarine and lagoon systems such as Incomati, Maputo, St Lucia and Umfolozi; (xiv) Quadrats 156 and 169 (65, 56 spp.) three major non-permanent tributaries of the Orange River and its estuary; (xv) Quadrats 178 and 190 (97, 112 spp.) Lesotho Mountains and their drainage into the Indian Ocean; (xvi) Quadrat 215 (82 spp.) the drainage of Groot Swartberg Mountains with several major estuaries in the Indian Ocean.

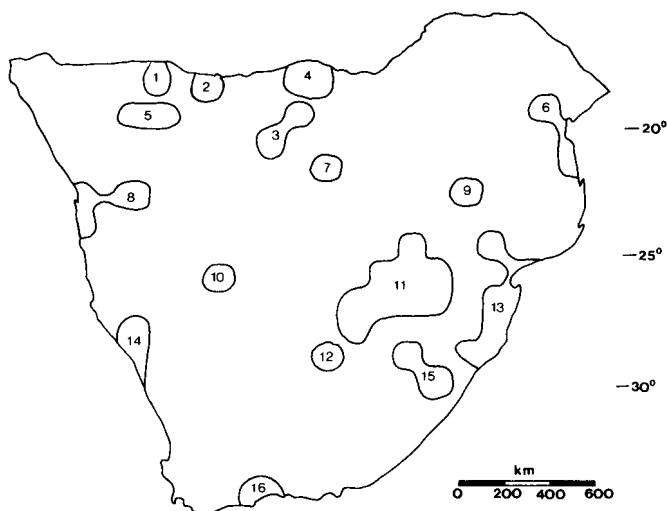
### Impoundments

The artificial creation of aquatic habitat may modify waterbird distribution and species richness considerably, sometimes fostering large aggregations of birds (Siegfried, Ball, Frost & McKinney 1975). Moreover, various waterbird guilds respond differently to impoundments in xeric and mesic rainfall regimes (Table 5). We interpret the positive correlations between species richness of resident waterbirds (S–R), Anatidae (T–AN) and Alcedinidae (T–AL) and density of impoundments (ID) in xeric quadrats to be a consequence of the absence or relatively ephemeral nature of their preferred natural habitat(s). Two results of these analyses are consistent with this interpretation. First, the lack of any significant correlations between ID and the species richness of any guild within the more mesic quadrats in the east, which presumably encompass adequate amounts of preferred habitat throughout the year. Second, migrant species richness (S–M) is not significantly correlated with ID in the xeric quadrats, since the natural habitats utilized by migrants are normally available while they are in southern Africa

The dichotomy between the species richness for guilds which appear to be dependent primarily on impoundment volume, e.g. Accipitridae (T–AC) and Charadriidae (T–CH), and those which may rely more on impoundment area, e.g. Scolopacidae (T–SC) and Laridae (T–LA), may be a consequence of two alternative but not mutually exclusive ecological strategies. The first strategy is adopted by relatively sedentary birds which appear to depend primarily on temporally reliable water habitat (as reflected by relatively high values for measures of impoundment volume). The second strategy is employed by more mobile waterbirds which often occur in large flocks and utilize the littoral zone. These species can also exploit relatively ephemeral water bodies, especially when they occur in large expanses (as reflected by relatively high values of measures of impoundment area).

### Deficiencies and remedies

Large-scale biogeographical syntheses such as this suffer from certain obvious deficiencies. First and foremost, the biotic data underpinning most such studies, e.g. checklists, 'birds of . . .' type books, are descriptive, rather than explicitly quantitative. They have been collected without such syntheses in mind, using a variety of sampling methods and intensities. Moreover,



**Figure 10** Hypothetical waterbird refugia during dry climatic phases as suggested by a multiple regression analysis of resident species richness (S–R) against measures of environmental diversity. All refugia quadrats are at least one standard deviation above the regression line.

they lack the temporal dimension necessary to give statistically robust predictions. This is essential if we hope to infer the effects of seasonal and/or cyclic climatic variations, e.g. droughts vs wet cycles, which in southern Africa are the rule and not the exception. This limitation is most troublesome when inherently mobile taxa such as waterbirds are studied. Similar criticisms apply, but perhaps to a lesser extent, to the use of environmental data. The primary difficulty in this instance is the applicability of gross information which can be extracted from maps, dam registers, etc., and of 'normal' or mean climatic statistics from fixed weather stations, in some instances far from sites at which biotic data were collected.

Although regional bird atlases (e.g. Cyrus & Robson 1980; M. Kemp & A.C. Kemp in prep.; Hockey 1983) provide much better bird distributional information, the enforced static representation of their results limits their utility as data bases. However, the primary data upon which they are based do not suffer from this limitation, provided that precise information as to date, sampling method/intensity, locality, abundance (preferably absolute counts or densities) and status (resident, vagrant, migrant) are noted. These broad-scale data can be 'calibrated' with long-term data for representative ecosystems which have been protected and monitored over long periods, e.g. Barberspan (Milstein 1975), Rondevlei (Middlemiss 1974; Banks 1980), and Lake St Lucia (Berruti 1980). Ornithological data should be curated by centres for bird study, e.g. along the lines of the British Trust for Ornithology or the proposed South African Bird Populations Data Bank within the South African Bird Ringing Unit (Prŷs-Jones 1984), which have suitably trained staff and adequate computer facilities for data capture, manipulation and archival. These centres should coordinate their activities with other organizations (e.g. agricultural and environmental affairs departments, nature conservancies, museums, meteorological stations) which collect ancillary biotic and abiotic data useful in identifying factors which determine patterns of biotic distribution. This would allow relatively easy analysis and exchange of information, and ensure a closer linkage between data used to identify patterns of biotic distribution and those used to explain them.

Even if high quality distributional data are available, it is difficult to compare communities and biotas. For example, although two quadrats or localities may have the same waterbird diversity, the species comprising their biotas may have markedly different biologies. In this study, we used the normal 'guild' approach to this problem, i.e. analysing species with common biological attributes, e.g. large size, preference for similar food, etc. However we felt constrained by the lack of basic morphological and natural history data on waterbirds. Indeed, for some of the 'borderline' waterbird species (e.g. certain passerine and wader species) there was not complete consensus among colleagues and references consulted as to their dependence on aquatic biotopes. Detailed single-species studies, e.g. Geldenhuys (1979) on the South African shelduck, and syntheses along the lines of Rowan (1963), are needed to provide quantifiable, high quality data for species to be studied. This strategy will allow researchers to employ multivariate analysis of large suites of species [see Capen (1981); Gauch (1982) and Adams (1985) for recent reviews], rather than having to resort to many univariate analyses of potentially arbitrarily defined, non-representative guilds. Moreover, a multivariate approach to community comparisons can help to identify species which form 'true' guilds, and which control or indicate important biological processes.

Lastly, these clearly preliminary results of our studies of

relationships between waterbirds and impoundments indicate an urgent need to repeat similar analyses when detailed bird and impoundment data are available for the whole study area. Given the economic importance of impoundments (Noble & Hemens 1978) and the critical conservation status of inland wetlands (Huntley 1978), a comparative study of the use of impoundments and natural aquatic biotopes, especially in relatively xeric parts of southern Africa could contribute considerably to our understanding of inter-relationships between waterbirds and their habitats.

### Acknowledgements

This research was funded, in part, by grants from the Foundation for Research Development of the Council for Scientific and Industrial Research. T.M.C. acknowledges the Frank M. Chapman Fund of the American Museum of Natural History for support during data analysis and manuscript preparation. In addition to the sources mentioned in the references, waterbird distribution, relative abundance data and/or information on waterbird natural history were obtained from: The South African Avifauna Series of the Percy FitzPatrick Institute of African Ornithology, K. Bonde, R.K. Brooke, other colleagues at the FitzPatrick Institute, Director of Orange Free State Division of Nature Conservation, C. Heyl, M.P.S. Irwin, A.C. Kemp and R. Liversidge. We are grateful to R.K. Brooke, W.R. Siegfried and two anonymous referees for their constructive comments. We thank the South African Bird Ringing Unit for access to its data base on African bird body mass. We acknowledge the assistance of: Anna A. Crowe with the statistical analyses and illustrations, L.P. Adams and H. Ruther with the development and implementation of the digitization of aquatic biotope availability, and S.E. Piper during data capture and display. We thank D.P. Zietsman, A. Hattle and P. Webster for information concerning impoundments. Data analysis was done on Sperry 1100 computers at the Universities of Cape Town and Rome.

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**Appendix 1** Southern African waterbirds analysed in this study and their guild and distributional characteristics (see Figure 5 for a key to zone codes)

Species	Guild types and codes						Characteristic species
	T <sup>a</sup>	B	T	F	M	M <sup>b</sup>	
	A	M	P	O	S	O	
	X	S	H	R	T	B	
Great crested grebe							
<i>Podiceps cristatus</i>	3 <sup>c</sup>	1	2	1	2		
Blacknecked grebe							
<i>Podiceps nigricollis</i>	2	1	2	2	3		
Dabchick							
<i>Tachybaptus ruficollis</i>	2	2	2	1	2		
Pinkbacked pelican							
<i>Pelecanus rufescens</i>	4	1	1	1	2		
White pelican							
<i>Pelecanus onocrotalus</i>	4	1	1	1	2		
Whitebreasted cormorant							
<i>Phalacrocorax carbo</i>	4	1	2	1	2		
Reed cormorant							
<i>Phalacrocorax africanus</i>	3	1	2	1	2		
Darter							
<i>Anhinga melanogaster</i>	3	1	2	1	2		
Grey heron							
<i>Ardea cinerea</i>	1	3	1	3	1	2	
Blackheaded heron							
<i>Ardea melanocephala</i>	1	3	1	3	1	2	
Goliath heron							
<i>Ardea goliath</i>	1	4	1	3	1	2	Zone I
Purple heron							
<i>Ardea purpurea</i>	1	3	1	3	1	2	Zone I
Great white egret							
<i>Egretta alba</i>	1	3	1	3	1	2	Zone I
Little egret							
<i>Egretta garzetta</i>	1	3	1	3	1	2	
Yellowbilled egret							
<i>Egretta intermedia</i>	1	3	2	3	1	2	Zone I
Cattle egret							
<i>Bubulcus ibis</i>	1	2	2	3	1	2	
Squacco heron							
<i>Ardeola ralloides</i>	1	2	2	3	1	2	Zone I
Greenbacked heron							
<i>Butorides striatus</i>	1	2	1	3	1	1	Zone I
Black egret							
<i>Egretta ardesiaca</i>	1	2	1	3	1	2	Zone I
Slaty egret							
<i>Egretta vinaceigula</i>	1	2	1	3	1	2?	
Rufousbellied heron							
<i>Butorides rufiventris</i>	1	2	1	3	1	2	Zone I
Dwarf bittern							
<i>Ixobrychus sturmii</i>	1	2	2	3	2	3	
Little bittern							
<i>Ixobrychus minutus</i>	1	2	2	3	1	1	
Night heron							
<i>Nycticorax nycticorax</i>	1	3	1	3	1	2	Zone I
Whitebacked night heron							
<i>Gorsachius leuconotus</i>	1	2	1	3	1	1	
Bittern							
<i>Botaurus stellaris</i>	1	3	1	3	1	1	
Hamerkop							
<i>Scopus umbretta</i>	2	1	3	1	2		
Marabou							
<i>Leptoptilos crumeniferus</i>	2	4	1	3	1	2	

**Appendix 1** Continued

Species	Guild types and codes						Characteristic species
	T <sup>a</sup>	B	T	F	M	M <sup>b</sup>	
	A	M	P	O	S	O	
	X	S	H	R	T	B	
Openbill							
<i>Anastomus lamelligerus</i>	2	3	2	3	2	3	Zone Ib
Saddlebill							
<i>Ephippiorhynchus senegalensis</i>	2	4	1	3	1	2	Zone Ib
Yellowbilled stork							
<i>Mycteria ibis</i>	2	3	1	3	2	3	
Woollynecked stork							
<i>Ciconia episcopus</i>	2	4	2	3	1	2	Zone Ib
Black stork							
<i>Ciconia nigra</i>	2	4	1	3	1	3	
White stork							
<i>Ciconia ciconia</i>	2	4	2	3	2	3	
Sacred ibis							
<i>Threskiornis aethiopicus</i>	3	2	3	1	2		
Glossy ibis							
<i>Plegadis falcinellus</i>	3	2	3	2	2		
African spoonbill							
<i>Platalea alba</i>	3	2	3	1	2		Zone I
Greater flamingo							
<i>Phoenicopterus ruber</i>	4	2	3	1	2		
Lesser flamingo							
<i>Phoeniconaias minor</i>	3	3	3	1	2		
Spurwinged goose							
<i>Plectropterus gambensis</i>	3	4	3	1	1	2	Zone I
Egyptian goose							
<i>Alopochen aegyptiacus</i>	3	4	3	1	1	2	
African shelduck							
<i>Tadorna cana</i>	3	3	2	1	1	2	Zone Ia
Knobbilled duck							
<i>Sarkidiornis melanotos</i>	3	3	3	1	2	2	
Pygmy goose							
<i>Nettapus auritus</i>	3	2	3	2	1	2	
European shoveller							
<i>Anas clypeata</i>	3	3	2	1	2	2	
Cape shoveller							
<i>Anas smithii</i>	3	3	2	1	1	2	
Black duck							
<i>Anas sparsa</i>	3	3	2	1	1	1	
Yellowbilled duck							
<i>Anas undulata</i>	3	3	3	1	1	2	
Redbilled teal							
<i>Anas erythrorhyncha</i>	3	3	3	1	1	2	
Garganey							
<i>Anas querquedula</i>	3	2	3	1	2	2	Zone Ib
Cape teal							
<i>Anas capensis</i>	3	3	2	1	1	2	
Hottentot teal							
<i>Anas hottentota</i>	3	2	3	1	1	2	
Whitefaced whistling duck							
<i>Dendrocygna viduata</i>	3	3	3	1	1	2	
Fulvous whistling duck							
<i>Dendrocygna bicolor</i>	3	3	3	1	1	2	
Redeyed pochard							
<i>Netta erythrophthalma</i>	3	3	3	2	1	2	
Maccoa duck							
<i>Oxyura maccoa</i>	3	3	2	2	1	2	
Whitebacked duck							
<i>Thalassornis leuconotus</i>	3	3	3	2	1	1	
Fish eagle							
<i>Haliaeetus vocifer</i>	4	4	1	4	1	1	
European marsh harrier							
<i>Circus aeruginosus</i>	4	3	1	6	2	2	
African marsh harrier							
<i>Circus ranivorus</i>	4	3	1	6	1	1	
Osprey							
<i>Pandion haliaetus</i>	4	3	1	4	1	2	
Water rail							
<i>Rallus caerulescens</i>	5	2	2	3	1	1	

## Appendix 1 Continued

Species	Guild types and codes						Characteristic species
	T <sup>a</sup>	B	T	F	M	M <sup>b</sup>	
	A	M	P	O	S	O	
	X	S	H	R	T	B	
African crane							
<i>Crex egregia</i>	5	2	2	3	2	3	
Striped crane							
<i>Aenigmatolimnas marginalis</i>	5	2	2	3	2	3	
Spotted crane							
<i>Porzana porzana</i>	5	2	2	3	2	3	
Baillon's crane							
<i>Porzana pusilla</i>	5	1	2	3	1	1	Zone I
Black crane							
<i>Amaurornis flavirostris</i>	5	2	2	3	1	1	Zone I
Whitewinged flufftail							
<i>Sarothrura ayresi</i>	5	2	2	3	2	3?	Zone Ia
Redchested flufftail							
<i>Sarothrura rufa</i>	5	2	2	3	1	1	Zone I
Streakybreasted flufftail							
<i>Sarothrura boehmi</i>	5	2	3	3	2	3?	Zone Ib
Purple gallinule							
<i>Porphyrio porphyrio</i>	5	3	3	5	1	1	
Lesser gallinule							
<i>Porphyrola alleni</i>	5	3	3	5	1	3	Zone I
Moorhen							
<i>Gallinula chloropus</i>	5	2	2	3	1	1	
Lesser moorhen							
<i>Gallinula angulata</i>	5	2	3	3	2	3	Zone I
Redknobbed coot							
<i>Fulica cristata</i>	5	3	3	1	1	2	
Finfoot							
<i>Podica senegalensis</i>	3	2	2	1	1		Zone I
Crowned crane							
<i>Balearica regulorum</i>	4	1	3	1	2		Zone I
Wattled crane							
<i>Grus carunculata</i>	4	1	3	1	1		Zone I
African jacana							
<i>Actophilornis africanus</i>	2	2	5	1	1		Zone I
Lesser jacana							
<i>Microparra capensis</i>	1	2	5	1	1		Zone I
Painted snipe							
<i>Rostratula benghalensis</i>	2	2	3	1	2		
Ringed plover							
<i>Charadrius hiaticula</i>	6	1	2	3	2	3	
Whitefronted sandplover							
<i>Charadrius marginatus</i>	6	1	2	3	1	1	
Chestnutbanded sandplover							
<i>Charadrius pallidus</i>	6	1	2	3	1	2	
Threebanded sandplover							
<i>Charadrius tricollaris</i>	6	1	2	3	1	1	
Grey plover							
<i>Pluvialis squatarola</i>	6	2	2	3	2	3	
Blacksmith plover							
<i>Vanellus armatus</i>	6	2	2	3	1	2	
Whitecrowned plover							
<i>Vanellus albiceps</i>	6	2	2	3	1	3	Zone Ib
Wattled plover							
<i>Vanellus senegallus</i>	6	2	2	3	1	1	
Longtoed plover							
<i>Vanellus crassirostris</i>	6	2	2	3	1	1	
Great snipe							
<i>Gallinago media</i>	7	2	2	3	2	3	Zone I
Ethiopian snipe							
<i>Gallinago nigripennis</i>	7	2	2	3	1	1	
Curlew sandpiper							
<i>Calidris ferruginea</i>	7	1	2	3	2	3	
Pectoral sandpiper							
<i>Calidris melanotos</i>	7	1	2	3	2	2	
Little stint							
<i>Calidris minuta</i>	7	1	2	3	2	3	
Broadbilled sandpiper							
<i>Limicola falcinellus</i>	7	1	2	3	2	3	

## Appendix 1 Continued

Species	Guild types and codes						Characteristic species
	T <sup>a</sup>	B	T	F	M	M <sup>b</sup>	
	A	M	P	O	S	O	
	X	S	H	R	T	B	
Ruff							
<i>Philomachus pugnax</i>	7	2	2	3	2	3	
Terek sandpiper							
<i>Xenus cinereus</i>	7	1	2	3	2	3	
Common sandpiper							
<i>Tringa hypoleucos</i>	7	1	2	3	2	3	
Green sandpiper							
<i>Tringa ochropus</i>	7	2	2	3	2	3	
Marsh sandpiper							
<i>Tringa stagnatilis</i>	7	1	2	3	2	3	
Greenshank							
<i>Tringa nebularia</i>	7	2	2	3	2	3	
Wood sandpiper							
<i>Tringa glareola</i>	7	1	2	3	2	3	
Bartailed godwit							
<i>Limosa lapponica</i>	7	2	2	3	2	3	
Curlew							
<i>Numenius arquata</i>	7	3	2	3	2	3	
Whimbrel							
<i>Numenius phaeopus</i>	7	3	2	3	2	3	
Avocet							
<i>Recurvirostra avosetta</i>	2	2	3	1	2		
Stilt							
<i>Himantopus himantopus</i>	2	2	3	1	2		
Water dikkop							
<i>Burhinus vermiculatus</i>	2	2	3	1	1		
Redwinged pratincole							
<i>Glareola pratincola</i>	1	2	3	1	3		
Whitecollared pratincole							
<i>Glareola nuchalis</i>	1	2	3	1	3		Zone Ib
Southern blackbacked gull							
<i>Larus dominicanus</i>	8	3	2	3	1	2	
Lesser blackbacked gull							
<i>Larus fuscus</i>	8	2	2	2	1	2	Zone Ib
Greyheaded gull							
<i>Larus cirrocephalus</i>	8	2	2	3	1	2	
Caspian tern							
<i>Hydroprogne caspia</i>	8	3	1	4	1	1	
Gullbilled tern							
<i>Gelochelidon nilotica</i>	8	2	2	4	1	2	Zone Ib
Whitewinged black tern							
<i>Chlidonias leucopterus</i>	8	1	2	4	2	3	
Whiskered tern							
<i>Chlidonias hybridus</i>	8	2	1	4	1	2	
Skimmer							
<i>Rynchops flavirostris</i>	2	1	4	1	1		
Black coucal							
<i>Centropus bengalensis</i>	2	2	6	1	3		
Copperytailed coucal							
<i>Centropus cupreicaudus</i>	2	1	6	1	1		Zone Ib
Whitebrowed coucal							
<i>Centropus superciliosus</i>	2	1	3	1	1		Zone I
Grass owl							
<i>Tyto capensis</i>	3	1	6	1	1		Zone I
Marsh owl							
<i>Asio capensis</i>	2	1	6	1	1		Zone I
Fishing owl							
<i>Scotopelia peli</i>	3	1	4	1	1		Zone I
Natal nightjar							
<i>Caprimulgus natalensis</i>	1	2	6	1	1		
Pied kingfisher							
<i>Ceryle rudis</i>	9	2	1	4	1	2	
Giant kingfisher							
<i>Ceryle maxima</i>	9	2	1	4	1	2	
Halfcollared kingfisher							
<i>Alcedo semitorquata</i>	9	1	1	4	1	1	Zone I
Malachite kingfisher							
<i>Alcedo cristata</i>	9	1	2	4	1	1	

## Appendix 1 Continued

Species	Guild types and codes						Characteristic species
	T <sup>a</sup>	B	T	F	M	M <sup>b</sup>	
	A	M	P	O	S	O	
	X	S	H	R	T	B	
Mangrove kingfisher	9	2	1	4	2	3	
<i>Halcyon senegaloides</i>							
European sandmartin							
<i>Riparia riparia</i>		1	2	6	2	3	
African sandmartin							
<i>Riparia paludicola</i>		1	2	6	1	2	
Cape reed warbler							
<i>Acrocephalus gracilirostris</i>	10	1	2	6	1	1	
Rufous reed warbler							
<i>Acrocephalus rufescens</i>	10	1	2	6	1	1	Zone Ib
African marsh warbler							
<i>Acrocephalus baeticatus</i>	10	1	2	6	2	3	
European sedge warbler							
<i>Acrocephalus schoenobaenus</i>	10	1	2	6	2	3	
African sedge warbler							
<i>Bradypterus baboecala</i>	10	1	2	6	1	1	Zone I
Fantailed warbler							
<i>Schoenicola brevirostris</i>	10	1	2	6	1	3	
Moustached warbler							
<i>Melocichla mentalis</i>	10	1	2	6	1	1	Zone Ib
Palecrowned cloud cisticola							
<i>Cisticola brunnescens</i>	10	1	2	6	1	1	
Shortwinged cisticola							
<i>Cisticola brachyptera</i>	10	1	2	6	1	1	Zone Ib
Blackbacked cisticola							
<i>Cisticola galactotes</i>	10	1	2	6	1	1	
Chirping cisticola							
<i>Cisticola pipiens</i>	10	1	2	6	1	1	Zone Ib
Le Vaillant's cisticola							
<i>Cisticola tinniens</i>	10	1	2	6	1	1	
Yellow warbler							
<i>Chloropeta natalensis</i>	10	1	2	6	1	1	
African pied wagtail							
<i>Motacilla aguimp</i>	11	1	2	6	1	2	
Cape wagtail							
<i>Motacilla capensis</i>	11	1	2	6	1	2	
Longtailed wagtail							
<i>Motacilla clara</i>	11	1	2	6	1	1	
Yellowthroated longclaw							
<i>Macronyx croceus</i>	11	1	2	6	1	1	
Pinkthroated longclaw							
<i>Macronyx ameliae</i>	11	1	2	6	1	1	
West African boubou							
<i>Laniarius bicolor</i>		1	2	6	1	1	Zone Ib
Coppery sunbird							
<i>Nectarinia cuprea</i>		1	2	6	1	2	Zone Ib
Yellow weaver							
<i>Ploceus subaureus</i>	12	1	3	5	1	1	
Golden weaver							
<i>Ploceus xanthops</i>	12	1	3	5	1	1	
Brownthroated golden weaver							
<i>Ploceus xanthopterus</i>	12	1	3	5	1	1	Zone Ib
Masked weaver							
<i>Ploceus velatus</i>	12	1	3	5	1	1	
Thickbilled weaver							
<i>Amblyospiza albifrons</i>	12	1	3	5	1	2	
Redheaded quelea							
<i>Quelea erythrops</i>	12	1	3	5	1	2?	
Red bishop							
<i>Euplectes orix</i>	12	1	3	5	1	1	
Cape widow							
<i>Euplectes capensis</i>	12	1	3	5	1	1	
Golden bishop							
<i>Euplectes afer</i>	12	1	3	5	1	2	Zone I
Yellowbacked widow							
<i>Euplectes macrourus</i>	12	1	3	5	1	1	Zone Ib
Redshouldered widow							
<i>Euplectes axillaris</i>	12	1	3	5	1	1	

## Appendix 1 Continued

Species	Guild types and codes						Characteristic species
	T <sup>a</sup>	B	T	F	M	M <sup>b</sup>	
	A	M	P	O	S	O	
	X	S	H	R	T	B	
Orangebreasted waxbill							
<i>Sporaeginthus subflavus</i>	12	1	3	5	1	1	
Common waxbill							
<i>Estrilda astrild</i>	12	1	3	5	1	2	
Quail finch							
<i>Ortygospiza atricollis</i>	12	1	3	5	1	2	
Locust finch							
<i>Ortygospiza locustella</i>	12	1	3	5	1	2	Zone Ib
Pintailed whydah							
<i>Vidua macroura</i>	12	1	3	5	1	2	

<sup>a</sup>Guild types, and <sup>c</sup>guild codes as in Table 1.

<sup>b</sup>1 = purely local movements; 2 = irregular-opportunistic movements, sometimes over great distances; 3 = regular and/or great distance movements.

? = uncertain whether their mobility score is 2 or 3.



**Appendix 2** Results of the southern African waterbird cluster analyses showing numbers of dendrogram terminal points and quadrats which they comprise, as synthesized in Figure 4

Resident cluster		Migrant cluster	
Terminal points	Quadrat numbers	Terminal points	Quadrat numbers
1:	16, 33, 48, 114	1:	9, 16, 29, 33, 34, 37, 48, 52, 58, 69, 82-84, 86, 93, 97-99, 114, 124, 143, 145, 146, 158, 159, 162, 182, 183, 192, 200
2:	106	2:	85
3:	124, 140, 155	3:	20
4:	34, 85, 86, 98-100, 158	4:	96
5:	37, 38	5:	40, 60, 74
6:	84, 130-132	6:	130
7:	29, 68, 81, 95, 125, 145-147, 159, 161	7:	129, 131, 132
8:	52	8:	42, 95, 125
9:	47, 129	9:	197, 206, 207, 213, 214
10:	10, 28, 49, 51, 64, 67, 69, 70, 82, 83, 93, 96, 97, 108, 111, 113, 127, 143, 183, 199, 200	10:	67, 111
11:	207	11:	73, 141
12:	197, 206, 213, 214	12:	28, 64, 106, 108, 157, 170, 171, 199
13:	43	13:	46, 75, 76, 92
14:	54, 116	14:	107
15:	75, 76, 90, 91	15:	91
16:	55, 56, 72	16:	202, 210
17:	15, 30, 184, 193	17:	10, 49
18:	73, 115	18:	47, 94
19:	9, 11, 12, 17	19:	113, 127
20:	39, 40	20:	155
21:	141, 182, 191		

**Appendix 2** Continued

Resident cluster		Migrant cluster	
Terminal points	Quadrat numbers	Terminal points	Quadrat numbers
22:	160, 162	21:	147, 160
23:	65, 66, 78, 80, 94, 110, 112, 126, 128, 142, 144, 157, 170-172, 192, 194, 198, 201-204, 208-210	22:	191
24:	26, 41, 42, 58, 59	23:	17, 19, 44
25:	44, 61	24:	110
26:	46, 92, 107, 122, 123	25:	30, 54, 70, 100, 115
27:	19, 20	26:	68, 116, 161, 198
28:	3, 4, 7, 8, 62	27:	51
29:	1, 2, 5, 23; 24, 60, 74	28:	126
30:	13, 14, 31, 32, 50, 79, 109	29:	109, 208
31:	77, 156, 169	30:	203, 204
32:	18	31:	148, 173, 174, 185
33:	21, 22, 35, 36, 53, 71	32:	172, 194, 209
34:	133, 148, 153, 216	33:	90, 122, 123
35:	6, 25, 57	34:	21, 22, 35, 36, 53, 55, 56, 71, 72
36:	27, 45, 63, 87-89, 101-105, 117-121, 134-139, 149, 150-152, 154, 163-168, 173-181, 185-190, 195, 196, 205, 211, 212, 215	35:	13, 18
		36:	11, 12, 59, 61, 66, 80, 87-89, 101-105, 117, 119, 120, 133, 137, 138, 167, 189
		37:	1, 2, 5, 6, 14, 15, 23-27, 31, 32, 38, 39, 41, 45, 50, 57, 63, 65, 77-79, 112, 118, 121, 128, 134-136, 139, 144, 149, 150-154, 163-166, 168, 169, 175-181, 186-188, 190, 195, 196, 205, 211, 212, 215
		38:	3, 4, 7, 8, 43, 62, 81, 140, 142, 153, 156, 184, 193, 201, 216