Waterfowl abundance and diversity in relation to season, wetland characteristics and land-use in semi-arid South Africa

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We studied waterfowl abundance and diversity in relation to season (wet *vs* dry), wetland characteristics (vegetation and morphometrics) and land-use in a semi-arid agricultural region of South Africa to determine how waterfowl respond to various wetland characteristics, particularly those of permanent agricultural ponds. Wetlands were visited during the wet (n = 215) and dry (n = 178) seasons of 1997 and species' abundances, and wetland and upland characteristics were recorded. Canonical correspondence analyses and multiple regressions determined which wetland and upland characteristics were most strongly associated with waterfowl density and species richness for both the wet and dry season. Overall, diving ducks were not abundant in the wet season, and were rare to absent in the dry season. Divers only responded positively to the characteristics of natural wetlands, including greater surface area, percent coverage of emergent vegetation, and high (ungrazed) shoreline vegetation. Of six species of dabbling ducks present during the wet season, occurrence of three co-varied with wetland and upland characteristics associated with agriculture, namely permanent water, and agricultural grains in the dry season. Being largely grazers, geese responded positively to the higher proportions of bare shoreline, characteristically surrounding agricultural ponds. Because only a few species associated with artificial waterbodies, natural wetlands should be conserved to protect waterfowl diversity in semi-arid South Africa.

Key words: semi-arid, South Africa, waterfowl abundance, environmental characteristics, artificial waterbodies.

INTRODUCTION

Many of the natural wetlands used by waterfowl in the semi-arid interior of South Africa are ephemeral and tend to dry up during the winter dry season (Petrie 1998). The availability of native terrestrial and aquatic seeds consumed by waterfowl also declines throughout winter (Petrie 1996; Petrie & Rogers 1996). Presumably, historical reductions in water and food availability meant that waterfowl once migrated from semi-arid areas to riverine and subtropical regions during winter. However, European settlement resulted in wide-scale changes to terrestrial as well as aquatic habitats throughout semi-arid regions. Increased water requirements, largely for crop and livestock production, resulted in the loss and alteration of many of South Africa's natural wetland systems (Breen & Begg 1989; Petrie & Rogers 1997). For instance, some wetlands were lost through drainage and the lowering of water tables, whereas others were impacted by dam construction (Tarboton & Batchelor 1981; Higgins *et al.* 1996). Agricultural expansion also resulted in the need for water throughout the year and led to the creation of permanent and semi-permanent waterbodies (impoundments and dugouts) for irrigation and stock watering. Consequently, cereal grain farming and the provision of permanent water have provided a novel food source and permanent aquatic habitats in semi-arid regions (Petrie & Rogers 1996, 1997; Petrie 2005) that now allow certain species to remain in semi-arid regions throughout the annual wet and dry seasons (Petrie & Rogers 1996, 1997).

Unfortunately, much of what is known about habitat use and requirements in the family Anatidae is a product of research conducted in north-temperate and arctic systems (*cf.* Petrie 1996, 1998). For instance, waterfowl use of agricultural

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ponds in north-temperate regions increases with pond size, pond age, presence of loafing sites, emergent vegetation, shoreline irregularity, and proximity to other ponds (Lokemoen 1973; Evrard 1975; Hudson 1983; Belanger & Couture 1988). By comparison, little is known about how waterfowl species respond to wetland characteristics and seasonal changes in wetland availability in semi-arid regions of South Africa.

Owing to differences in ecological requirements and foraging capabilities, extensive land-use change and the provision of permanent waterbodies should have a strong influence on the distribution and abundance of certain anatid species, particularly in winter. For instance, dabbling ducks and geese that feed in fields should respond to anthropogenically provided waterbodies and associated cereal grains during the dry season (Johnsgard 1978; Petrie & Rogers 1997; Petrie 1998). Diving ducks do not field feed, and most permanent stock and irrigation ponds generally do not support large quantities of waterfowl food in winter due to rapidly fluctuating water levels (irrigation ponds), winter senescence, and trampling by cattle (stock ponds) (S. Petrie, pers. obs.). Therefore, most species of diving ducks should migrate out of semi-arid regions in winter.

The objectives of this study were to determine how species respond to variation in natural and agricultural waterbodies in the winter dry season by comparing which vegetation and morphometric wetland characteristics, and associated land-use, are the primary determinants of wetland use by waterfowl during each season. This study will provide a better understanding of how anthropogenic landscape changes have influenced waterfowl abundance and diversity in semi-arid regions and will also provide information useful for the management of semi-arid occurring waterfowl and their aquatic habitats.

METHODS

Study area

The Springbok Flats of Limpopo Province, South Africa, is a region characterized by a semi-arid climate. These conditions are the result of high summer temperatures (mean daily = 29°C), low annual rainfall (average of 623 mm), and an annual evaporation rate that is nearly double the precipitation rate (Huntley & Morris 1978; Frost 1987). Consequently, most of the natural wetlands within the Springbok Flats are either seasonal or ephemeral. Therefore, although natural wetlands in this region can provide a large amount of habitat and food for breeding waterfowl when flooded, they tend to dry up during winter (Uys & MacLeod 1967; Tarboton & Batchelor 1981).

A 3643 km^2 semi-arid area of the Springbok Flats, southeast of the town of Naboomspruit (now called Mookgopong) was selected for study. A total of 292 wetlands was surveyed from each of four regions within the flats. One area in the 'northwest' included the Nyl River floodplain, and several other areas of unbroken bushveld. The 'southwest' area contained numerous wetlands and was extensively cultivated. The 'northeast' area was also extensively cultivated, but contained fewer wetlands than the 'southwest'. Lastly, the 'southeast' area was characterized by irrigated agricultural land surrounded by bushveld.

Field methods

Waterfowl and wetland surveys were performed during the wet (23 February – 3 April) and dry seasons (31 July – 22 August) of 1997. Each wetland was visited once per season to count waterfowl by species (all waterfowl species, scientific names and guild groupings are listed in Appendix 1) and to record wetland and upland characteristics. The percentage of emergent vegetation, submerged vegetation, and open water of a pond's surface area were visually estimated. The percentages of the shoreline (within approximately 5 m from shore) containing tall vegetation (over 0.6 m), grazed vegetation, or no vegetation (bare) were also recorded. The percentages of the pond with water depths above and below 1 m were estimated by taking numerous water depth measurements around the pond and then visually estimating the proportion above and below 1 m. Each pond was assigned one of the following categorical variables based on pond depth and associated degree of permanency; 1 = ephemeral/seasonal wetlands that likely dry up each dry season, 2 = semi-permanent wetlands that dry up during some years, and 3 = permanent wetlands that rarely dry up. The percentage of elevated shoreline that provided loafing areas suitable for predator detection was visually estimated at each wetland. Water turbidity was measured (cm) using a modified secchi disk. We also recorded whether ponds were constructed (dugouts) or altered (impoundments) for agricultural purposes (collectively referred to as artificial ponds) or if wetlands were largely unaffected (collectively referred to as natural wetlands). Total surface area of large ponds was estimated using pond width, length, and configuration dimensions acquired from 1:50 000 base maps. Small pond dimensions were estimated by pacing off the length and width of each waterbody. To have a comparable measure of waterfowl use between ponds of different sizes, raw abundance values were divided by the total surface area of the pond for a measure of waterfowl density on a pond. Only ponds containing water were used in the analyses.

Uplands associated with each pond (within approximately 100 m of the pond) were classified as natural, grazed, or cultivated. When more than one type of upland habitat was present, the percentage of each type was estimated using 1:50 000 base maps and visual estimation. A categorical measure of grazing intensity was also recorded and included; 0 = no grazing, 1 = light grazing intensity, 2 = moderate grazing intensity, and 3 = high grazing intensity.

Statistical methods

A discriminant function analysis (DFA) was performed for each season to determine which wetland and upland characteristics best discriminated between natural and agricultural ponds. A contingency table was developed to determine if the number of ponds with water differed by type (agricultural or natural), or by season (wet or dry). Log-linear analyses were performed to determine if ponds differed in their permanence, or grazing intensity by pond type. Two-way ANOVAs were performed to determine if pond area, or pond turbidity differed by pond type, or season.

Canonical correspondence analysis (CCA) is a gradient analysis technique that creates axes of linear combinations of environmental variables to which community composition information (guild density or species richness of a guild) is applied (ter Braak 1986). To generate more powerful statistical comparisons, we categorized waterfowl species into their respective guilds prior to conducting CCAs: divers, dabblers, or geese. Knob-billed ducks (*Sarkidiornis melanotos*) were included with geese because they are more phylogenetically and ecologically similar to the geese than the ducks in this region. The knob-billed duck belongs to the same tribe as the spur-winged goose (Cairinini) (*Plectropterus gambensis*), and with the Egyptian goose, share a predominantly vegetarian diet consisting of soft aquatic plant material, and native and agricultural grasses and seeds (Clancey 1967). We used season-specific CCAs to determine which wetland and upland characteristics were most closely associated with overall patterns in guild density. We then used CCA to relate environmental data to patterns of species richness for each guild during each season. Multiple regressions were then used to test for relationships between guild density or richness (response variables) and 14 continuous environmental characteristics (predictor variables). The results of the DFAs, CCAs, and multiple regressions together facilitated an assessment of whether and how permanent waterbodies and cereal grain cultivation in this semi-arid region affect the intra- and inter-seasonal distribution and abundance of divers, dabblers, and geese. Significance for all statistical tests was assessed at $P < 0.05$.

Statistical analyses were performed with SPSS Version 12.0 (SPSS, Chicago, IL) and PC-ORD Version 4.0 Multivariate Analysis of Ecological Data (MjM Software Design, Gleneden Beach, OR) statistical software.

RESULTS

Seasonal wetland characteristics

There were more agricultural ponds than natural ponds with water in the wet season (90.2 *vs* 9.8%, $n = 215$), as well as during the dry season (89.3 *vs* 10.7%, $n = 178$). There was, however, no significant interaction between season and pond type on the number of ponds containing water ($\chi^2 = 0.09$, d.f. = 1, $P = 0.77$). Agricultural ponds were more permanent with respect to water retention than were natural ponds ($\chi^2 = 87.6$, d.f. = 2, $P < 0.001$). Agricultural ponds also had higher intensity grazing of associated uplands than did natural ponds ($\chi^2 = 39.4$, d.f. = 2, $P < 0.001$). Although water turbidity did not vary significantly with pond type ($F = 0.85$, d.f. = 1,386, $P = 0.36$), there was some indication that turbidity was higher in the dry season ($F = 3.21$, d.f. = 1,386, $P = 0.07$). Total pond surface area was greater for natural ponds (15.1 ± 40.2 ha, $n = 40$) than agricultural ponds (1.9 ± 4.2 ha, $n = 353$) ($F = 34.50$, d.f. = 1,389, $P < 0.001$) and there was some indication that pond surface area declined somewhat between the summer wet and the winter dry season ($F = 3.52$, d.f. = 1,386, $P = 0.06$).

In the wet season, DFA clearly discriminated between natural and agricultural ponds based on their measured environmental variables, with very little within-pond type variation (Wilks' λ =

Table 1. Seasonal mean (±S.D.) values for environmental variables of agricultural and natural ponds, and corresponding standardized canonical discriminant function coefficients for the first discriminant function (r).

Environmental characteristic[a]	Wet season			Dry season		
	Agricultural	Natural	r	Agricultural	Natural	r
Turb (cm)	289.5 ± 234.0	379.5 ± 202.9	–0.17	420.2 ± 328.0	410.5 ± 266.4	0.07
SA (m^2)	2.0 ± 4.7	19.0 ± 45.5	–0.32	1.8 ± 3.6	10.9 ± 34.0	–0.34
PO (%)	66.7 ± 36.5	6.7 ± 16.2	1.16	68.5 ± 35.4	10.1 ± 22.4	–0.79
PE (%)	24.3 ± 30.3	86.6 ± 27.6	0.33	23.4 ± 29.7	85.0 ± 23.4	–1.22
PS (%)	8.5 ± 18.5	1.9 ± 3.7	0.82	8.1 ± 15.6	4.9 ± 8.0	n/a[b]
<1 m (%)	59.3 ± 36.1	92.6 ± 22.6	0.09	64.0 ± 32.7	98.4 ± 5.0	0.17
>1 m (%)	39.7 ± 36	7.4 ± 22.6	0.28	35.3 ± 32.4	1.6 ± 5.0	0.43
Elev (%)	58.9 ± 38.8	5.2 ± 12.9	0.47	57.5 ± 38.1	8.4 ± 23.6	0.36
SB (%)	29.3 ± 36.6	1.0 ± 4.4	–0.80	37.2 ± 41.4	0.2 ± 0.7	0.34
SG (%)	25.3 ± 28.5	18.1 ± 30.3	–0.58	27.6 ± 31.3	13.3 ± 24.9	0.21
SHV (%)	44.7 ± 40.2	81.0 ± 32.0	–0.82	34.8 ± 38.8	86.6 ± 24.8	0.06
UN (%)	25.6 ± 42.1	47.6 ± 51.2	–0.02	21.2 ± 39.7	47.4 ± 51.3	0.25
UG (%)	45.7 ± 48.9	52.4 ± 51.2	0.11	50.5 ± 49.4	52.6 ± 51.3	0.67
UC (%)	28.6 + 42.9	0.0 ± 0.0	n/a[b]	29.0 ± 43.4	0.0 ± 0.0	0.56

[a]Turb = turbidity of the water; SA = surface area; PO = open water on the pond; PE = emergent vegetation on the pond; PS = submerged vegetation on the pond; <1 m = depth <1 m; >1 m = depth 0–1 m; Elev = elevated shoreline; SB = bare shoreline; SG = grazed shoreline; SHV = high vegetation on the shoreline; UN = natural upland; UG = grazed upland; UC = cultivated upland.

[b]Variable excluded from analysis due to high collinearity.

0.58, $\chi^2 = 112.25$, d.f. = 13, $P < 0.0001$). The DFA correctly classified 95.3% of natural ponds and 89.2% of agricultural ponds. The percentages of pond surface area with open water and submerged vegetation were strongly correlated with the first discriminant function (DF1) and varied together (Table 1). The model showed that agricultural ponds had much higher proportions of open water, and submerged vegetation than did natural ponds (Table 1). The percentages of shoreline with tall vegetation and bare shoreline were also strongly correlated with DF1 (Table 1). Natural ponds had higher proportions of their shoreline occupied by high vegetation than agricultural ponds, and less of their shoreline was bare as compared to agricultural ponds (Table 1).

The dry season DFA also clearly distinguished between natural and agricultural ponds (Wilks' $\lambda = 0.57$, $\chi^2 = 95.88$, d.f. = 13, $P < 0.0001$). This model correctly classified 94.7% of natural ponds and 89.3% of agricultural ponds. The percentages of pond surface area with emergent vegetation and open water were strongly correlated with the dry season DF1 and varied together (Table 1). As with the wet season, agricultural ponds had a greater proportion of surface area open than natural ponds in the dry season (Table 1). Emergent vegetation was much more prevalent in natural than in agricultural ponds (Table 1). The percentage of the upland that was grazed, and that which was cultivated also helped to explain some variation between agricultural and natural ponds (Table 1). Natural ponds were never surrounded by cultivated upland, whereas over 25% of upland surrounding agricultural ponds was cultivated (Table 1). Agricultural ponds also tended to have more of their water depth greater than 1 m than did natural ponds (Table 1).

Waterfowl abundance

During the wet season, divers (southern pochard, *Netta erythrophthalma*; white-backed duck, *Thalassornis leuconotus*; and Maccoa duck, *Oxyura maccoa*) tended to occur on dammed portions of natural wetlands with deep water and ample emergent vegetation. During the dry season, divers were uncommon on agricultural as well as natural ponds (Fig. 1). Overall dabblers occur regularly on all pond types, with particularly high abundance in the dry season (Fig. 1). On agricultural ponds in the wet and dry season, and on natural ponds in the wet season, white-faced whistling ducks (*Dendrocygna viduata*) made up 89, 86, and 71% of dabbling duck occurrence, respectively. Of six white-faced whistling duck broods observed during the study, five were on agricultural ponds and one was on a natural vlei. Red-billed teal (*Anas erythrorhyncha*), yellow-billed ducks (*Anas undulata*), and Hottentot teal (*Anas hottentota*) were the next three most common species (Fig. 1). Fulvous

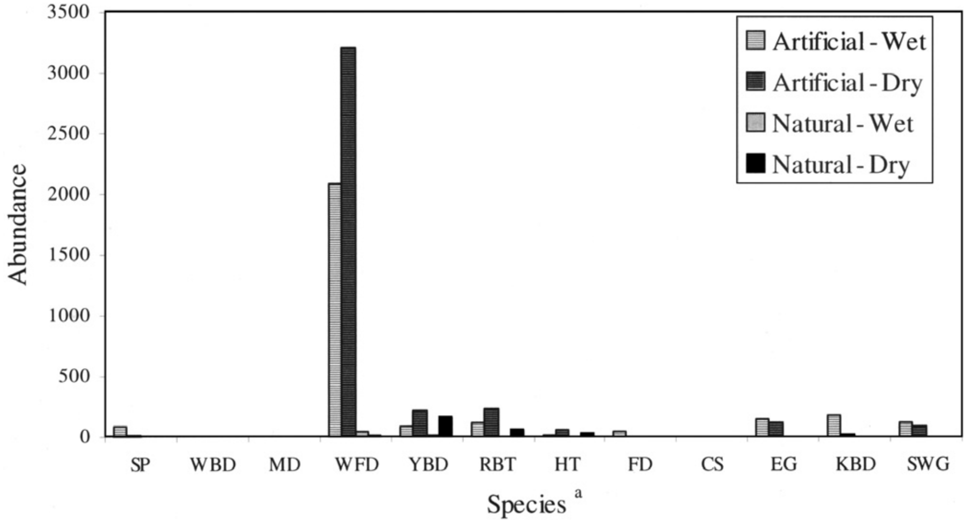

Fig. 1. Total abundance for waterfowl species on natural and artificial waterbodies in Limpopo Province, South Africa during the wet and dry season of 1997. ([a]SP = southern pochard; WBD = white-backed duck; MD = Maccoa duck; WFD = white-faced whistling duck; YBD = yellow-billed duck; RBT = red-billed teal; HT = Hottentot teal; FWD = fulvous whistling duck; CS = Cape shoveller; EG = Egyptian goose; KBD = knob-billed duck; SWG = spur-winged goose).

whistling ducks (*Dendrocygna bicolor*) were rarely seen on either pond type, during either season and Cape shovellers (*Anas smithii*) were almost never seen (Fig. 1). Egyptian geese, knob-billed ducks, and spur-winged geese were seen occasionally on agricultural ponds during wet and dry seasons (Fig. 1) but were rarely seen on natural ponds during either season. Four Egyptian goose (*Alopochen aegyptiaca*) broods were observed during the study and all were on irrigation and stock watering ponds.

Overall, in the wet season, on natural and agricultural ponds, and during the dry season on agricultural ponds, waterfowl abundance was dominated by the white-faced whistling duck. In the dry season on natural ponds, waterfowl abundance was low, but consisted primarily of yellow-billed ducks and red-billed teal.

Seasonal waterfowl density and richness

CCA revealed an association between guild density and wetland/upland characteristics (r = 0.08, P = 0.048) in the wet season. The percentages of variance accounted for by the fist three canonical axes were 16.8, 6.7, and 1.4%, respectively. Diving duck density tended to increase with the percentages of upland that was natural, shoreline with high vegetation, and surface area of the pond (Table 2). Diver density tended to decrease with increasing amount of open water on a pond and the proportion of bare shoreline (Table 2). Dabbler density was most strongly positively associated with a higher percentage of cultivated upland and turbidity, but was negatively correlated with percentage of grazed upland (Table 2). Goose density was positively associated with the percentages of grazed upland, bare shoreline, and open water area (Table 2). Goose density was negatively associated with higher percentages of cultivated upland, natural upland, tall shoreline vegetation, emergent vegetation in the pond, and turbidity (Table 2). In the dry season, CCA revealed no significant association between guild density structure and the 14 environmental variables analysed (r = –0.034, P = 0.40).

CCA also revealed an association between guild species richness and the environment in the wet season (r = 0.072, P = 0.045). The percentages of variance accounted for by the first three canonical axes were 13.2, 5.0, and 2.1%, respectively. Species richness of the diving guild was positively associated with pond surface area, percentage of natural surrounding upland, and presence of emergent vegetation (Table 3), and negatively influenced by turbidity, bare shoreline, and grazed upland (Table 3). Species richness of dabbling ducks was positively associated with pond surface area, and negatively associated with the amount of natural upland surrounding the pond, percentage of high shoreline vegetation, proportion of elevated shoreline, and pond depth (Table 3). Species richness of geese was positively associated with pond

Table 2. Biplot scores for a canonical correspondence analysis investigating the associations between guild density and the environment during the wet season.

Variable	Score		
	Axis 1	Axis 2	Axis 3
Guild[a]			
Diver density	0.85	**4.56**	**22.88**
Dabbler density	**–0.32**	–0.09	–0.01
Goose density	**3.48**	**–1.22**	0.07
Environment[b]			
Turbidity (cm)	**–0.38**	0.02	–0.13
Surface area (m^2)	0.15	0.29	**0.71**
% Pond open water	–0.01	**–0.41**	–0.18
% Emergent pond vegetation	–0.01	**0.43**	0.12
% Submerged aquatic vegetation	0.03	0.10	0.23
% Pond depth 0–1 m	0.08	–0.11	–0.18
% Pond depth >1 m	–0.12	0.13	0.18
% Elevated shoreline	–0.05	–0.22	0.04
% Bare shoreline	–0.16	**–0.40**	–0.03
% Grazed shoreline	0.29	–0.12	–0.09
% Tall shoreline vegetation	0.04	**0.55**	0.01
% Natural upland	0.19	**0.67**	**0.36**
% Grazed upland	**0.37**	–0.03	–0.09
% Cultivated upland	**–0.44**	–0.24	–0.06

[a]Guild loadings that were considered important are in bold face.

[b]Environmental variable scores ≥0.35 were considered important (in bold face).

Table 3. Biplot scores for a canonical correspondence analysis investigating the associations between guild species richness and the environment during the wet season.

Variable	Score		
	Axis 1	Axis 2	Axis 3
Guild[a]			
Diver richness	**1.66**	**4.09**	0.83
Dabbler richness	**0.97**	–0.43	**–1.03**
Goose richness	0.83	**–1.03**	**2.20**
Environment[b]			
Turbidity (cm)	**–0.37**	0.03	–0.32
Surface area (m^2)	**0.43**	0.16	–0.25
% Pond open water	0.02	**–0.35**	**0.58**
% Emergent pond vegetation	–0.16	**0.39**	**–0.42**
% Submerged aquatic vegetation	0.17	0.12	**–0.46**
% Pond depth 0–1 m	–0.22	–0.14	**–0.68**
% Pond depth >1 m	0.23	0.15	**0.61**
% Elevated shoreline	0.04	0.17	**0.45**
% Bare shoreline	0.28	**–0.58**	0.21
% Grazed shoreline	0.18	0.12	0.23
% Tall shoreline vegetation	**–0.44**	**0.35**	–0.34
% Natural upland	–0.11	**0.64**	–0.12
% Grazed upland	0.11	**–0.39**	0.02
% Cultivated upland	–0.01	–0.23	0.10

[a]Guild loadings that were considered important are in bold face.

[b]Environmental variable scores ≥0.35 were considered important (in bold face).

Table 4. Seasonal (wet and dry) multiple regression coefficients for guild densities and environmental variables. Significant results ($P < 0.05$) indicated by bold face.

Environmental variable[a,b]	Divers				Dabblers				Geese			
	Wet		Dry		Wet		Dry		Wet		Dry	
	β^c	P	β	P	β	P	β	P	β	P	β	P
Turb (cm)	–0.15	0.06	0.09	0.33	0.16	0.05	–0.18	0.05	–0.05	0.52	0.16	0.09
SA (m^2)	0.11	0.14	–0.02	0.78	–0.03	0.71	0.01	0.95	0.03	0.73	–0.02	0.82
PO (%)	–0.07	0.80	–0.12	0.37	0.01	0.97	0.07	0.61	0.12	0.70	0.02	0.85
PE (%)	0.09	0.72	0.01	0.95	0.06	0.82	0.01	0.88	0.04	0.87	0.03	0.70
PS (%)	0.13	0.36	0.05	0.88	0.02	0.89	0.11	0.75	0.06	0.71	0.32	0.35
<1 m (%)	–0.04	0.92	–0.06	0.86	0.15	0.70	0.20	0.55	–0.16	0.68	0.32	0.35
>1 m (%)	0.15	0.68	0.05	0.60	0.14	0.71	0.17	0.07	–0.24	0.54	–0.05	0.60
Elev (%)	0.08	0.31	–0.11	0.84	–0.06	0.49	–0.51	0.31	0.07	0.42	–0.69	0.18
SB (%)	**–1.26**	**0.00**	–0.06	0.88	0.01	0.98	–0.59	0.12	0.07	0.85	–0.70	0.07
SG (%)	**–1.08**	**0.00**	0.10	0.86	–0.11	0.70	–0.65	0.20	0.08	0.79	–0.96	0.07
SHV (%)	**–1.55**	**0.00**	–0.12	0.79	–0.22	0.60	–0.05	0.90	0.02	0.97	0.03	0.94
UN (%)	0.12	0.14	–0.02	0.97	–0.06	0.48	–0.20	0.69	–0.05	0.52	0.14	0.79
UC (%)	0.01	0.89	–0.15	0.75	0.17	0.07	–0.11	0.80	–0.03	0.77	0.16	0.72

[a]Turb = turbidity of the water; SA = surface area; PO = open water on the pond; PE = emergent vegetation on the pond; PS = submerged vegetation on the pond; <1 m = depth <1 m; >1 m = depth 0–1 m; Elev = elevated shoreline; SB = bare shoreline; SG = grazed shoreline; SHV = shoreline with tall vegetation; UN = natural upland; UC = cultivated upland.

[b]UG (%) = grazed upland; was excluded from analysis due to high collinearity.

[c]β is the standardized beta coefficient.

surface area, percentage of open water, water depth, bare and elevated shoreline, and grazed upland (Table 3), and negatively associated with the percentage of natural upland, high vegetation on the shoreline, emergent vegetation on the pond's surface, and turbidity (Table 3). In the dry season, CCA revealed no association between guild species richness composition and the environmental variables analysed (r = –0.048, P = 0.22).

In the wet season, multiple regression analysis showed that diving duck density was negatively associated with the percentages of bare, grazed, and high vegetation shoreline (R^2 = 0.14, d.f. = 13, F = 2.51, P = 0.003) (Table 4). Dabbler density (R^2 = 0.06, d.f. = 13, F = 0.98, P = 0.47), and goose density (R^2 = 0.037, d.f. = 13, F = 0.59, P = 0.86) were not significantly associated with environmental variables in the wet season. In the dry season, multiple regressions showed that diver (R^2 = 0.043, d.f. = 13, F = 0.57, P = 0.88), dabbler (R^2 = 0.12, d.f. = 13, F = 1.70, P = 0.07), and goose densities (R^2 = 0.077, d.f. = 13, F = 1.04, P = 0.42) were not associated with the environmental variables (Table 4).

In the wet season, diving duck species richness was negatively correlated with the percentages of bare shoreline, shoreline with high vegetation, and turbidity, but was positively correlated with greater surface area (R^2 = 0.12, d.f. = 13, F = 2.10, P = 0. 016) (Table 5). Surface area of the pond was the only environmental variable associated with diver species richness in the dry season (R^2 = 0.144, d.f. = 13, F = 2.10, P = 0.017) (Table 5). Dabbler species richness was also positively correlated with surface area in the wet (R^2 = 0.131, d.f. = 13, F = 2.30, P = 0.007) (Table 5) and dry (R^2 = 0.155, d.f. = 13, F = 2.29, P = 0.008) season (Table 5). Goose species richness was not related to with any environmental variables in the wet season (R^2 = 0.077, d.f. = 13, F = 1.27, P = 0.23). In the dry season goose species richness was positively correlated with pond surface area, and negatively correlated with the percentage of shoreline having high vegetation (R^2 = 0.188, d.f. = 13, F = 2.88, P = 0.001) (Table 5).

DISCUSSION

Wetlands

The number of natural ponds containing water did not change substantially between the wet and dry season (0.9% of ponds became dry) likely due to the fact that the study was conducted during a particularly wet year. In a typical year, most natural wetlands, such as those associated with the Nyl

Table 5. Seasonal (wet and dry) multiple regression coefficients for guild species richness and environmental variables. Significant results ($P < 0.05$) indicated by bold face.

Environmental variable[a,b]	Divers				Dabblers				Geese			
	Wet		Dry		Wet		Dry		Wet		Dry	
	β^c	P	β	P	β	P	β	P	β	P	β	P
Turb (cm)	**–0.22**	**0.01**	0.04	0.63	–0.13	0.10	0.02	0.83	–0.09	0.25	0.09	0.29
SA (m^2)	**0.16**	**0.03**	**0.28**	**0.00**	**0.26**	**0.00**	**0.31**	**0.00**	0.11	0.13	**0.35**	**0.00**
PE (%)	–0.06	0.82	0.06	0.64	–0.33	0.24	0.15	0.22	–0.30	0.31	0.19	0.11
PS (%)	0.05	0.83	0.02	0.78	–0.23	0.38	0.01	0.90	–0.22	0.39	–0.01	0.89
<1 m (%)	0.10	0.50	–0.04	0.90	0.06	0.66	0.12	0.72	–0.09	0.53	0.18	0.57
>1 m (%)	0.00	1.00	0.00	0.99	0.25	0.50	0.14	0.68	–0.27	0.48	0.39	0.22
Elev (%)	0.15	0.68	0.10	0.29	0.35	0.33	0.09	0.36	–0.08	0.83	–0.07	0.44
SB (%)	0.14	0.09	–0.18	0.71	–0.08	0.31	–0.36	0.47	–0.01	0.92	–0.82	0.09
SG (%)	**–0.75**	**0.04**	–0.03	0.94	–0.22	0.54	–0.32	0.39	0.19	0.62	**–0.78**	**0.03**
SHV (%)	–0.49	0.09	–0.06	0.91	–0.24	0.40	–0.32	0.52	0.10	0.74	**–1.12**	**0.02**
UN (%)	**–0.84**	**0.04**	–0.12	0.77	–0.50	0.22	–0.17	0.68	0.01	0.99	–0.18	0.67
UG (%)	0.15	0.07	–0.03	0.95	–0.01	0.88	–0.13	0.79	–0.05	0.55	–0.10	0.85
UC (%)	–0.04	0.66	–0.23	0.59	0.08	0.37	–0.25	0.57	–0.01	0.96	–0.17	0.69

[a]Turb = turbidity of the water; SA = surface area; PE = emergent vegetation on the pond; PS = submerged vegetation on the pond; <1 m = depth <1 m; >1 m = depth 0–1 m; Elev = elevated shoreline; SB = bare shoreline; SG = grazed shoreline; SHV = shoreline with tall vegetation; UN = natural upland; UG = grazed upland; UC = cultivated upland.

[b]PO (%) = open water on the pond; was excluded from analysis due to high collinearity.

[c]β is the standardized beta coefficient.

River floodplain, contain little or no standing water in the dry season (Noble & Hemens 1978). Most agricultural ponds surveyed were dugouts, or parts of natural floodplains that have been dammed to retain water for stock watering and irrigation. Therefore, agricultural ponds were generally much deeper to assure reliable water retention for agricultural purposes. Natural ponds in this study were most often vleis, pans, shallow inundated reed beds or plains. Many natural wetlands were associated with the Nyl River floodplain and inundation depends on the magnitude and timing of flooding events along the waterway (Tarboton & Bachelor 1981; Higgins *et al.* 1996). A large amount of water in these natural wetlands is lost through runoff, ground seepage, and evaporation over the large surface area of the waterbody (Tarboton & Batchelor 1981; Higgins *et al.* 1996).

Agricultural ponds tend to have less emergent vegetation than natural ponds, as the depth of permanent standing water restricts the development of these macrophytes. Consequently, the surface area of agricultural ponds was predominately open, sometimes with submerged vegetation. Agricultural ponds are usually created for use in areas of high human/cattle disturbance since the land surrounding these ponds is usually devoted to grazing or cultivation. This cultivation and grazing and trampling by livestock can also decrease littoral grass, and aquatic macrophyte densities (Whyte & Cain 1981; Colahan 1984). The difference in disturbance between natural and agricultural ponds provides some explanation for the disparity in the amount of high vegetation on their shorelines. Consequently, the proportion of tall vegetation on a pond's shoreline provides a good basis for discriminating between agricultural and natural ponds during the summer wet season. However, in winter the amount of tall vegetation in the littoral area surrounding natural ponds is diminished because of declining water levels and temperatures, and foraging by wildlife and termites (Day *et al.* 1988; Petrie 1998). This explains why this characteristic no longer provided a clear distinction between natural and agricultural ponds in the dry season.

Waterfowl response to landscape change

During the wet season, divers tended to select dammed portions of natural wetlands, which had high shoreline vegetation, large surface area, and ample emergent vegetation. Divers tended to avoid ponds with large proportions of open water, which is generally a characteristic of stock-watering and irrigation ponds. This can be attributed to their requirements for emergent vegetation for over-water nesting and cover for broods in the wet season (Siegfried *et al.* 1976; Clark 1980; Irwin 1981; Brickell 1988; Maclean 1997a). Divers, such as the southern pochard, that happened to occur on agricultural ponds in the wet season, were likely able to utilize them because of their greater depth and clarity (Maclean & Harrison 1997). Also, most of the agricultural ponds used by southern pochard were dammed portions of natural wetlands, which tend to support more submerged and emergent macrophyte growth than stock and irrigation ponds. The white-backed duck was rarely observed, and only on dammed areas of natural wetlands. This can be attributed to its need for secluded water with plentiful surface vegetation (Irwin 1981). Although overall abundance of diving ducks was relatively low, their consistent occupation of ponds with characteristics typical of natural waterbodies reveals important information on their environmental requirements.

Overall, dabblers did not respond to characteristics of one pond type over another in the wet season. This is likely attributed to the ability of certain dabbling duck species to utilize a wide variety of resources on both natural and agricultural ponds. White-faced whistling ducks made extensive use of agricultural ponds during the summer breeding season and five of six broods observed occurred on stock and irrigation ponds (Petrie, pers. obs.). Yellow-billed ducks were observed on both natural and agricultural ponds, during both the wet and dry season. Yellow-billed ducks are year-round, opportunistic breeders that use natural and agricultural ponds in South Africa (Brickell 1988; Maclean 1997b). Red-billed teal are physiologically capable of breeding when encountering dry conditions with limited quantities of macro-invertebrates. They do this by effectively assimilating protein from seeds of native grasses that characteristically surrounded both pond types throughout the year (Petrie 1996). This, combined with the ability to feed in agricultural fields, provides an explanation for their ability to utilize artificial ponds in both seasons. Hottentot teal have a very wide, although localized distribution (Johnsgard 1978), which may account for their low abundance in this study. Colahan (1984) also reported a low abundance of Hottentot teal in KwaZulu-Natal province, south east of our study area. In KwaZulu-Natal, Hottentot teal favoured the eutrophic waters of sewage ponds (Colahan 1984), which comprised only a small number of ponds in the Springbok Flats. Although fulvous whistling ducks breed on larger inland floodplains with plentiful aquatic vegetation (Irwin 1981; Hockey *et al.* 2005), similar to the Nyl River floodplain, few were recorded during this study in the wet season, and this species was absent in the dry season. Maclean (1997c) found that reporting rates for fulvous whistling ducks are relatively low in southern Africa, and their distribution is mainly concentrated around major wetlands in South Africa in the summer. Cape shovellers likely avoided the many deep, artificial ponds surveyed in this study due to their specialized preference for shallow, plankton-rich waters (Brickell 1988), especially the eutrophic waters of sewage ponds (Colahan 1984). Froneman *et al.* (2001) also found a higher diversity of waterbirds in the summer on large farm ponds that offered more shallow water areas with suitable food resources.

Geese responded positively to the greater proportions of grazed shoreline associated with many agricultural ponds during the wet season, and were rarely observed on natural ponds during either season. This selection of agricultural ponds is likely related to the fact that they prefer to forage in the short grasses and cultivated fields that surround most artificial ponds (Johnsgard 1978), and do not feed in the high vegetation that surrounds natural ponds in summer. Colahan (1984) quantitatively matched this habitat characteristic to Egyptian geese in an analysis of farm dam suitability for waterfowl. Geese occasionally occurred on natural ponds in winter, however much of the high shoreline vegetation had died back at this time, leaving more suitable habitat for grazing.

In the dry season, no guild responded to characteristics of one pond type more than another. This can be attributed primarily to the fact that only three of nine species observed during this study were regularly observed during the dry season. White-faced whistling duck abundance dramatically increased on stock and irrigation ponds in the winter dry season because they are capable of eating cereal grains on surrounding cultivated fields (Petrie & Rogers 1997; Petrie 1998). As previously mentioned, yellow-billed ducks and red-billed teals are capable of finding suitable habitat and food resources on a variety of pond types throughout the year (Brickell 1988; Petrie 1996; Maclean 1997b). These two dabbler species likely increased in abundance in the dry season because of immigration, or perhaps because they were more easily detected after the breeding season.

The white-faced whistling duck was the only species that was abundant on agricultural wetlands during the dry season. Although southern pochards use dammed vleis during the wet season, divers and specialist dabbler (Cape shovellers) were rare during the dry season and rarely ever occurred on stock-watering and irrigation ponds. The results of this study indicate that the occurrence of these species is strongly linked to the characteristics and availability of natural wetlands. Unfortunately, although natural wetlands provide essential agricultural, municipal, and ecological services in semi-arid South Africa (Breen & Begg 1989), they are continually being impacted by drainage and development. Consequently, natural wetlands are becoming increasingly scarce in southern Africa (Breen & Begg 1989; Petrie & Rogers 1997). Our results suggest that natural wetlands need to be protected in order to maintain waterfowl diversity in the semi-arid regions of South Africa.

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Appendix 1. Species of waterfowl observed in Springbok Flats, of Limpopo Province, South Africa in 1997.

Guild	Common name	Latin name
Divers	Southern pochard	*Netta erythrophthalma*
	White-backed duck	*Thalassornis leuconotus*
	Maccoa duck	*Oxyura maccoa*
Dabblers	White-faced whistling duck	*Dendrocygna viduata*
	Red-billed teal	*Anas erythrorhyncha*
	Yellow-billed duck	*Anas undulata*
	Hottentot teal	*Anas hottentota*
	Fulvous whistling duck	*Dendrocygna bicolor*
	Cape shoveller	*Anas smithii*
Geese	Egyptian goose	*Alopochen aegyptiaca*
	Knob-billed duck	*Sarkidiornis melanotos*
	Spur-winged goose	*Plectropterus gambensis*