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Monthly and seasonal changes in the aquatic avifauna at Rondevlei Bird Sanctuary (Cape Province, South Africa)

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Abstract - Patterns of long-term temporal variation in waterbird abundance and species richness at Rondevlei Bird Sanctuary are studied. Waterbird utilisation shows a strong seasonal variation which is correlated with variation in abiotic factors, especially water depth, rainfall and water and ambient temperature. Relationships between the utilisation of different waterbird taxo-morpho-eco-ethological and status groupings and the environment, are mediated through the presence of shallow water and mud habitats, and the ecological density of food. These waterbird-environmental relationships may be complex, especially when influenced by lag and threshold effects. Future research needs are reviewed.

Key words: waterbirds, South Africa, habitat, ecological density, long-term.

Since many African waterbird species depend on dramatically fluctuating, often ephemerally superabundant, resources, they are characteristically highly mobile and opportunistic in their utilisation of aquatic ecosystems (Guillet & Crowe 1985, 1986). The availability of these resources is affected by local natural (*e.g.* heavy and unpredictable rainfall in sub-desertic catchment areas) and man-induced (*e.g.* artificially regulated impoundment regimes) changes in the availability of surface water. Therefore, it is necessary to put broad scale studies of distribution and diversity of waterbirds (*e.g.* Reichholf 1975; Guillet & Crowe 1985, 1986) into a biologically meaningful context by estimating seasonal and between-year variation in waterbird community structure at representative aquatic ecosystems.

In this paper, we analyse 12 years of monthly count data for waterbirds at Rondevlei Bird Sanctuary, an important waterbird reserve in the southwestern Cape Province, South Africa. Short-term studies, *e.g.* Banks (1980) and Guillet & Crowe (1981, 1983), suggest that the fluctuating environment at Rondevlei causes periodic variation in waterbird utilisation patterns. The aims of this study are to determine if there is long-term regular, monthly and/or year-to-year variation in waterbird species richness and abundance at Rondevlei, and to relate any patterns found to variation in abiotic factors (*e.g.* precipitation, temperature, water depth) at the Sanctuary.

STUDY AREA AND METHODS

Study area

Rondevlei Bird Sanctuary (34° O4' S 18° 30' E) is a 'coastal vlei' (flattish expanded stretch of river with marshy vegetation and seasonal standing water), a relatively common South African aquatic biotope (Noble & Hemens 1978). Middlemiss (1974), Banks (1980) and Guillet & Crowe (1983) provide a more detailed discussion of Rondevlei and its environs. The Sanctuary is an important nature reserve which provides food, shelter and breeding grounds for large populations of many waterbird species (Middlemiss 1974).

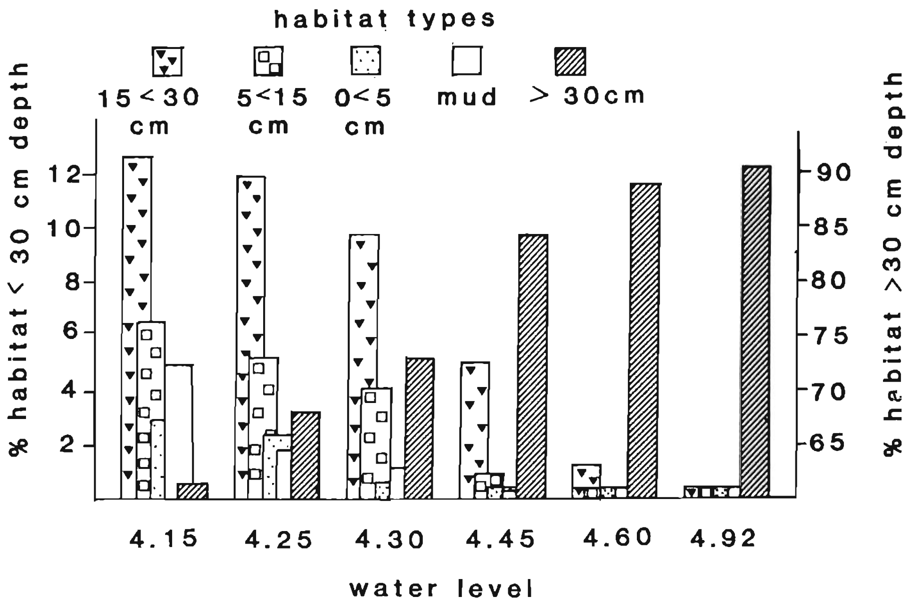

FIGURE 1. Availability of a selected number of water depth and mud habitats, at different water levels at Rondevlei (after Banks 1980).

The conservation importance of Rondevlei is enhanced by its location, since it is the only protected, large aquatic biotope amidst the highly developed suburbs of Cape Town.

The results of Banks' (1980) unpublished 13-month study of Rondevlei's waterbird community suggest that the seasonally fluctuating water levels at the Sanctuary have profound effects on its waterbird species richness and abundance. More particularly, she found that under high water depth conditions (>4.45 m a.s.l. as measured at the Sanctuary's water depth gauge), the availability of very shallow water (< 15 cm) and mud habitats is greatly diminished (Fig. 1), leading to a decrease in the species richness and abundance of waterbirds, primarily waders, dependent on these habitats. Under relatively low vlei depth conditions (<4.45 m a.s.l.), the availability of these habitats increases dramatically (Fig. 1) at the expense of deep water (> 30 cm deep) habitat, which is used primarily by diving waterbirds (*e.g.* Dabchick *Tachybaptus ruficollis* and Redeyed Pochard *Netta erythrophthalma*).

Data base

The data base for this study is 130 monthly counts for 27 waterbird species and abiotic environmental data (Tab. I-IV) collected by Rondevlei's wardens between 1965 and 1976. In order to identify possible lag effects of environmental variables, abiotic data for the month immediately preceding each bird count were also analysed. The waterbird species studied include resident and both Palaearctic and intra-African migrant species which feed at the Sanctuary, and encompass a broad range of body mass, trophic and foraging behaviour groups (Tab. I). The study period includes the maximum climatic variation experienced at Rondevlei (Middlemiss 1974), encompassing months of relatively low, high and normal temperature, rainfall and water depth.

TABLE I. Waterbird species and groups analysed in this study. Body mass 1, 2, 3 = < 400 g, > 400 g, < = 1200g, > 1200 g. Diet 1, 2, 3 = prevalently vertebrate, invertebrate, plant food. Foraging behaviour 1 - 5 = swimming, diving, large and small pecker, other. Status 1, 2 = resident, migrant.

	Groups			
	Body mass	Diet	Foraging behaviour	Status
Dabchick *Tachybaptus ruficollis*	1	2	2	1
White Pelican *Pelecanus onocrotalus*	3	1	1	1
Reed Cormorant *Phalacrocorax africanus*	2	1	2	1
Grey Heron *Ardea cinerea*	3	1	3	1
Little Egret *Egretta garzetta*	2	1	3	1
Yellowbilled Egret *Egretta intermedia*	2	2	3	1
Sacred Ibis *Threskiornis aethiopicus*	3	2	3	1
Spoonbill *Platalea alba*	3	2	3	1
Greater Flamingo *Phoenicopterus ruber*	3	2	3	1
Lesser Flamingo *Phoenicopterus minor*	3	3	3	1
Spurwing Goose *Plectropterus gambensis*	3	3	3	1
Egyptian Goose *Alophochen aegyptiacus*	3	3	3	1
Cape Shoveller *Anas smithii*	2	2	1	1
Yellowbilled Duck *Anas undulata*	2	3	1	1
Redbilled Teal *Anas erythrorhyncha*	2	3	1	1
Cape Teal *Anas capensis*	2	2	1	1
Fulvous Whistling Duck *Dendrocygna bicolor*	2	3	1	1
Redeyed Pochard *Netta erythrophthalma*	2	3	2	2
Maccoa Duck *Oxyura maccoa*	2	2	2	1
Moorhen *Gallinula chloropus*	1	2	1	1
Redknobbed Coot *Fulica cristata*	2	3	1	1
Curlew Sandpiper *Calidris ferruginea*	1	2	4	2
Little Stint *Calidris minuta*	1	2	4	2
Ruff *Philomachus pugnax*	1	2	4	2
Avocet *Recurvirostra avosetta*	1	2	4	2
Stilt *Himantopus himantopus*	1	2	4	1
Whitewinged Black Tern *Chlidonias leucopterus*	1	2	5	2

Numerical methods

Cluster analysis (Field & McFarlane 1968) and multidimensional scaling (Shepard 1980) were used to identify patterns of similarity between the study months in terms of waterbird community structure. The Bray & Curtis (1957) measure of similarity and a group average sorting method (Lance & Williams 1967) were used in the cluster analysis. Cluster analysis allows the detection of hierarchical patterns of similarity (*i.e.* grouping patterns), whereas multidiminsional scaling is more suitable for detecting possible gradients within and between clusters (Field, Clarke & Warwick 1982). Multidimensional scaling is thus a heuristic aid in determining possible gradient effects of abiotic factors on waterbird utilisation patterns. Waterbird and environmental variables which characterize groups of months resulting from cluster analysis were identified by comparing each cluster with the remaining months using one-way analysis of variance (BMDP-P7D; Dixon 1983). Correlation analysis (BMDP-P7D) was used to identify one-to-one relationships between environmental and waterbird variables.

RESULTS

Patterns of waterbird utilisation

Mean values of monthly counts for all bird species studied are given in Table II. The cluster and multidimensional scaling analyses (Fig. 2a and b) divide the study months

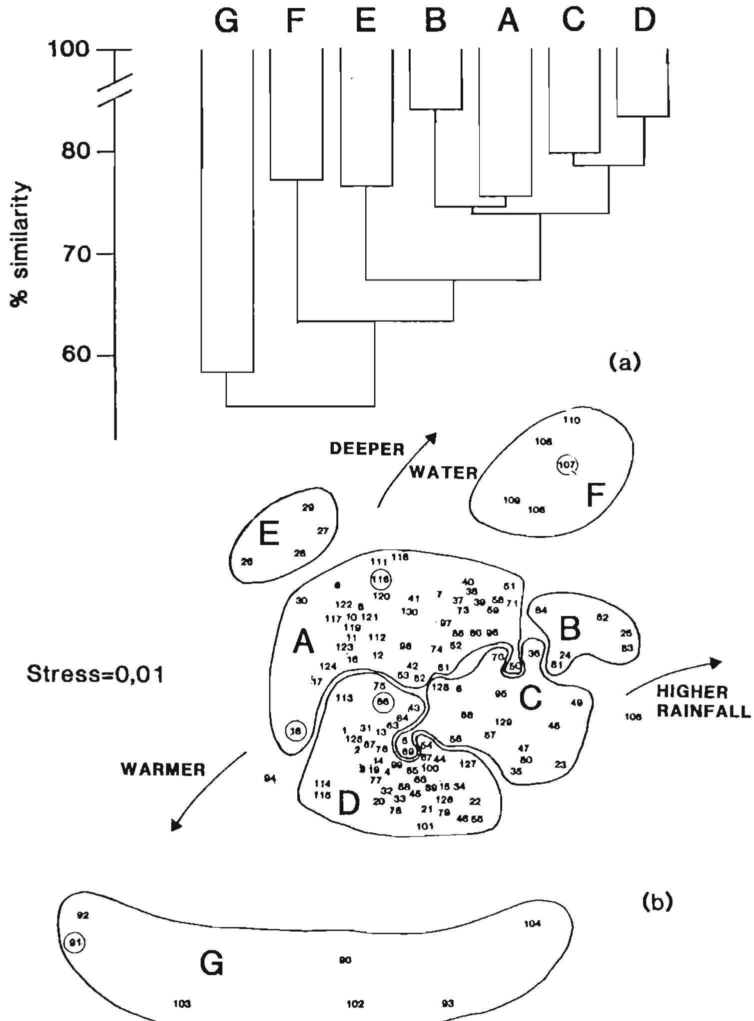

FIGURE 2. Patterns of waterbird Sanctuary utilisation during 130 months reflected by: a) cluster analysis, and b) multidimensional scaling. See Tab. IV for information concerning month codes (1-130), and text, for month-cluster codes (A-G). Encircled month codes are discussed in the text.

into two major clusters, A and D. Cluster A consists primarily of austral winter-spring months (July-November) and cluster D of summer-autumn months (January-April). Cluster D is characterized by relatively high waterbird species richness and abundance, particularly of species which forage in shallow water, and by relatively low (though increasing) rainfall, normal (but decreasing) water level, and high temperature conditions. Cluster A is characterized by low waterbird species richness and abundance (particularly in species which forage in shallow water, *e.g.* waders),

TABLE II. Monthly mean counts for waterbirds at Rondevlei 1965-1976.

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
Dabchick	37.0	28.3	25.6	17.0	11.0	13.8	20.8	19.6	20.9	21.1	22.1	32.8
White Pelican	86.4	113.2	113.0	62.5	38.7	54.7	60.0	49.0	42.7	65.1	56.1	71.0
Reed Cormorant	43.1	37.2	32.2	31.3	23.7	22.2	21.4	17.1	13.8	23.5	35.5	48.1
Grey Heron	8.4	11.0	13.3	11.7	7.6	7.2	5.4	3.3	3.3	4.5	4.8	4.3
Little Egret	6.2	10.7	7.8	4.3	2.9	2.0	0.8	5.5	9.1	8.6	7.2	5.9
Yellowbilled Egret	11.9	8.1	5.6	3.1	2.7	3.0	0.8	2.7	4.5	5.0	6.5	6.9
Sacred Ibis	1.2	1.5	2.1	1.2	1.6	1.4	2.1	2.0	4.1	7.2	6.2	8.3
Spoonbill	6.5	9.7	9.1	5.4	5.7	2.9	1.5	2.4	1.8	2.3	5.7	6.2
Greater Flamingo	371.0	348.2	332.8	289.6	145.1	233.0	166.6	212.7	223.6	435.8	209.4	339.3
Lesser Flamingo	4.6	40.0	62.3	140.5	55.0	87.5	103.5	83.4	15.2	10.0	2.2	7.1
Spurwing Goose	9.8	10.4	17.6	15.7	13.2	8.1	5.9	6.0	1.6	1.6	2.3	4.6
Egyptian Goose	7.0	7.9	5.9	8.3	4.4	4.9	4.9	3.8	4.1	6.8	5.7	8.1
Cape Shoveller	463.0	324.9	211.6	239.3	85.1	133.6	180.1	138.7	145.3	256.1	375.9	438.6
Yellowbilled Duck	127.3	146.8	188.2	72.0	83.6	51.5	55.8	47.6	41.5	62.9	76.2	74.3
Redbilled Teal	43.6	26.6	12.3	10.0	7.8	9.6	24.2	29.6	18.6	12.5	32.4	36.4
Cape Teal	7.1	7.9	8.6	9.8	11.4	32.2	20.4	31.7	15.0	13.0	12.9	6.4
Fulvous Whistling Duck	1.6	1.0	1.1	0.0	0.0	1.5	0.1	0.3	0.9	0.5	0.3	1.4
Redeyed Pochard	84.2	47.7	6.0	6.9	5.2	8.0	21.2	31.7	72.4	107.8	116.0	67.1
Maccoa Duck	1.5	2.1	1.0	1.2	0.4	0.6	1.6	3.8	3.5	2.7	2.0	0.3
Moorhen	49.1	51.5	64.4	60.5	54.1	55.7	51.4	34.8	34.8	40.1	31.4	47.1
Redknobbed Coot	465.6	453.4	375.2	282.8	127.0	139.2	125.0	146.8	237.5	279.3	479.6	513.2
Curlew Sandpiper	10.3	39.0	61.2	76.8	27.2	10.0	1.3	0.7	1.5	1.0	2.4	10.3
Little Stint	32.6	34.9	111.0	120.5	98.5	17.9	2.5	2.3	0.5	2.6	2.7	8.4
Ruff	9.3	16.8	20.2	14.9	7.0	0.0	0.0	0.0	0.0	1.1	0.9	5.0
Avocet	53.5	118.4	112.9	90.0	41.5	36.2	6.1	4.0	5.8	4.0	4.3	11.7
Stilt	9.7	12.2	13.4	19.9	14.6	10.7	8.3	3.1	3.1	5.7	5.0	8.3
Whitewinged Black Tern	294.1	352.8	660.4	124.1	50.2	0.0	0.4	0.1	3.1	18.5	72.5	161.5

high water levels, normal (but decreasing) rainfall and low (but increasing) ambient/water temperature.

Cluster C (May-June/July) is transitional between clusters D and A. Clusters B, E, F and G comprise groups of months with generally low species richness. The results of analyses of variance (Tab. V) and the month-cluster's relative position in Fig. 2b suggest that environmental factors which influence waterbird community structure at Rondevlei include: ambient and water temperature, rainfall and water level. Month-clusters in the upper right side of Fig. 2b (*e.g.* B and F) tended to have higher rainfall and lower temperatures than those on the lower left side (*e.g.* D and G). Month-clusters at or near the top of this fugure (*e.g.* A, B, E and F) had deeper water than those at the bottom (*e.g.* D and G). This pattern is particularly highlighted by the positions of atypical months in Fig. 2b in terms of one or more environmental conditions. For example, December 1966 (month no. 18 in Fig. 2b), although typical in water level and rainfall, had abnormally high ambient temperature. Thus, although it falls within cluster A, it is positioned closer to the normally warmer months which comprise cluster D. May 1975 (month no. 116), which had an abnormally high water level, is within cluster A rather than D. Conversely, November 1972 (month no. 86), which had a low water level, is in cluster D rather than A. April 1973 (month no. 91),

TABLE III. Measures of waterbird total and group richness (RICH) and abundance (AB), and of environmental variation analysed in this study; their abbreviations for current and preceding (PR) months (see text and Tab. I for explanation)

Abbreviations	Description
Waterbirds	
TOT-RICH	total number of waterbird species
RES-RICH	number of resident waterbird species
MIG-RICH	number of migrant waterbird species
TOT-AB	total number of resident waterbirds
RES-AB	number of resident waterbirds
MIG-AB	number of migrant waterbirds
BM1-AB	number of body mass class 1 waterbirds
BM2-AB	number of body mass class 2 waterbirds
BM3-AB	number of body mass class 3 waterbirds
DV-AB	number of prevalently vertebrate eating waterbirds
DI-AB	number of prevalently invertebrate eating waterbirds
DH-AB	number of prevalently plant eating waterbirds
FS-AB	number of waterbirds which obtain food by swimming
FD-AB	number of waterbirds which obtain food by diving
FBP-AB	number of big pecker waterbirds
FSP-AB	number of small pecker waterbirds
Environment	
RF / PR	Sanctuary total monthly rainfall (in mm)
WL / PR	mean monthly water level (in m a.s.l.) as measured at the Sanctuary's water depth gauge
WT / PR	mean monthly water temperature (in °C)
TMAX / PR	mean monthly maximum ambient temperature (in °C)
TMIN / PR	mean monthly minimum ambient temperature (in °C)

which had relatively high water and ambient temperature, is in cluster G rather than D. Conversely, August 1974 (month no. 107) which falls within cluster F rather than A, had relatively high rainfall.

Richness and abundance of waterbirds and environmental correlations

In general, waterbird species richness and abundance are positively correlated with ambient and water temperature and negatively correlated with rainfall (especially values for the previous month) and water level (Tab. VI). The few species whose abundance is positively correlated with water level (*e.g.* Cape Shoveller *Anas smithii* and Redeyed Pochard) belong to the swimmer and diver groups, and are more strongly correlated with water level conditions in the previous month. However, examination of Fig. 3 shows that the correlation pattern between waterbird and environmental variables is complex. The greatest increase in waterbird abundance occurs during November-March as water level is decreasing from relatively high values, and the abundance of resident waterbirds peaks in January (at the 4.45 m a.s.l. level), whereas migrant waterbird abundance peaks in March (at the 4.15 m a.s.l. level).

TABLE IV. 130 months of bird count data for Rondevlei analysed in this study. Month codes are those used in Fig. 2.

Code	Mth/year	Code	Mth/Year	Code	Mth/Year	Code	Mth/Year
1	Jan 1965	34	Apr 1968	67	Apr 1971	100	Jan 1974
2	Feb 1965	35	May 1968	68	May 1971	101	Feb 1974
3	Mar 1965	36	Jun 1968	69	Jun 1971	102	Mar 1974
4	Apr 1965	37	Jul 1968	70	Jul 1971	103	Apr 1974
5	May 1965	38	Aug 1968	71	Aug 1971	104	Mar 1974
6	Jun 1965	39	Sep 1968	72	Sep 1971	105	Jun 1974
7	Jul 965	40	Oct 1968	73	Oct 1971	106	Jul 1974
8	Aug 1965	41	Nov 1968	74	Nov 1971	107	Aug 1974
9	Sep 1965	42	Dec 1968	75	Dec 1971	108	Sep 1974
10	Oct 1965	43	Jan 1969	76	Jan 1972	109	Oct 1974
11	Nov 1965	44	Feb 1969	77	Feb 1972	110	Nov 1974
12	Dec 1965	45	Mar 1969	78	Mar 1972	111	Dec 1974
13	Jan 1966	46	Apr 1969	79	Apr 1972	112	Jan 1975
14	Feb 1966	47	May 1969	80	May 1972	113	Feb 1975
15	Mar 1966	48	Jun 1969	81	Jun 1972	114	Mar 1975
16	Oct 1966	49	Jul 1969	82	Jul 1972	115	Apr 1975
17	Nov 1966	50	Aug 1969	83	Aug 1972	116	May 1975
18	Dec 1966	51	Sep 1969	84	Sep 1972	117	Jun 1975
19	Jan 1967	52	Oct 1969	85	Oct 1972	118	Jul 1975
20	Feb 1967	53	Nov 1969	86	Nov 1972	119	Aug 1975
21	Mar 1967	54	Dec 1969	87	Dec 1972	120	Sep 1975
22	Apr 1967	55	Jan 1970	88	Jan 1973	121	Oct 1975
23	May 1967	56	Feb 1970	89	Feb 1973	122	Nov 1975
24	Jun 1967	57	Mar 1970	90	Mar 1973	123	Dec 1975
25	Jul 1967	58	Jul 1970	91	Apr 1973	124	Jan 1976
26	Aug 1967	59	Aug 1970	92	May 1973	125	Feb 1976
27	Sep 1967	60	Sep 1970	93	Jun 1973	126	Mar 1976
28	Oct 1967	61	Oct 1970	94	Jul 1973	127	Apr 1976
29	Nov 1967	62	Nov 1970	95	Aug 1973	128	May 1976
30	Dec 1967	63	Dec 1970	96	Sep 1973	129	Jun 1976
31	Jan 1968	64	Jan 1971	97	Oct 1973	130	Jul 1976
32	Feb 1968	65	Feb 1971	98	Nov 1973		
33	Mar 1968	66	Mar 1971	99	Dec 1973		

DISCUSSION

Patterns of waterbird utilisation

Waterbird utilisation at Rondevlei shows a clear seasonal pattern (Figs. 2 and 3). However, the Sanctuary's waterbird 'seasons' do not coincide precisely with traditional austral seasons (summer = November-February; winter = June-September). The January-April 'season' (D in Fig. 2 and Tab. V) is characterized by high waterbird species richness and abundance for both residents and migrants. Banks (1980), in her short term study, also found high values for waterbird species richness and abundance at the Sanctuary during January-April and attributed these to increased availability of shallow water (< 30 cm) and mud habitat, due primarily to the effects of low water level. Strong positive correlations between Banks' (1980) and long-term monthly mean values for rainfall, water level, maximum and minimum ambient

TABLE V. Waterbird total abundance and richness statistics for month-clusters in Figs 3a & 3b. Significant results of the analysis of variance between month-clusters in terms for abundance/richness measures of waterbird species and groups, and of environmental diversity. Abbreviations as in Tabs I and III significantly over- (+) and under- (-) represented at the P < = 0,05 (*), and P < = 0.01 (**), and P < = 0.001 (***) levels; NA = zero counts within the cluster under study.

	Month cluster						
	A	B	C	D	E	F	G
Waterbird mean total abundance	1325	1191	1090	2209	1381	494	1781
Waterbird mean richness	19	17	20	24	16	13	17
SPECIES: Dabchick				(+)*	(-)NA		(-)**
White Pelican				(+)***		(-)*	(-)*
Reed Cormorant		(-)*		(+)***		(-)**	(-)*
Grey Heron	(-)***			(+)***	(-)NA	(-)**	
Little Egret							
Yellow-billed Egret							
Sacred Ibis						(-)NA	
Spoonbill				(+)*			
Greater Flamingo		(+)*		(+)**		(-)*	
Lesser Flamingo	(-)**	(+)***			(-)NA		
Spurwing Goose	(-)***		(+)*	(+)***		(-)*	
Egyptian Goose	(-)*		(-)*	(+)***			
Cape Shoveller		(-)*	(-)*	(+)**			(-)*
Yellowbilled Duck				(+)***			
Redbilled Teal	(+)**				(-)NA		
Fulvous Duck					(-)NA	(-)NA	(-)NA
Redeyed Pochard			(-)*		(+)***		(-)NA
Maccoa Duck					(+)***	(-)NA	(-)NA
Moorhen			(+)**	(+)*	(-)NA		(-)**
Redknobbed Coot			(-)*	(+)**			(-)*
Curlew Sandpiper	(-)***			(+)***			(+)**
Little Stint	(-)***	(-)NA		(+)***	(-)NA	(-)NA	(+)***
Ruff	(-)***	(-)NA		(+)***	(-)NA	(-)NA	
Avocet	(-)***		(+)**	(+)***	(-)NA	(-)NA	
Stilt	(-)***		(+)**	(+)***		(-)*	
Whitewinged Black Tern		(-)NA				(-)NA	(+)***
GROUPS: TOT-AB	(-)*		(-)*	(+)***		(-)**	
RES-AB			(-)**	(+)***		(-)**	(-)***
MIG-AB	(-)**			(+)*			(+)***
BM1-AB	(-)**			(+)*			(+)***
BM2-AB		(-)**	(-)**	(+)***			(-)**
BM3-AB	(-)*	(-)***		(+)**		(-)*	
DV-AB				(+)***		(-)*	
DI-AB	(-)*			(+)***		(-)*	(+)*
FS-AB		(-)**	(-)*	(+)***			(-)***
FD-AB		(-)*	(-)		(+)***		(-)*
FBP-AB		(-)***		(+)**		(-)*	
FSP-AB	(-)***			(+)***			(+)*
TOT-RICH	(-)*	(-)*		(+)***	(-)**	(-)***	(-)**
RES-RICH				(+)***	(-)**	(-)***	(-)***
MIG-RICH	(-)***	(-)***		(+)***	(-)*	(-)***	
ENVIRONMENT							
RF			(+)**	(-)***		(+)*	
RF-PR	(+)*			(-)***		(+)***	
WL	(+)***		(-)**	(-)***	(+)**	(+)***	(-)***
WL-PR	(+)***	(-)*	(-)***		(+)*	(+)**	(-)***
WT	(-)*	(-)***	(-)***	(+)***			
WT-PR	(-)***	(-)**		(+)***	(-)*	(-)**	(+)**
TMAX		(-)**	(-)***	(+)***		(-)*	
TMIN		(-)**	(-)***	(+)***		(-)*	
TMIN-PR	(-)***	(-)**		(+)***	(-)*	(-)**	(+)*

TABLE VI. Correlations between waterbird and environmental variables. Abbreviations as in Tabs I and III. P = 0.05, r = 0.18; P = 0.01, r = 0.23; P = 0.001, r = 0.29.

	RF	RF-PR	WL	WL-PR	WT	WT-PR	TMAX	TMAX-PR	TMIN	TMIN-PR
RF-PR	0.37									
WL	0.15	0.47								
WL-PR	-0.18	0.16	0.83							
WT	-0.67	-0.65	-0.32	0.11						
WT-PR	-0.43	-0.68	-0.66	-0.30	0.82					
MAX	-0.64	-0.63	-0.28	0.10	0.89	0.73				
MAX-PR	-0.43	-0.66	-0.63	-0.27	0.76	0.90	0.73			
MIN	-0.59	-0.67	-0.26	0.13	0.92	0.79	0.91	0.76		
MIN-PR	-0.46	-0.61	-0.61	-0.25	0.79	0.93	0.75	0.91	0.80	
Dabchick	-0.10	-0.05	0.16	0.22	0.11	0.07	0.11	0.08	0.14	0.10
White Pelican	-0.22	-0.22	-0.09	0.01	0.27	0.33	0.31	0.33	0.31	0.37
Reed Cormorant	-0.14	-0.27	-0.10	0.02	0.22	0.24	0.32	0.33	0.24	0.22
Grey Heron	-0.12	-0.34	-0.37	-0.28	0.31	0.48	0.32	0.46	0.32	0.49
Little Egret	-0.10	-0.08	0.05	0.11	0.09	0.03	0.13	0.08	0.10	0.05
Yellowbilled Egret	-0.12	-0.12	0.07	0.16	0.17	0.13	0.20	0.15	0.19	0.12
Sacred Ibis	-0.09	-0.07	0.12	0.15	-0.01	-0.08	0.23	-0.01	0.05	-0.05
Sponbill	-0.15	-0.26	-0.22	-0.09	0.23	0.30	0.38	0.34	0.31	0.32
Greater Flamingo	-0.12	-0.14	-0.15	-0.12	0.10	0.09	0.18	0.18	0.09	0.11
Lesser Flamingo	0.07	-0.04	-0.27	-0.32	-0.09	0.05	-0.06	0.06	-0.10	0.04
Spurwing Goose	-0.04	-0.25	-0.34	-0.27	0.17	0.41	0.14	0.36	0.20	0.40
Egiptian Goose	-0.20	-0.26	-0.22	-0.07	0.31	0.29	0.32	0.26	0.32	0.27
Cape Schoveller	-0.25	-0.19	0.16	0.31	0.38	0.24	0.32	0.16	0.39	0.23
Yellowbilled Duck	-0.04	-0.18	-0.10	0.00	0.32	0.30	0.21	0.25	0.27	0.27
Redbilled Teal	-0.16	-0.12	0.18	0.28	0.22	0.09	0.14	0.02	0.20	0.17
Cape Teal	0.14	0.09	0.15	-0.04	-0.27	-0.23	-0.24	-0.32	-0.27	-0.28
Fulvous Duck	-0.06	-0.03	0.09	0.04	0.12	0.08	0.08	0.02	0.09	0.06
Redeyed Pochard	-0.18	-0.07	0.30	0.40	0.16	-0.05	0.14	-0.05	0.15	-0.07
Maccoa Duck	0.03	0.06	0.23	0.23	-0.12	-0.20	-0.07	-0.15	-0.11	-0.20
Moorhen	-0.03	-0.08	-0.10	-0.10	-0.06	0.06	-0.03	0.06	-0.08	0.01
Redknobbed Coot	-0.25	-0.21	0.15	0.31	0.35	0.21	0.30	0.28	0.34	0.24
Curlew S'piper	-0.12	-0.33	-0.52	-0.32	0.31	0.47	0.28	0.49	0.27	0.49
Little Stint	-0.09	-0.29	-0.65	-0.50	0.24	0.47	0.20	0.47	0.20	0.45
Ruff	-0.19	-0.30	-0.38	-0.20	0.38	0.46	0.34	0.42	0.36	0.45
Avocet	-0.15	-0.30	-0.43	-0.23	0.30	0.47	0.27	0.43	0.28	0.47
Stilt	-0.06	-0.27	-0.44	-0.36	0.14	0.34	0.11	0.37	0.09	0.34
Whitewinged Tern	-0.15	-0.17	-0.19	-0.11	0.19	0.22	0.22	0.26	0.21	0.26
TOT-RICH	-0.32	-0.38	-0.35	-0.12	0.53	0.55	0.51	0.55	0.54	0.56
RES-RICH	-0.16	-0.30	-0.15	-0.04	0.26	0.27	0.26	0.28	0.29	0.28
MIG-RICH	-0.43	-0.56	-0.50	-0.18	0.70	0.73	0.66	0.72	0.67	0.74
TOT-AB	-0.35	-0.41	-0.21	0.01	0.51	0.48	0.51	0.53	0.50	0.51
RES-AB	-0.32	-0.33	0.02	0.20	0.45	0.34	0.44	0.38	0.44	0.35
MIG-AB	-0.17	-0.23	-0.32	-0.20	0.25	0.33	0.27	0.36	0.26	0.37
BM1-AB	-0.18	-0.24	-0.32	-0.20	0.26	0.34	0.27	0.37	0.26	0.38
BM2-AB	-0.31	-0.28	0.20	0.40	0.49	0.30	0.41	0.30	0.48	0.31
BM3-AB	-0.11	-0.18	-0.24	-0.21	0.10	0.16	0.20	0.23	0.10	0.17
DV-AB	-0.25	-0.31	-0.13	0.01	0.33	0.38	0.41	0.43	0.37	0.41
DI-AB	-0.28	-0.33	-0.29	-0.12	0.38	0.40	0.42	0.45	0.39	0.44
DH-AB	-0.24	-0.27	0.07	0.24	0.41	0.29	0.34	0.33	0.38	0.30
FS-AB	-0.31	-0.29	0.15	0.35	0.49	0.34	0.41	0.33	0.48	0.35
FD-AB	-0.22	-0.15	0.29	0.42	0.23	0.03	0.24	0.06	0.23	0.02
FBP-AB	-0.09	-0.16	-0.23	-0.21	0.08	0.12	0.17	0.20	0.07	0.13
FSP-AB	-0.16	-0.39	-0.66	-0.43	0.36	0.60	0.32	0.58	0.32	0.59

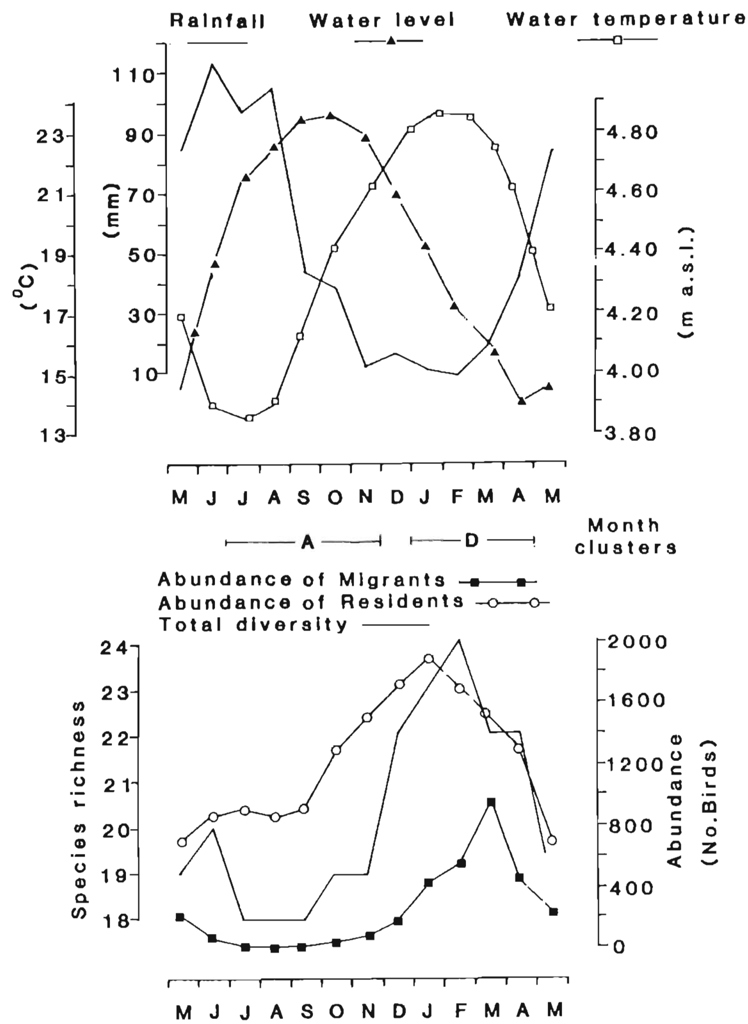

FIGURE 3. Temporal relationship between monthly means for waterbird total species richness and resident and migrant abundance, rainfall, water level and temperature. A and D are month clusters in Fig. 2.

temperature, total waterbird abundance, and species richness ($r = 0.91, 0.93, 0.88, 0.89, 0.73$; $P < 0.01$) indicate that a similar habitat availability hypothesis could explain water bird species richness and abundance pattern in Rondevlei over the longer term.

Indirect supporting evidence of this habitat availability hypothesis is the fact that Palaearctic migrant waterbirds, although present in the southwestern Cape in October (Blaker & Winterbottom 1968; Pringle & Cooper 1977) do not come to Rondevlei in numbers until January-February (Tab. II), when the water level at the vlei is low enough to allow a significant amount of shallow water habitat (Fig. 1). Moreover, during the relatively warm January-April 'season', the 'quality' of the various habitats is improved by a proliferation of plant, invertebrate and vertebrate prey for waterbirds (Harrison 1958, 1962; Middlemiss 1974; Guillet & Crowe 1981, 1983; Guillet & Furness 1985).

Cluster A, the July-November waterbird 'season' is characterized (Tab. V) by cool, deep water, conditions with a low availability of shallow water and mud habitats. Not unexpectedly, the primary reason for its low waterbird species richness and abundance is the absence of migrants.

The clusters of low waterbird species richness (B, E, F and G in Figs. 2a and b) represent extreme environmental conditions and usually low waterbird abundance (Tab. V). For example, in cluster E, the Red-eyed Pochard, Maccoa Duck *Oxyura maccoa* and Yellowbilled Duck *Anas undulata* are 'overrepresented', presumably exploiting the relatively deep water conditions at the vlei (high values for WL and WL-PR). Conversely, cluster B is characterized by months in two different years (June-July 1967 and June-September 1972) with low water level conditions, and high abundance values for Greater and Lesser Flamingos *Phoenicopterus ruber* and *Phoenicopterus minor*. In months comprising cluster G (April-May 1973 and March-April 1974) there were persistent, extreme shallow water conditions. In fact, the vlei virtually dried out, and species which utilise shallow water/mud habitat, such as the Little Stint *Calidris minuta*, Curlew Sandpiper *C. ferruginea* and Whitewinged Black Tern *Chlidonias leucopterus* were among the few present in numbers. Cluster F comprises months with extremely low temperatures and high rainfall and water level conditions (July-November 1974, the highest rainfall season of the study period). Its low richness/abundance and lack of characteristic species might therefore reflect the overall unsuitable conditions for the waterbird species investigated in this study.

Waterbird species richness and abundance and environmental correlations

The results of this study support Banks' (1980) primary conclusion, that the fluctuating water level at Rondevlei affects the waterbird community at the Sanctuary via its effects on habitat availability. However, they also indicate that there is a threshold-like relationship between waterbird richness/abundance and water level. For example, only once water level drops below 4.45 m a.s.l. does the availability of shallow water and mud habitats increase dramatically (Fig. 1). The increased availability of these habitats is soon followed by an increase in the species richness and abundance of waders. Moreover, this study also suggests that relatively strong positive correlations found between water and ambient temperature and the presence of waterbirds are presumably mediated through the effects of warmer conditions on the availability of a broad array of plant and animal food types (see below). The differential impact of water level and temperature on waterbird utilisation at Rondevlei, is perhaps best reflected by differences in the correlation pattern between members of the foraging and body mass groups and environmental variables. The abundance of members of the medium mass (BM2-AB) and swimmer (FS-AB) groups is more strongly correlated with temperature variables, whereas the abundance of small mass, wading waterbirds (BM1-AB and FSP-AB) is more strongly correlated with water level. This correlation pattern is consistent with the idea that the availability of habitat might be a primary limiting factor to the utilisation of 'shallow water' smaller waterbirds, and that of food to the 'warm, deeper water' waterbirds.

Rainfall

Rainfall affects waterbird richness/abundance at Rondevlei primarily through the lag effect it has on water level. This lag relationship is illustrated by the significant positive correlation ($r = 0.47$; $P < 0.001$) between water level (WL) and rainfall for the preceding month (RF-PR) and the non-significant correlation ($r = 0.15$; $P > 0.05$) betwween WL and rainfall for the current month (RF) (Tab. VI). Moreover, the effects of rainfall on water level are cumulative and are typically associated with crossing a 90 mm 'threshold' (Fig. 3).

Rainfall might also have another indirect effect on waterbird abundance at Rondevlei through its influence on waterbird prey. For example, rainfall is thought to trigger spawning of the Clawed frog *Xenopus laevis* (Picker 1982), the commonest amphibian at Rondevlei (Middlemiss 1974). Clawed frog tadpoles might from an important component of the diet of the chicks of both the Reed Cormorant *Phalacrocorax africanus* (Middlemis 1974) and Grat White Pelican *Pelecanus onocrotalus* (J. Cooper pers. comm.; A. Guillet unpub. data).

Water level

As shown above, and by Banks (1980), the effect of water level on the aquatic avifauna at Rondevlei, appears to be mediated through its effects on the availability of shallow water (< 30 cm deep) and mud habitats. Kushlan (1978) also found a strong negative relationship between water level and waterbird habitat availability. Water level variation plays a major role in critical aspects of waterbird ecological fluctuations, such as variation in the availability of prey (Kushlan *et al.* 1975, Kushlan 1976); or foraging and nesting habitat (Whitfield & Blaber 1978, 1979a, 1979b).

The generally stronger positive correlations between the abundance of members of the swimmer grouping (FS) (e.g. Redknobbed Coot *Fulica cristata*) and diver group (FD) (e.g. Redeyed Pochard) with water level of previous months (WL-PR) probably reflect a lag effect in the variation of suitable foraging conditions in relatively deep water habitat. This could, for example, be the development/decay of flooded vegetation and its associated invertebrate fauna. The positive correlation between the abundance of members of the plant eater group (DH-AB) with WL-PR and not with WL (current month water level) may also be due to such a lag effect. Shallow water habitat, on the other hand, is apparently suitable immediately as it becomes available, hence the relatively strong negative correlations between shallow water species and water level of the current month.

Temperature

Independent of its negative correlation with water level, the relevance of temperature to waterbird ecology in Rondevlei is probably mediated through its effects on both the crude and ecological density (*sensu* Kahl 1964) of a broad array of food types from small crustaceans to fish (Harrison 1958, 1962; Middlemiss 1974; Guillet & Crowe

1981, 1983; Guillet & Furness 1985). This is reflected in the relatively strong positive correlation of waterbird variables in general, and resident abundance in particular, with temprature variables (Fig. 3, Tab. VI).

Future research

Several other biotic and abiotic factors may also have a major impact on waterbird utilisation at Rondevlei. First, the high density of the exotic Common Carp *Cyprinus carpio* at the vlei (Hamman *et al.* 1977) may affect the invertebrate prey community. One possible outcome of predation by carp is reduction of waterbird food resources both in the form of overall invertebrate biomass and submerged vegetation (Britton 1982). Indeed, Reichholf (1975) invokes competition between fish and waterbirds as being an important determinant of waterbird species richness in South America. Since the Great White Pelican is the only predator at Rondevlei capable of taking large carp, both species at Rondevlei need to be studied to identify the roles each plays in that ecosystem. Additional attention should also be directed to interactive processes between turbidity and flooded vegetation which are important component of Rondevlei's ecological fluctuations (Tschortner 1969; Banks 1980).

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RIASSUNTO

Variazioni mensili e stagionali nell'avifauna acquatica di Rondevlei Bird Sanctuary (Provincia del Capo, Sud Africa)

- Si è studiata la variazione temporale nella ricchezza ed abbondanza di avifauna di ambiente acquatico del Rondevlei Bird Sanctuary, nel periodo 1965-76, facendo ricorso a metodi statistici uni- e multi-variati.
- La periodicità sia nell'andamento della ricchezza che dell'abbondanza di uccelli acquatici è chiaramente stagionale ed è correlata a variazioni ambientali.
- Alti valori di ricchezza/abbondanza di uccelli acquatici caratterizzano i mesi dell'estate-autunno australi (gennaio-aprile), bassi valori, i mesi primaverili (luglio-novembre).
- I valori più alti di ricchezza-abbondanza di uccelli acquatici si riscontrano in periodi di declino di piovosità e profondità del lago, e di alta temperatura ambientale ed acquatica. Bassi valori di ricchezza/abbondanza si riscontrano in periodi di bassa temperatura ed alti livelli di profondità del lago.
- Relazioni fra la ricchezza/abbondanza di varie associazioni (tasso-morfo-eco-etologiche e di stato migratorio) di uccelli acquatici e l'ambiente, sono mediate dagli effetti che le modificazioni ambientali hanno sulla accessibilità (densità ecologica *sensu* Kahl 1964) di habitat e di risorse alimentari.
- Maggiori variazioni nella accessibilità di habitat sono associate alla variazione di livelli di profondità del lago, variazioni nell'accessibilità di risorse alimentari, a modifiche di temperatura e probabilmente anche di piovosità.
- I risultati di questo studio, condotto su un periodo relativamente lungo, confermano ed approfondiscono i risultati di uno studio di dettaglio sulla avifauna di Rondevlei (Banks 1980).

FIG. 1. Accessibilità di una selezione di habitat di differenti livelli di profondità del lago, a Rondevlei (da Banks 1980).
FIG. 2. L'andamento di utilizzazione del Santuario da parte di uccelli acquatici durante 130 mesi, secondo le analisi di: a) *cluster*, e b) *multidimensional scaling*. Vedi Tab. IV per informazioni riguardanti l'identificazione dei mesi (1-130), ed il testo per quelle riguardanti i raggruppamenti (*clusters*) di mesi (A-G). I mesi cerchiati sono discussi nel testo.
FIG. 3. Relazione temporale fra le medie mensili di ricchezza totale di uccelli acquatici e dell'abbondanza di specie stanziali e migratrici, piovosità, livelli di profondità del lago e temperature. Tipici mesi dei *clusters* analizzati.
TAB. I. Elenco delle specie di uccelli acquatici in questo studio, e categorizzazione in gruppi a seconda del peso, dieta (1 = dieta a prede vertebrate, 2 = invertebrati, 3 = vegetali), comportamento di alimentazione (1=nuoto,2=tuffo, 3,4=cammina, 5=altro), e status (1 = residente, 2 = migratore).
TAB. II. Conteggi medi mensili delle specie di uccelli acquatici a Rondevlei, 1965-1976.
TAB. III. Parametri di ricchezza totale di specie, di associazioni (ICH) e di abbondanza (AB) di uccelli acquatici, e della variazione ambientale analizzate nel presente studio; abbreviazioni impiegate per i mesi in corso, e per quelli precedenti (PR). Vedi testo e Tab. I per delucidazioni.
TAB. IV. I 130 mesi nei quali sono stati effettuati i censimenti a Rondevlei, e i relativi codici utilizzati in Fig. 2.
TAB. V. Dati statistici sulla abbondanza totale e la ricchezza di uccelli acquatici, riferentisi a *clusters* di mesi identificati in Fig. 3a, 3b). Risultati statisticamente significativi dell'analisi della varianza fra *clusters* di mesi in termini di misure di ricchezza/abbondanza totali e di associazioni di uccelli acquatici, e della diversità ambientale.
TAB. VI. Correlazioni fra dati su uccelli acquatici ed ambientali.

RESUME'

Variations mensuelles et saisonnières de l'avifaune aquatique de Rondevlei Bird Sanctuary (Provincie du Cap, Afrique du Sud)

-On a étudié la variation temporelle de richesse/abondance d'avifaune et d'ambiance aquatique à Rondevlei Bird Sanctuary pendant la période 1965-76, en employant des méthodes statistiques uni- et multivariées.
- Soit la périodicité de la variation de richesse soit celle d'abondance d'oiseaux aquatiques ont un caractère saisonnier et sont en corrélation avec la variation de l'ambiance.
- L'eté-automne australes (janvier-avril) sont characterizés par des hautes valeurs de la diveristé/abondance, tandis que l'hiver-printemps (juillet-novembre) montrent des basses valeurs.
- Les valeurs de richesse/abondance d'oiseaux aquatiques montrent un pic pendant la période de diminution de pluie et de profondeur du lac. Ces mêmes valeurs sont basses pendant la période de basse température et haute profondeur du lac.
- Les relations entre la richesse/abondance de différents group (taxo-morpho-eco-ethologiques) d'oiseaux aquatiques et l'ambiance, sont influencées par les repercussions de la variation ambientale sur la disponibilité (densité écologique *sensu* Kahl 1964) d'habitat et de ressources alimentaires.
- Les variations les plus hautes en disponibilité d'habitat sont liées à la variation de profondeur de l'eau du lac, tandis que les variations en disponibilité de ressources alimentaires sont liées à celles de la température et probablement aussi de précipitation pluvieuse.
- Les résultats de cette étude, qui couvre une période à long terme relatif, complémentent et élargissent les résultats d'une étude de détail sur l'avifaune aquatique de Rondevlei (Banks 1980).

FIG. 1. Disponibilité d'une sélection d'habitat de differente profondeur d'eau et de boux, en relation à différents niveaux de profondeur du lac à Rondevlei (de Banks 1980).
FIG. 2. La tendance d'utilisation du Sanctuaire de la part des oiseaux aquatiques pendant 130 mois, en tant que reconnue par les analyses de: a) *cluster*, et b) *multidimensional scaling*. Voir Tab. IV pour des informations concernant l'identification des mois (1-130), et le texte pour celles concernant les *clusters* de mois (A-G). Les mois encerclés sont discutés dans le texte.
FIG. 3. Relation temporelle entre les moyennes mensuelles de richesse totale d'oiseaux aquatiques et d'abondance d'éspèces résidentes et migratrices, précipitation, niveau de profondeur du lac et temperature. Les mois typiques des *clusters* étudiés.
TAB. I. Liste des espèces d'oiseaux aquatiques dans cette étude.
TAB. II. Résultats des recensements d'oiseaux aquatiques (moyennes mensuelles), 1965-1976.
TAB. III. Mesures de la richesse totale et de *groups* (RICH) et de l'abondance (AB) d'oiseaux aquatiques, et de la variation ambientale analysée dans cette étude; les abréviations employées pour les mois en cours et les mois précédent (PR) ceux-ci (voir le texte et la Tab. I pour des clarifications).

TAB. IV. Les 130 mois pour lesquelles on a recensé l'avifaune de Rondevlei, et leur codes utilizés dans la Fig. 2.
TAB. V. Données statistiques sur l'abondance totale et la richesse d'oiseaux aquatiques pour les *clusters* de mois en Fig. 3a et 3b. Résultats statistiquement significatifs de l'analyse de variance entre *clusters* de mois en termes de mésures de richesse/abondance d'éspèces et de *groups* d'oiseaux aquatiques, et de mésures de diversité ambientale.
TAB. VI. Corrélations entre données sur les oiseaux aquatiques et sur l'ambiance.

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