

# Is waterbird distribution within rice paddies of eastern Uganda affected by the different stages of rice growing?

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Rice paddies are becoming a common feature of Uganda's landscapes. This study aimed to establish the effect of the different stages of rice growing on the distribution of waterbirds in rice fields in eastern Uganda. Spatial variation in species diversity and the abundance of the most common species was examined between 1) Ploughed fields, 2) Fields with rice at Phase one, 3) Fields with rice at Phase two, and 4) Harvested fields. Eighty-two total counts of 26 4-ha plots were made, from which 43 waterbird species and 20,821 individuals from 15 families were recorded. Of the 15 families censused, the family Threskiornithidae represented 30%, Ardeidae 27%, Anatidae 16%, while the remaining 27% were accounted for by 12 waterbird families. Ploughed fields and fields with rice at phase one were more species diverse and supported higher abundances of species than phase two and harvested fields. The Cattle Egret (*Bubulcus ibis*), Yellow-billed Egret (*Egretta intermedia*), African Open-billed Stork (*Anastomus lamelligerus*), the Little Egret (*Egretta garzetta*), Squacco Heron (*Ardeola ralloides*), the Black-headed Heron (*Ardea melanocephala*) and the Grey Heron (*Ardea cinerea*) were among the most common birds. Findings of this study suggest that the rice farming practice creates a simple mosaic of habitats (heterogeneity) some of which are attractive to waterbirds. However, it is most likely that the observed spatial pattern of waterbirds is related to the abundance and distribution of other factors such as food, water depth and water quality, which were not tested by this study.

## INTRODUCTION

Rice paddies are one of the most productive and dependable agricultural systems devised by humans (Odum 1993). However, they differ from natural ecosystems in some important aspects. For example, the operation of a rice scheme typically involves use of fertilizers, herbicides, pesticides, and machinery. Rice, which is the dominant plant species, is under artificial rather than natural selection (Odum 1993). Because the primary goal of rice paddies is rice production, rice ecosystems are highly dynamic; their physical and chemical parameters and water levels change very quickly and their biological communities develop rapidly (González-Solís *et al.* 1996). Despite these and other artificial features of this freshwater marsh ecosystem, rice paddies can be important ecological areas throughout the world (Arinaitwe 1992, Fasola *et al.* 1996, Lane & Fujioka 1998, Tourenq *et al.* 2001). The impacts of the rice growing practice on waterbirds and other wildlife have been studied in North America (Elphick & Oring 2002), Japan (Fujioka *et al.* 2001, Maeda 2001), and in the Mediterranean (González-Solís *et al.* 1996). It is therefore important to assess if the observed changes are similar to what happens on Ugandan rice paddies. This is also important if we are to consider conservation options in rice fields.

In Uganda, rice agriculture has been an integral part of the economy since the 1940s when the government began to cultivate this at Doho and Kibimba swamps. Habitat use patterns of birds on rice fields in Uganda have been reported in limited studies (Arinaitwe 1992, Gumonye-Mafabi 1989), in

which rice growing has been shown to create favorable feeding conditions for waterbirds, particularly Ciconiiformes (Arinaitwe 1992). However, none of these studies has explained the effects of the rice phase on waterbirds. This study is the first rigorous attempt to understand the relationships between present agricultural practices and waterbirds on Ugandan rice fields. The aim was to explain the spatial variation in the distribution of waterbirds on rice paddies and, in addition, to provide a preliminary documentation of the diversity of waterbirds associated with rice paddies. Variation among waterbird diversity and abundance were examined by comparing use of ploughed fields, fields with rice at Phase one, fields with rice at Phase two, and harvested fields.

## METHODS

### The rice growth cycle

Rice is cultivated in lowland fields at these rice schemes and the rice cycle ranges from 120–150 days. The process of rice growing involves ploughing of fields, planting or seeding and harvesting. Rice fields are traditionally flooded for about one week before ploughing. The rice seeds are then broadcast on the fields shortly after ploughing. The fields are then kept dry for 10–25 days after sprouting, and in the case of transplanting the fields are kept dry for 14 days and then flooded again. At this phase there is a continuous flow of water through the fields and the depth of water is usually maintained at approximately 10 cm for better growth and to suppress the growth of

weeds. The rice then grows very fast, achieving ear formation and ear ripening. The start of harvesting is determined by the degree of moisture of mature rice grains. Following harvest of the rice crop, the fields are re-flooded almost immediately for 10–15 days. For the purposes of this study, I divided the entire rice cycle into 4 phases namely: Ploughed fields, Fields with rice before ear development (Phase one), fields with rice after ear development (Phase two) and Harvested fields. Until recently rice growing at Doho and Kibimba rice scheme was seasonal. Farmers have adopted a staggered type of agriculture, which means that whole blocks or sections of blocks were at different phases of the rice growth cycle every month, creating an entire array of habitats from which to sample.

### Sampling design

Rice fields are divided into blocks for water management purposes; these are further subdivided into plots that are separated by earth levees. The sampling units were 4ha plots established in each block and these plots were monitored monthly from May to September in 2003. Sometimes two plots were established in the same block if it had more than one phase/habitat and each month new plots became available. The nature of the rice fields prevented complete randomization in selecting plots with respect to the rice cycle. However, I selected plots such that the various phases of rice cultivation were spatially interspersed (more than 300 m apart) in order to reduce the likelihood that unknown spatial factors could confound the results. A total of 82 plot counts from 26 4-ha plots were made (there was repeated sampling). Out of the 82 plot counts, 17 were on ploughed fields, 33 on fields with rice at Phase one, 21 on fields with rice at Phase two, and 11 on Harvested fields.

### Waterbird count

I censused plots on foot, counting all waterbirds from locations along levee perimeters which maximized observations and minimized disturbance by being 150 m away. This was done using 22× spotting scopes and 8×40 binoculars. Given the open nature of the habitats, these counts were likely to assess absolute abundance accurately for most species except

for the small waders. Birds disturbed from a field or standing on the bands at the edges of the plot and on internal earthen levees, as well as those flying just above and around the plot were included in the samples; birds seen flying overhead were not.

### Waterbird composition and species diversity

Waterbirds were classified into families and species and abundances of each were calculated. The Shannon–Weaver ( $H'$ ) diversity index (Magurran 2003) and the abundance of the common species were also calculated per count (details in Nachuha 2006). Simple linear regression analysis using Generalised Linear Mixed Model (GLMM), in Genstat version 8.1(VSN Intl.2003) was done to determine if the waterbird community was dependant on the rice phase. Plot was used as a random effect to control for pseudoreplication (Hurlbert 1984). One-sample Kolmogrov test showed that the species diversity conformed to the normal distribution, however, the abundance of each of the common species was not, therefore data were log transformed.

## RESULTS

### Waterbird community composition

I observed a total of 20,821 waterbirds of 43 species from 15 families (Table 1). Families Threskiornithidae (wading birds), Ardeidae (wading birds), Anatidae (waterfowl) and Ciconiidae (mainly wading birds) were the most abundant and frequent, contributing 82% of the total abundance, and were recorded in more than 50% of the counts (except Anatidae) (Table 1). Of these, family Ardeidae was the most species-rich (10 species), and Threskiornithidae, the most abundant, although this contributed only 4 species. Overall species diversity ranged from 0 to 2.63 birds, with a mean of  $1.56 \pm 0.07$  birds (Table 2).

Of all the observed species, the Cattle Egret (*Bubulcus ibis*), Yellow-billed Egret (*Egretta intermedia*), African Open-billed Stork (*Anastomus lamelligerus*), the Little Egret (*Egretta garzetta*), Squacco Heron (*Ardeola ralloide*), the Black-headed Heron (*Ardea melanocephala*) and the Grey

**Table 1.** Waterbird families and their abundances, richness and frequency in all plots.

Number	Family	Abundance <sup>a</sup>	%Abundance <sup>b</sup>	Richness	%Richness <sup>c</sup>	Frequency <sup>d</sup>
1	Alcedinidae	13	0.06	1	2.33	6
2	Anatidae	3311	15.9	5	11.63	33
3	Ardeidae	5568	26.74	10	23.26	82
4	Charadriidae	404	1.94	3	6.98	31
5	Ciconiidae	2018	9.69	5	11.63	63
6	Gruidae	215	1.03	1	2.33	24
7	Jacaniidae	128	0.61	1	2.33	12
8	Laridae	642	3.08	2	4.65	18
9	Phalacrocoracidae	40	0.19	1	2.33	12
10	Rallidae	249	1.20	4	9.30	25
11	Recurvirostridae	867	4.16	1	2.33	15
12	Scolopacidae	738	3.54	3	6.98	23
13	Scopidae	9	0.04	1	2.33	8
14	Sternidae	430	2.07	1	2.33	1
15	Threskiornithidae	6189	29.72	4	9.30	45
	Total	20,586		43		

<sup>a</sup> Sum of observations from the 82 counts. <sup>b</sup> Summed counts from the 82 counts divided by the 20,586 bird total. <sup>c</sup> Number of species divided by the 43 species recorded. <sup>d</sup> Number of counts in which species from this family were recorded.

**Table 2.** Summary of diversity and individual species abundances in all the counts, and in the four phases of rice growing.

Variable	All counts		Rice phase			Statistics P-value
	Mean ± SE (range)	Ploughed fields (17) Mean ± SE (range)	Phase one (33) Mean ± SE (range)	Phase two (21) Mean ± SE (range)	Harvested fields (11) Mean ± SE (range)	
Shannon diversity (H')	1.56±0.07 (0–2.63)	1.90±0.12 (1.01–2.63)	1.77±0.09 (0.46–2.56)	1.08±0.11 (0–2.05)	1.27±0.14 (0.36–1.82)	<0.001
Cattle Egret	22.1±3.6 (0–200)	42.9±2.0 (0–200)	28.7±5.0 (0–124)	4.7±2.0 (0–30)	3.4±1.8 (0–20)	<0.001
Yellow-billed Egret	20.9±3.7 (0–150)	26.4±8.5 (0–120)	34.3±7.2 (0–150)	1.9±0.9 (0–16)	8.4±1.8 (0–18)	<0.001
African Open-billed Stork	17.9±3.4 (0–150)	33.9±8.8 (0–130)	13.7±3.8 (0–85)	17.6±8.8 (0–150)	5.9±2.7 (0–30)	<0.001
Little Egret	12.3±2.5 (0–150)	16.9±8.8 (0–150)	14.8±2.5 (0–54)	10.0±5.1 (0–72)	2.0±0.7 (0–7)	<0.001
Squacco Heron	4.6±1.2 (0–80)	10.6±4.6 (0–80)	5.1±1.7 (0–43)	0.5±0.3 (0–5)	2.0±0.9 (0–6)	<0.001
Black-headed Heron	4.12±0.83 (0–52)	7.6±3.1 (0–52)	3.6±0.7 (0–15)	1.1±0.3 (0–6)	6.0±2.9 (0–25)	<0.057
Grey Heron	2.4±0.6 (0–35)	6.6±2.3 (0–35)	1.9±0.4 (0–7)	0.2±0.1 (0–1)	1.3±0.7 (0–7)	<0.001

The statistic column is results of a Generalised Linear Mixed Model examining the relationship between waterbird community variables with rice phase. Only those species detected in ≥50% of plot counts are shown. Natural log transformed values were used for the abundance of the individual species.

**Table 3.** Relative abundance of 43 waterbird species observed in rice paddies in Doho and Kibimba rice schemes, eastern Uganda.

No.	Species	Scientific name	All phases						Phases of rice growing					
			Abund <sup>a</sup>	%Abund <sup>b</sup>	Freq <sup>c</sup>	Ploughed fields Abund <sup>d</sup>	%Abund <sup>e</sup>	Phase one Abund <sup>d</sup>	%Abund <sup>e</sup>	Phase two Abund <sup>d</sup>	%Abund <sup>e</sup>	Harvested fields Abund <sup>d</sup>	%Abund <sup>e</sup>	
53	Glossy Ibis	<i>Plegadis falcinellus</i>	5138	24.68	37.8	4105	19.72	1033	4.96	0	0	0	0	0
59	Fulvous-whistling Duck	<i>Dendrocygna bicolor</i>	1829	8.78	7.32	1829	8.78	0	0	0	0	0	0	0
32	Cattle Egret	<i>Bubulcus ibis</i>	1812	8.7	75.61	730	3.51	947	4.55	98	0.47	37	0.18	0.18
38	Yellow-billed Egret	<i>Egretta intermedia</i>	1710	8.21	70.73	448	2.15	1131	5.43	39	0.19	92	0.44	0.44
43	African Open-billed Stork	<i>Anastomus lamelligerus</i>	1464	7.03	70.73	577	2.77	452	2.17	370	1.78	65	0.31	0.31
36	Little Egret	<i>Egretta garzetta</i>	1010	4.85	58.54	288	1.38	490	2.35	210	1.01	22	0.11	0.11
282	Black-winged Stilt	<i>Himantopus himantopus</i>	867	4.16	18.29	533	2.56	334	1.6	0	0	0	0	0
60	White-faced whistling Duck	<i>Dendrocygna viduata</i>	683	3.28	25.61	240	1.15	443	2.13	0	0	0	0	0
51	Hadada Ibis	<i>Bostrychia olivacea</i>	647	3.11	29.27	145	0.7	495	2.38	7	0.03	0	0	0
50	Yellow-billed Stork	<i>Mycteria ibis</i>	533	2.56	48.78	305	1.46	207	0.99	18	0.09	2	0.01	0.01
306	Grey-headed Gull	<i>Larus cirrocephalus</i>	508	2.44	10.98	60	0.29	448	2.15	0	0	0	0	0
80	Knob-billed Duck	<i>Sarkidiornis melanotos</i>	469	2.25	15.85	247	1.19	222	1.07	0	0	0	0	0
320	Gull-billed Tern	<i>Gelochelidon nilotica</i>	430	2.07	1.22	0	0	430	2.07	0	0	0	0	0

Names and numbers following Britton (1980)

<sup>a</sup> Sum of observations from the 82 counts. <sup>b</sup> Summed counts from the counts divided by the 20,586 bird total. <sup>c</sup> % of counts where species was recorded. <sup>d</sup> Sum of observations in each phase. <sup>e</sup> Summed counts from the counts in each phase divided by the 20,586 bird total.

**Table 3.** (Continued) Relative abundance of 43 waterbird species observed in rice paddies in Doho and Kibimba rice schemes, eastern Uganda.

No.	Species	Scientific name	All phases			Phases of rice growing							
			Abund <sup>a</sup>	%Abund <sup>b</sup>	Freq <sup>c</sup>	Abund <sup>d</sup>	%Abund <sup>e</sup>	Abund <sup>d</sup>	%Abund <sup>e</sup>	Abund <sup>d</sup>	%Abund <sup>e</sup>	Abund <sup>d</sup>	%Abund <sup>e</sup>
30	Squacco Heron	<i>Ardeola ralloides</i>	380	1.83	50.00	180	0.86	167	0.8	11	0.05	22	0.11
257	Greenshank	<i>Tringa erythropus</i>	362	1.74	19.51	117	0.56	245	1.18	0	0	0	0
278	Black-tailed Godwit	<i>Limosa limosa</i>	351	1.69	10.98	332	1.59	17	0.08	2	0.01	0	0
27	Black-headed Heron	<i>Ardea melanocephala</i>	338	1.62	65.85	129	0.62	120	0.58	23	0.11	66	0.32
79	Spur-winged Geese	<i>Plectropterus gambensis</i>	323	1.55	24.39	91	0.44	230	1.1	0	0	2	0.01
55	African Spoonbill	<i>Platalea alba</i>	319	1.53	39.02	149	0.72	148	0.71	14	0.07	8	0.04
201	Black Crane	<i>Limnocorax flavirostris</i>	243	1.17	28.05	6	0.03	14	0.07	222	1.07	1	0
249	Spur-winged Plover	<i>Vanellus spinosus</i>	227	1.09	32.93	160	0.77	67	0.32	0	0	0	0
194	Grey-crowned Crane	<i>Balearica regualum</i>	215	1.03	29.27	52	0.25	145	0.7	4	0.02	14	0.07
25	Grey Heron	<i>Ardea cinerea</i>	195	0.94	50.00	112	0.54	65	0.31	4	0.02	14	0.07
245	Long-toed Plover	<i>Vanellus crassirostris</i>	175	0.84	30.49	101	0.49	73	0.35	1	0	0	0
318	White-winged Black Tern	<i>Chlidonias leucopterus</i>	134	0.64	14.63	88	0.42	37	0.18	9	0.04	0	0
225	African Jacana	<i>Actophilornis africanus</i>	128	0.61	14.63	120	0.58	8	0.04	0	0	0	0
54	Sacred Ibis	<i>Threskiornis aethiopica</i>	85	0.41	24.39	31	0.15	54	0.26	0	0	0	0
34	Great-white Egret	<i>Egretta alba</i>	57	0.27	10.98	18	0.09	39	0.19	0	0	0	0
28	Purple Heron	<i>Ardea purpurea</i>	50	0.24	28.05	11	0.05	10	0.05	25	0.12	4	0.02
17	Long-tailed Cormorant	<i>Phalacrocorax carbo</i>	40	0.19	14.63	15	0.07	21	0.1	4	0.02	0	0
262	Common Snipe	<i>Gallinago gallinago</i>	25	0.12	3.66	25	0.12	0	0	0	0	0	0
48	Saddle-billed Stork	<i>Ephippiorhynchus senegalensis</i>	17	0.08	8.54	7	0.03	10	0.05	0	0	0	0
33	Green-backed Heron	<i>Butorides striatus</i>	13	0.06	7.32	5	0.02	8	0.04	0	0	0	0
466	Malachite kingfisher	<i>Alcedo cristata</i>	13	0.06	7.32	0	0	0	0	13	0.06	0	0
42	Hammerkop	<i>Scopus umbreta</i>	9	0.04	9.76	1	0	7	0.03	0	0	1	0
66	Red-billed Teal	<i>Anas erythroorhynchus</i>	7	0.03	2.44	6	0.03	1	0	0	0	0	0
23	Little Bittern	<i>Ixobrychus minutus</i>	3	0.01	1.22	3	0.01	0	0	0	0	0	0
202	Allen's Gallinule	<i>Porphyrio alleni</i>	3	0.01	1.22	0	0	3	0.01	0	0	0	0
44	Abdim's Stork	<i>Ciconia abdimii</i>	2	0.01	2.44	0	0.01	2	0	0	0	0	0
46	Woolly-necked Stork	<i>Ciconia episcopus</i>	2	0.01	2.44	0	0	2	0.01	0	0	0	0
204	Striped Crane	<i>Porzana marginalis</i>	2	0.01	2.44	0	0	2	0.01	0	0	0	0
248	Wattled Plover	<i>Vanellus senegalensis</i>	2	0.01	1.22	2	0	0	0.01	0	0	0	0
199	Common Moorhen	<i>Gallinula chloropus</i>	1	0	1.22	0	0	1	0	0	0	0	0
	Total abundance		20,821			11,268		8,128		1,074		351	
	% Proportion of total abundance		100%			54%		39%		5.2%		1.7%	
	Total number of species		43			36		38		18		14	

Names and numbers following Britton (1980)

<sup>a</sup> Sum of observations from the 82 counts. <sup>b</sup> Summed counts from the counts divided by the 20,586 bird total. <sup>c</sup> % of counts where species was recorded. <sup>d</sup> Sum of observations in each phase. <sup>e</sup> Summed counts from the counts in each phase divided by the 20,586 bird total.

Heron (*Ardea cinerea*) were the most frequent, occurring in more than 50% of the counts (Table 3). With the exception of the Squacco Heron and, the Black-headed and Grey Herons, the remaining species were also among the most abundant in addition to the Glossy Ibis (*Plegadis falcinellus*) and the Fulvous Whistling-Duck (*Dendrocygna bicolor*), contributing 62% (12,963 individuals) (see Tables 2 & 3). In contrast, slightly more than one quarter of the birds occurred infrequently (<10% of plot counts).

### Bird-habitat relationship

Rice phase had an effect on the distribution of birds (Table 2:  $\chi^2 = 39.32$ ,  $df = 3$ ,  $P < 0.001$ , and Fig. 1). Ploughed fields and fields with rice at Phase one were most species diverse (Table 2:  $1.90 \pm 0.12$ ,  $1.77 \pm 0.09$  birds respectively), while fields with rice at Phase two and harvested fields had low waterbird diversities ( $1.08 \pm 0.11$ ,  $1.27 \pm 0.14$  birds respectively). The abundance of individual species (most common ones) also varied among the phases of rice growing, with higher abundances recorded on Ploughed fields and fields with rice at Phase one. Also worth mentioning is that the Black Crake (*Limnecorax flavirostris*) and Purple Heron (*Ardea purpurea*) were more common on fields with rice at Phase two of its development (see Table 3).

## DISCUSSION

### Spatial variation

My data indicate that the distribution of waterbirds was non-random and related to rice phase. Ploughing, flooding and harvesting changed field conditions on commercial rice fields in Uganda, and this had an effect on waterbird distribution on these fields as observed elsewhere in the world (Elphick & Oring 2002, Fujioka *et al.* 2001, Maeda 2001). Waterbirds were more common on Ploughed fields and fields with rice at Phase one and less common on fields with rice at Phase two and Harvested fields. This is probably because ploughed fields and fields with rice at Phase one are characterized by soft muddy areas, and sparse and short rice plants suitable as foraging grounds for most water birds that feed by probing in

mud and those that feed on aquatic organisms obtained from shallow waters (Fredrickson & Reid 1986). At this phase, rice fields are also similar to mud flats and wet meadows typically used for foraging by waterbirds worldwide for example in the Camargue (Isenmann 1993). These results indicate that the activity of waterbirds tends to be concentrated on fields not covered by rice vegetation or when rice vegetation is still short and sparse, and similar observations have been made in other habitats (Keith 1961, Weller & Spatcher 1965).

Generally waterbirds were much less common on Phase two and Harvested fields. Phase two is also characterized by the presence of people scaring away the passerine birds that feed on rice who may also have scared away the waterbirds. In addition, several studies (in pasture lands) have demonstrated that the abundance of some waterbirds, for example wading birds on grasslands, is predicted by vegetation height, which affects ease of movement and soil penetration when feeding, and hence prey intake rate (Milsom *et al.* 2000). Shorebirds have also been shown to frequent short-vegetation pastures (Colwell & Dodd 1995). Therefore the reduced use of fields with rice at Phase two could be partly attributed to the presence of tall, dense rice plants, which reduced accessibility of the fields and probably limited the ease of locating and obtaining food and movement while foraging (Butler & Gillings 2004). Furthermore, such vegetation structure may also increase predation risk, since predator vigilance is facilitated by short vegetation (Colwell & Dodd 1995). Rice fields are drained before harvesting starts, and this reduces the availability of aquatic prey, which probably explains the low species diversity and waterbird abundances on harvested fields.

The Cattle Egret, Yellow-billed Egret, the Little Egret, Squacco Heron, the Black-headed Heron, and the Grey Heron belong to the Heron family Ardeidae. These species together with the African Open-billed Stork were the most frequent. Some herons have been known to colonize farmland, for example rice fields (Fasola *et al.* 1996, Fasola & Ruiz 1996, Subramanya 1996). The presence of higher numbers of Purple Herons and Black Crakes on fields with rice at Phase two (Table 3) indicates that, as the rice plants get taller, they create suitable habitats for bird species that prefer tall vegetation. However, rice fields do not compensate for loss of papyrus that is suitable for papyrus endemics such as the

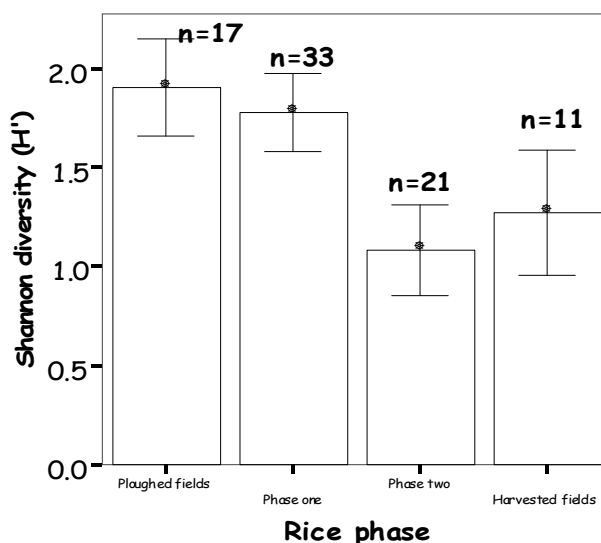


Fig. 1. Species diversity (mean  $\pm$  SE) in each rice phase.  $P < 0.001$  as given in Table 2. Sample sizes for each phase are given above each bar.

Swamp Warbler (*Acrocephalus rufescens*), Papyrus Gonolek (*Laniarius mufumbiri*) and other waterbirds such as the Shoebill (*Balaeniceps rex*) (Arinaitwe 1992). Waterbirds such as the Slaty Egret (*Egretta vinaceigula*) in the Zambezi plain in southern Africa and the Humbolt's Heron (*Ardea humboldti*) in Madagascar have been severely affected as natural wetlands are drained for the creation of rice fields (Kushlan & Hafner 2000). Rice growing has also been found to have a negative effect on sedentary waterbird species (Gumonye-Mafabi 1989). Therefore the needs of food production for human consumption should be balanced against the conservation of endemic species.

## CONCLUSION AND MANAGEMENT IMPLICATIONS

Human management has greatly reduced biodiversity in most agro-ecosystems (Odum 1993). However, alternating periods of ploughing, flooding and drying during the rice growth cycle creates spatial heterogeneity that seems to have important consequences for the diversity, abundance and distribution patterns of waterbirds in rice fields. I suggest that in order to maintain the value of rice fields for waterbirds, manager/farmers in eastern Uganda should maintain a mosaic of fields on their farms during the rice growing process, as this seems to provide good conditions for both waterbirds and non-waterbirds (pers. obs.). However, birds could be responding to another unmeasured aspect of the environment. Determining the cause of the remaining variability would provide greater insight into the relative importance of rice phase to waterbirds.

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