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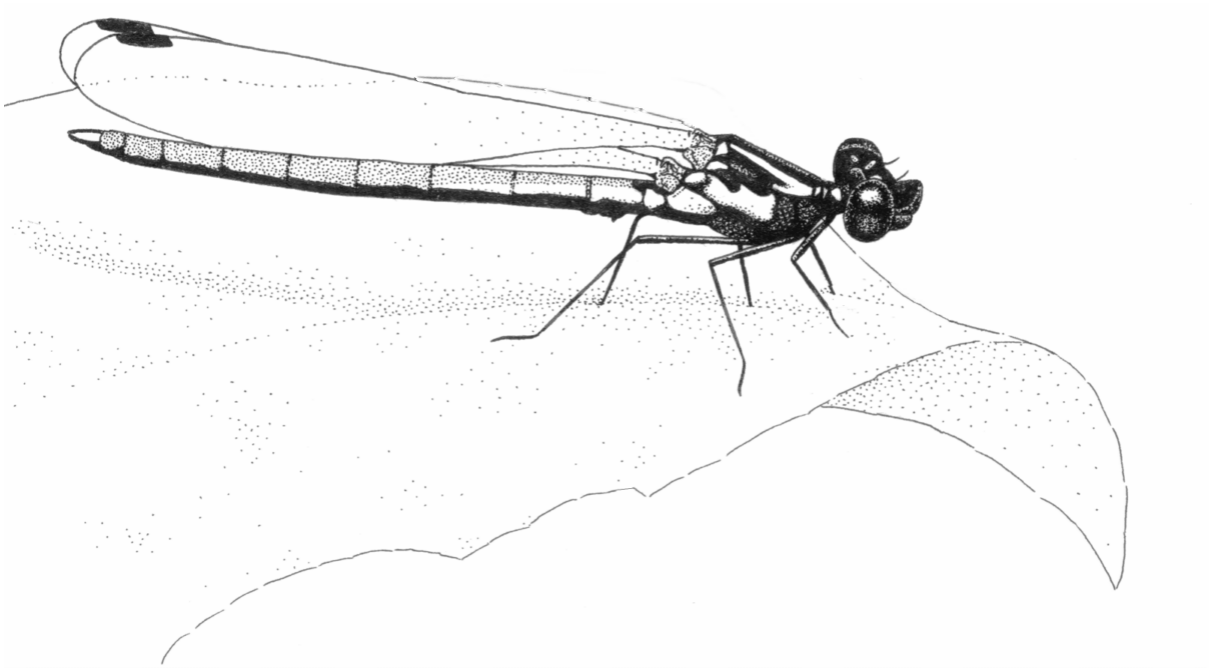

A Journal of Biodiversity

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BIRDS OF AN EXTENSIVE PAPYRUS SWAMP IN UGANDA AND THEIR CONSERVATION

Micheal Kibuule
Nature Uganda, P.O. Box 27034 Kampala, Uganda
mkibuule@gmail.com

George Kaphu
Uganda Wildlife Authority, P.O. Box 3550. Kampala, Uganda
Kaphygeorge01@gmail.com

David Ochanda
Total E&P Uganda, P.O. Box 34867 Kampala, Uganda
david.ochanda@total.com

Derek Pomeroy
Department of Zoology, Makerere University, P.O. Box 7298, Kampala, Uganda
derekp@cantab.net

ABSTRACT

The delta of the Nile as it enters Lake Albert is part of a Ramsar site and supports 35 km^2 of papyrus swamp through which run channels of the river. For 12 months in 2017-2018, we made monthly bird counts, each of ten minutes, at 20 points along swamp edges. Overall, 143 species were recorded, of which 13 were particularly common in the papyrus, and a similar number along the channels. Of seven papyrus-restricted species observed, three are globally red-listed notably papyrus gonolek and shoebill. Most species are resident, but white-winged terns and several hirundine species were seasonally common. Our baseline counts should be repeated in future years as well as recording potential threats—climate change, oil and gas operations and other human activities. Most, but not all, of the Ramsar site is within Murchison Falls National Park, which is well-protected; if possible, the protection should be extended to the whole site.

Keywords: Murchison Falls National Park, papyrus birds, Ramsar site

INTRODUCTION

The Murchison Falls – Lake Albert Delta Wetland System is a Ramsar site in north-west Uganda, and it contains the largest protected papyrus swamp in East Africa, extending to some 35 km^2. It is also part of a proposed Key Biodiversity Area (Plumptre *et al.,* 2019). The Ramsar site extends upstream along the River Nile to the Falls, and there are several islands within this part of the river, up to a kilometre long, and mainly covered with papyrus. Our survey of this swamp had two components, one being the larger waterbirds that frequented the river channels through the swamp and its margins, together with adjacent areas of Lake Albert (reported in Pomeroy *et al.,* 2020), and the other the birds which are found in the papyrus swamp itself, the subject of this paper.

Permanent swamps (mainly of *Cyperus papyrus* L., but some dominated by *Miscanthus violaceus* (K.Schum.) Pilg.), are extensive in Uganda, the papyrus-dominated swamps amounting to about 6910 km^2 in the 1960s (Langdale-Brown *et al.*, 1964). Since then, many have been lost and by 2010 the remaining area of these swamps in Uganda was estimated at 4810 km^2 (WCS & eCountability, 2016). Maclean *et al.* (2014) found a similar, but lower rate of loss for papyrus swamps in south-west Uganda. Many remaining swamps have been degraded—for example, some are burnt annually by hunters with dogs, hoping to kill a sitatunga *Tragelaphus spekii* Speke 1863—and many have been drained or degraded, especially the numerous relatively small swamps in the south-west of Uganda, and particularly around their edges (Maclean *et al.,* 2011a). Nevertheless,

extensive areas of fairly intact but unprotected papyrus remain today. Most of these surviving swamps in Uganda are around the Lake Kyoga system in central Uganda, and along the shores of Lake Victoria.

The sedge *Cyperus papyrus* is the world's largest, normally reaching a height of several metres and often in stands which are almost monocultures, growing in shallow waters bordering lakes and slow-flowing rivers. Papyrus dominates floodplain swamps throughout central and southern Africa and in shallow lake systems, such as Lake Victoria and parts of Lake Albert. The entangled rhizomes often form floating mats, thus providing a sheltered habitat for fish, and even crocodiles, although this only occurs in fairly stable hydrological regimes, where seasonal changes in water levels are gradual (Thompson, 1976; Thompson & Hamilton, 1983). Papyrus in Uganda is used by people for various purposes and is therefore valued by local communities as an ecosystem service. Because the papyrus habitat is so unusual, and not well-known, we have provided some more detailed information about it in appendix 1.

Previous studies of birds in papyrus swamps have been made in Kenya by Britton (1978) and Owino & Oyugi (2008), and in south-west Uganda (Maclean *et al.,* 2014 and references therein). Each of these studies were in areas where the papyrus had been disturbed to varying degrees by human activity.

We studied the birds of the almost completely undisturbed Nile delta from September 2017 to August 2018. The term 'Nile delta' usually refers to the entry of the River Nile into the Mediterranean Sea in Egypt, but the term is also widely used in Uganda for the delta we are discussing here, despite the official Ramsar name being 'Albert', and we therefore retain its use in this paper.

From the swamps we first aimed to document the avifauna by recording all species using them and estimating the relative abundances of the most common species, which depend upon them to varying degrees (table 1). Entering mature papyrus swamps is difficult, and we describe a method of counting from the papyrus edge. Because we were at the edge, density estimates (*e.g.,* using the software Distance) were not practical, since the area of swamp was only that of a semi-circle, the other half being water. We therefore used encounter rates, as described below. Then, since there are plans to extract oil and gas from an area upstream of the swamp, we consider the potential threats from this and other possible causes, such as increasing rainfall and its effects on the water levels. This Ramsar site is important not only for conservation and as a breeding ground for aquatic animals such as fish, but increasingly for tourism too, since many birds can be seen along the open channels that carry most of the Nile waters to Lake Albert—notably the much sought-after shoebill *Balaeniceps rex* Gould, 1850.

MATERIAL AND METHODS

Study Area

As it approaches the northern end of Lake Albert, the River Nile forms a delta of about 35 km^2, most of which is covered by swamp vegetation. The river flows mainly through three channels, referred to as northern, southern, and central, the last being a branch of the southern channel (figure 1). These channels average about 130 m in width, and there are also a number of smaller branches, particularly towards the lake. The three main channels are readily navigable by small boats, including those used in this study, and are increasingly used by tourists and illegal fishermen.

The swamp vegetation is predominantly papyrus, *Cyperus papyrus*, which reaches a height of 3-4 m. Within the papyrus, there are a few open areas, supporting a wide variety of swamp vegetation, mostly less than 1 m in height. For much of their lengths, the channels are fringed by papyrus (figure 2), but in some places there are bands of the aquatic grass, *Vossia cuspidata* (Roxb.) Griff., with the papyrus beyond. This tall perennial grass, which rarely flowers, is largely restricted to this part of Uganda (Harker & Napper, 1960) (see table 1). Within the main areas of papyrus are occasional clumps of small trees, mainly *Ficus trichopoda* Baker (synonym *F. congensis* Engl.) (figure 3).

To achieve a wide coverage, and to minimise bias, we established sample points at 1 km intervals on the margins of the northern and southern channels, with two additional points, 2 km apart, on the central channel, in order to bring the total to 20 (figure 1). All of these points provided data both for the survey of larger waterbirds and for our assessment of the overall species diversity in the papyrus. As figure 1 shows, this set of sites gave a good coverage of the main channels running through the swamp area. Having the sample sites at the edge of the swamp (the only practicable way of having them) also has consequences, including edge effects *per se*, and more light for plant growth, so that many smaller plants grow between and on the papyrus. Successive points were on alternate sides of the channel, unless that place had no papyrus (for example, part of the north channel is fringed on its northern bank by adjacent savanna, macrophytes being absent). Further, seven of the 20 sites were fringed by up to 50 m of *Vossia cuspidata* (table 2).

Table 1. The mean monthly encounter rates of the commoner species, totalled across the 20 delta sites (B1-20). The species groupings follow Maclean et al (2003). G-VU and G-NT indicate globally Vulnerable and Near-threatened species. The less common species are listed in Appendix 2.

		Monthly	
Guild	Guild members	Mean	SD
Papyrus-restricted species	Papyrus gonolek *Laniarius mufumbiri* (G-NT)	23.08	6.82
	White-winged swamp warbler *Bradypterus carpalis*	1.42	0.9
	Carruthers' cisticola *Cisticola carruthersi*[b]	26.25	6.7
	Greater swamp warbler *Acrocephalus rufescens*[b]	15.42	4.21
	Papyrus yellow warbler *Calamonastides gracilirostris*[b] (G-VU)	0.42	0.67
	Shoebill *Balaeniceps rex* (G-VU)	0.5	0.67
	Papyrus canary *Serinus koliensis*[c]	0	0
Swamp-reliant species	Lesser swamp warbler *Acrocephalus gracilirostris*[de]	16.83	5.46
	Blue-headed coucal *Centropus monachus*[f]	17.83	4.97
	Swamp flycatcher *Muscicapa aquatica*[f]	16.42	3.6
Swamp-opportunist species	Winding cisticola *Cisticola marginatus*	3.25	2.05
	Yellow-backed weaver *Ploceus melanocephalus*	25.5	16.19
	Slender-billed weaver *Ploceceus pelzelni*	8.08	7.49
	Grey-capped warbler *Eminia lepida*	15.08	4.78
Generalised species	African mourning dove *Streptopelia decipiens*	17.92	9.98
	Common bulbul *Pycnonotus barbatus*	14.5	3.8
	Diedrick cuckoo *Chrysococcyx caprius*	2.08	1.98
	Common waxbill *Estrilda astrild*	5.5	10.18

Notes

a The first three are papyrus endemics
b In some areas, these species occur in other kinds of swamps
c Only one record for this area (GK)
d Can occur in other mycrophytic vegetation, but are papyrus endemics in the delta
e Given by Maclean *et al*. 2006 as an example
f our examples

Data collection

The birds fall into two main groups: birds of the swamps, considered in this paper, those on the wide-open water channels of the Nile which flow through the swamps (see Pomeroy *et al.*, 2020), together with those along the edges of the swamps, effectively an ecotone, such as swamp flycatcher *Muscicapa aquatica* Heuglin, 1864 and African jacana *Actophilornis africana* (Gmelin, 1789). Our main interest was in the papyrus-restricted and swamp-reliant species (table 1). We define encounter rates as the number of bids detected during ten-minute counts at each of the twenty points indicated in figure 1. At each site, the boat was moored next to the papyrus or *Vossia.* We allowed a two-minute quiet period before the count began, and then all birds seen or heard at any distance from within or above the papyrus were reported by two observers. Occasionally, two calls of the same species were heard fairly near to each other, and these were assumed to be from the same bird that had simply moved a short distance.

Both observers and the recorder, and the boat's three crew members, observed silence before and during the count, apart from the noting of records. Birds were counted if within the swamps, and also recorded (but separately) if flying over, so long as they belonged to species that were commonly found within the swamps. Counts were made monthly from September 2017 to August 2018, so that each site received twelve counts. The numbers of birds recorded varied with time of day, so we varied the order in which sites were counted, so that each site had earlier, later, and intermediate times.

Figure 1. Map of the western part of the Murchison Falls – Albert Delta Ramsar site, showing the distribution of the count sites along the three main channels (B1-20). The Ramsar boundary extends several kilometres into the lake.

Figure 2. A wall of papyrus fringes many kilometres of the main channels.

Figure 3. Clumps of fig trees provide perches for doves and other species.

Table 2. Main features of the 20 counts sites in the delta (B1-20) and four upstream (R1-4), which are also within the Ramsar site. The habitat opposite is included to give a broader view.

	Channel						
Count site	Location[a]	Width(m)	Side[b]	Current [c]	Vossia width (m)	Habitat opposite[d]	Notes
B1	S	430	S	S	-	Riverine forest	Grass swamp to 15 m
2	S	110	N	S	10	Vo 20/Pa	-
3	S	235	S	S	0	Vo 30/Pa	-
4	S	200	N	F	15	Vo 10/Pa	-
5	S	170	S	S	0	Vo 20/Pa	-
6	S	140	N	F	0	Pa	2 m of grass
7	S	105	S	F	0	Pa	-
8	S	80	N	F	30	2m grass then Pa	-
9	S	80	S	F	0	2m grass then Pa	-
10	M	115	N	S	5	Pa	Swamp for 5 m
11	M	90	S	F	0	Pa	-
12	N	110	S	F	0	Pa	
13	N	150	N	N	50	Riverine forest	Extensive *Vossia*
14	N	160	S	S	0	Riverine forest and swamp E	
15	N	70	S	F	0	Pa	
16	N	70	N	F	10	Pa	*Vossia* nearby
17	N	180	N	N	-	Pa	Mixed swamp vegetation[e]
18	N	220	S	F	0	Open swamp then savanna	
19	N	220	S	S	-	Savanna	Mixed vegetation for 30 m[f]
20	N	200	N	F	5	Vo 20/Pa	
R[g]1	U	110	S	S	0	Pa	
2	U	260	S	S	0	Riverine forest	
3	U	140	S	F	0	Riverine forest	
4	U	205	N	S	100	Pa	Riverine forest beyond

Notes
a S = South, N = North, M = Central channel, U = Upstream
b S = South, N = North bank
c N = Nil, S = slow, F = faster
d Pa = papyrus, Vo10 = 10 m of *Vossia*, then papyrus
e Similar to open swamps E and F
f Papyrus beyond
g River sites

So as to better assess their distributions, especially those of less common species such as the papyrus yellow warbler *Calamonastides gracilirostris* (Ogilvie-Grant, 1906), after the end of some counts, we played the calls of species that were thought likely to be present, but which had not been recorded within the ten minutes of the count, using the free-to-download *African Bird Sounds* in a mobile phone. Species thus recorded were not included in the counts. Some counts were also made on the upstream islands (R1-4, figure 1), to confirm that they had similar swamp bird populations to the delta.

Species names of birds are based on the 7-volume *Birds of Africa* (1982-2004) and the bird families are ordered according to Dickinson. & Remsen (2013) and Dickinson. & Christidis (2014).

For each count, we recorded the start time and shade temperature. In addition, flowering plants were recorded by Sam Mutebi (pers. comm.); any that could not be identified in the field were collected and checked at the Herbarium of the Department of Botany at Makerere University.

RESULTS

Encounter rates

From the 240 counts made in the 12-month period, a total of 134 species were recorded as using the swamps and adjacent channels in some way. Table 1 shows the mean numbers of records (encounter rates) of the main swamp species, the remainder being listed in appendix 2.

Three of the papyrus-restricted species, and all three of those that are swamp-reliant, were recorded in a mean of 15 or more of the 20 count sites, when considered over the whole year. They included the globally near-threatened papyrus gonolek *Laniarius mufumbiri* (Ogilvie-Grant, 1911) (figure 4). However, the two globally-threatened species, shoebill (figure 5) and papyrus yellow warbler, were only recorded in very small numbers.

Figure 4. The papyrus gonolek is common in the swamps. (Photo credit, John Caddick)

Of the less specialised species, both African mourning dove *Streptopelia decipiens* (Hartlaub & Finsch, 1870) and yellow-backed weaver *Ploceus melanocephalus* (Linnaeus, 1758), were particularly common. The dove was most often seen, and heard, near clumps of fig trees, whilst flocks of weavers were most common at the outer edges of the papyrus, where they also nested.

Over the twelve months of counts, a mean of about ten individuals were recorded at each of the twenty count sites, each month. However, these numbers could be affected by various factors, including temperature, time of day and time of year, as described in the following sections.

Figure 5. The shoebill is occasionally seen on the edges of the channel through the swamp and by Lake Albert. (Photo credit: Lwere Shakul)

Effects of time, temperature, and plant species diversity

The order in which counts were made was varied between months, since it was soon found, as expected, that counts made earlier in the day tended to produce more species. Time and temperature are of course correlated, but not perfectly—for example, a morning could start cloudy and cool, but later the sun comes out and it becomes much warmer. Figure 6 shows two representative data sets, in which the relationships, although negative, were not significant at $P = 0.05$. However, for the full set of 20 count sites, 13 showed clear negative slopes for species number against time, and 15 did so for temperature, implying that earlier counts are better in terms of numbers of birds recorded. In order to make comparisons between sites, we standardized the species number per site as the number estimated by regression for the time 08:00 h. They show a considerable range, from 4.1 to 9.9. These figures are compared to the numbers of plant species at each point in figure 7, on the assumption that a greater variety of plants (and therefore of their flowers and fruits) would provide a greater variety of food for birds and thus support more bird species. The correlation between these two variables is weak, however, perhaps because some of the plants found at the edge of the channel, and thus recorded by us, did not occur further into the papyrus (where light penetration will have been lower), and vice-versa. It may be noted that four of the five sites with a fringe of *Vossia* had fewer species of both plants and birds.

Seasons

Although they were all recorded from all 20 points, we found considerable month-to-month variation in the numbers of sites with records of all the commoner species within the swamps (figures 8 to 11), but in no month was any species recorded from all sites. Note that the swamp flycatcher is not included because it is only found at the water's edge. The opportunist and generalist species, which we assume are not confined to the swamps, may come and go from the adjacent dry lands. However, the lower numbers recorded for papyrus-restricted and swamp-reliant species (figures 8 and 9), particularly in the drier months around the turn of the year, implies that, although they were almost certainly there, they were not calling and were,

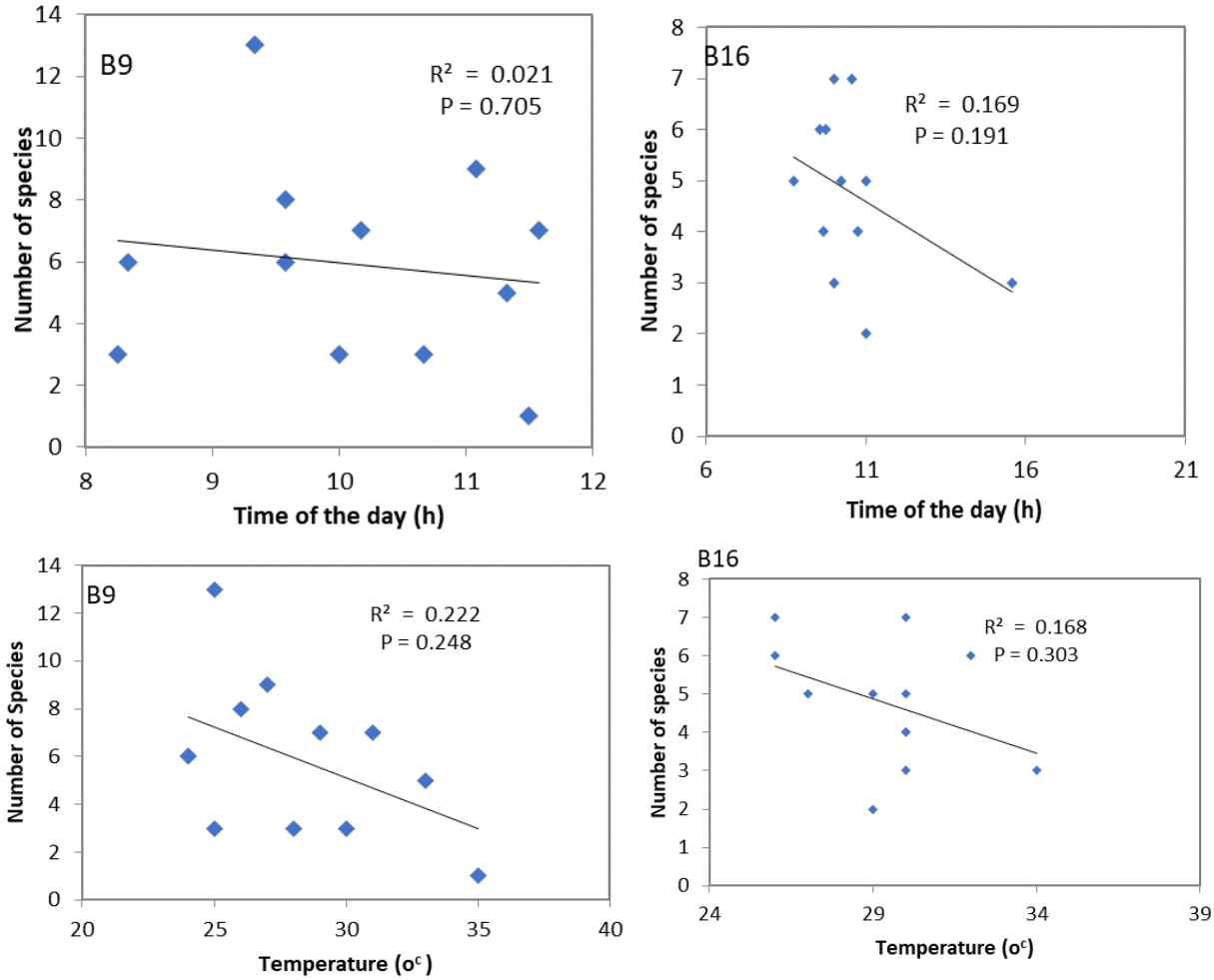

Figure 6. Numbers of species recorded by time of day (above) and temperature (below) for two representative count sites.

therefore, under-recorded by at least a quarter. As expected, most species called more often during their breeding seasons. Records of the two weaver species, unlike the others, were of birds seen.

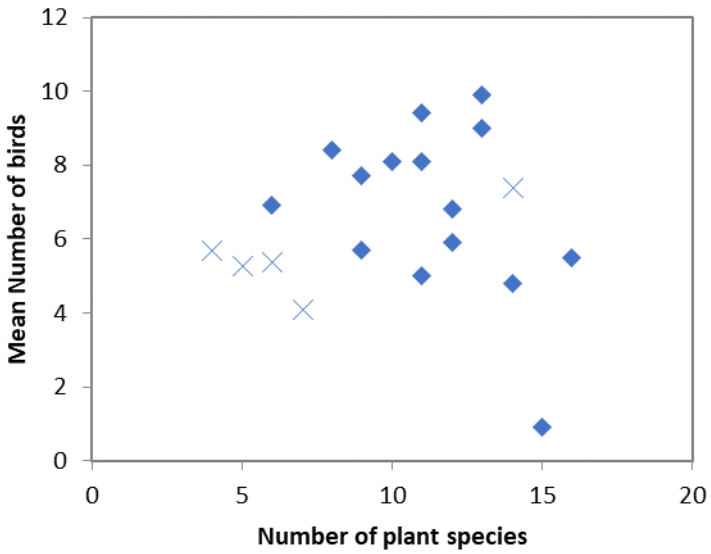

Figure 7. Relationship between the numbers of plant species and the mean number of bird species at the 20 delta sites. Sites with a band of Vossia *>= 10 m wide are represented by a cross (plant data from S Mutebi, pers comm).*

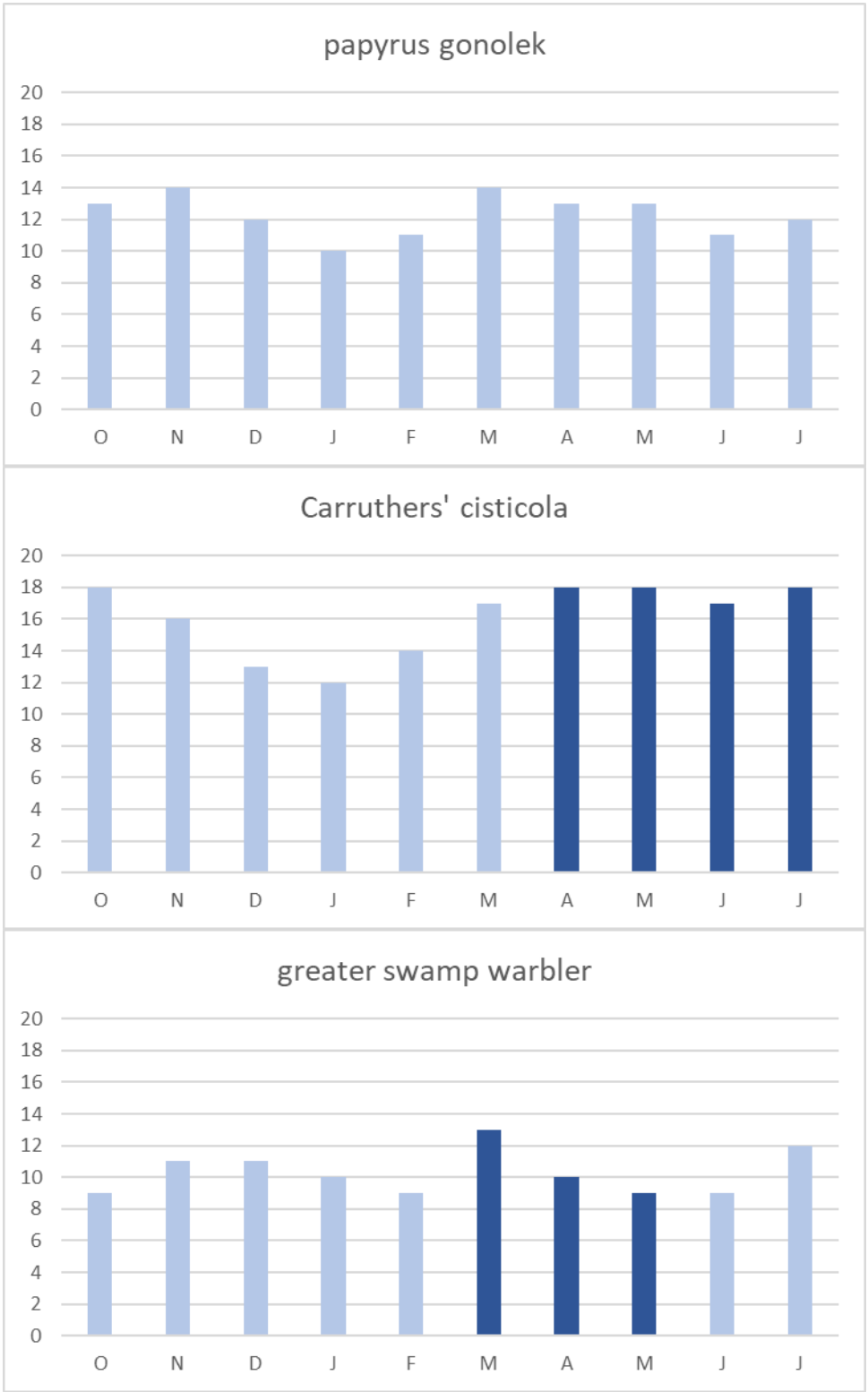

Figure 8. Monthly numbers of count sites (out of 20) with records of the three papyrus-restricted species. Data are three-point running means. The main egg–laying months (from Brown & Britton 1980) are shaded in darker blue. There are no known nesting data for the papyrus Gonolek.

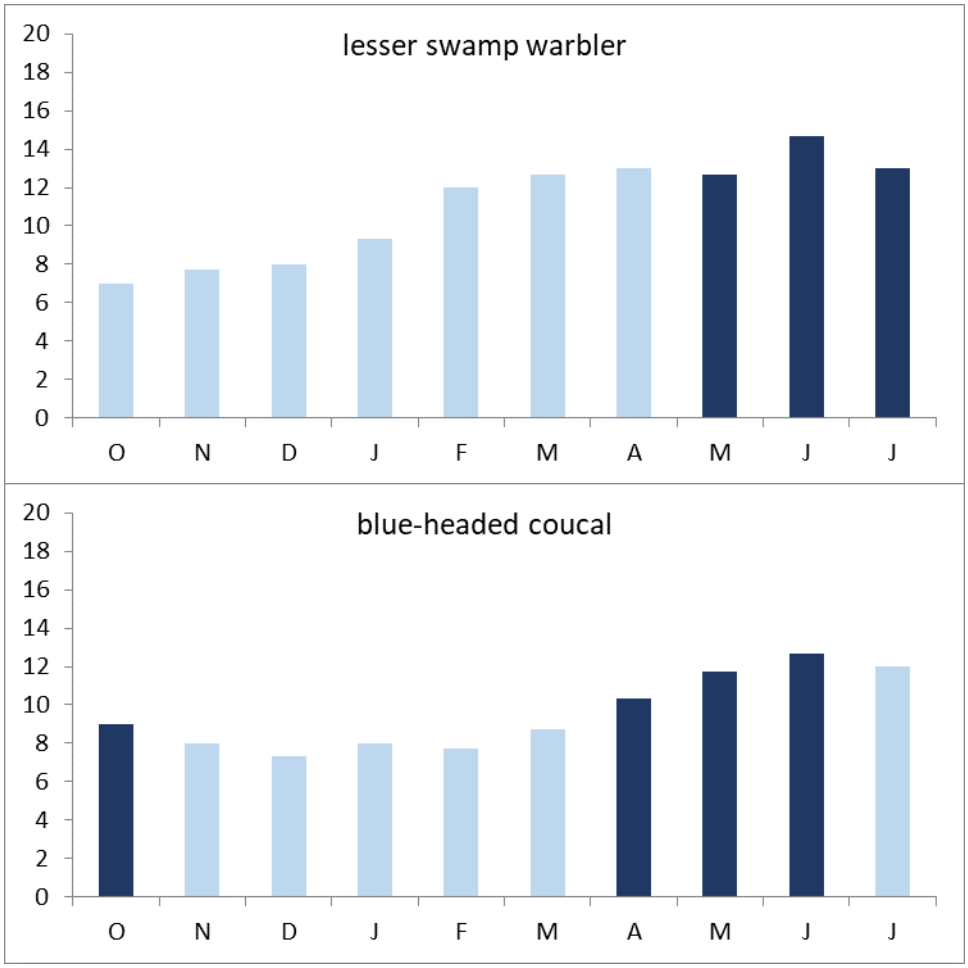

Figure 9. Monthly numbers of count sites (out of 20) with records of the two swamp-reliant species. Data are three-point running means. As in Fig.4, the main egg–laying months are shaded in darker blue.

Nesting

Apart from the weavers, whose nests are conspicuous along the swamp edges, and the papyrus gonolek, for which there are no known breeding records, most species' expected breeding seasons coincide with rainy periods (figure 7-12), sometimes extending a little beyond into a drier period; these are times when many plants flower and fruit, and insect life is abundant.

Duetting

In addition to the well-known duetting by the black-headed gonolek *Laniarius erythrogaster*, (Cretszchmar, 1829), duetting also occurs in both the papyrus gonolek (IMD Maclean, pers comm) and Carruthers's cisticola *Cisticola carruthersi* Ogilvie-Grant, 1909 (Fry *et al.,* 2000). For these species we therefore assume that most records represented two birds, although the data in table 1 and appendix 2 simply reflect the numbers of calls of these species. However, for all the others, except the weavers, which were invariably seen, we assume that only the males call, and therefore that the females remained unrecorded. Thus, the numbers of birds recorded by calls and songs will have been under-estimated.

Use of playback

In order to increase the numbers of records of birds in the papyrus swamps, we made use of playback recordings, particularly for the Globally Vulnerable papyrus yellow warbler and white-winged swamp warbler *Bradypterus carpalis* Chapin, 1916, both papyrus-restricted species, but for which we otherwise had few records. Playbacks, especially for these two species, were made in the absence of records during the ten-minute point count, and where the habitat seemed most suitable. The use of these recordings followed the recommendations of De Rosa *et al.* (2022).

Despite the recordings being (to the human ear) of high quality, of 121 times when we used a playback, only 23 were successful (19%), but the proportion varied between species (table 3), ranging from zero to

0.33. They also varied with time. For example, for the seven counts at B14 from February to August 2018, on four occasions the papyrus gonolek was recorded as being present, and on the other three we used playback. It only responded on one of these occasions, but was presumably there on the other two. Many similar examples could be quoted.

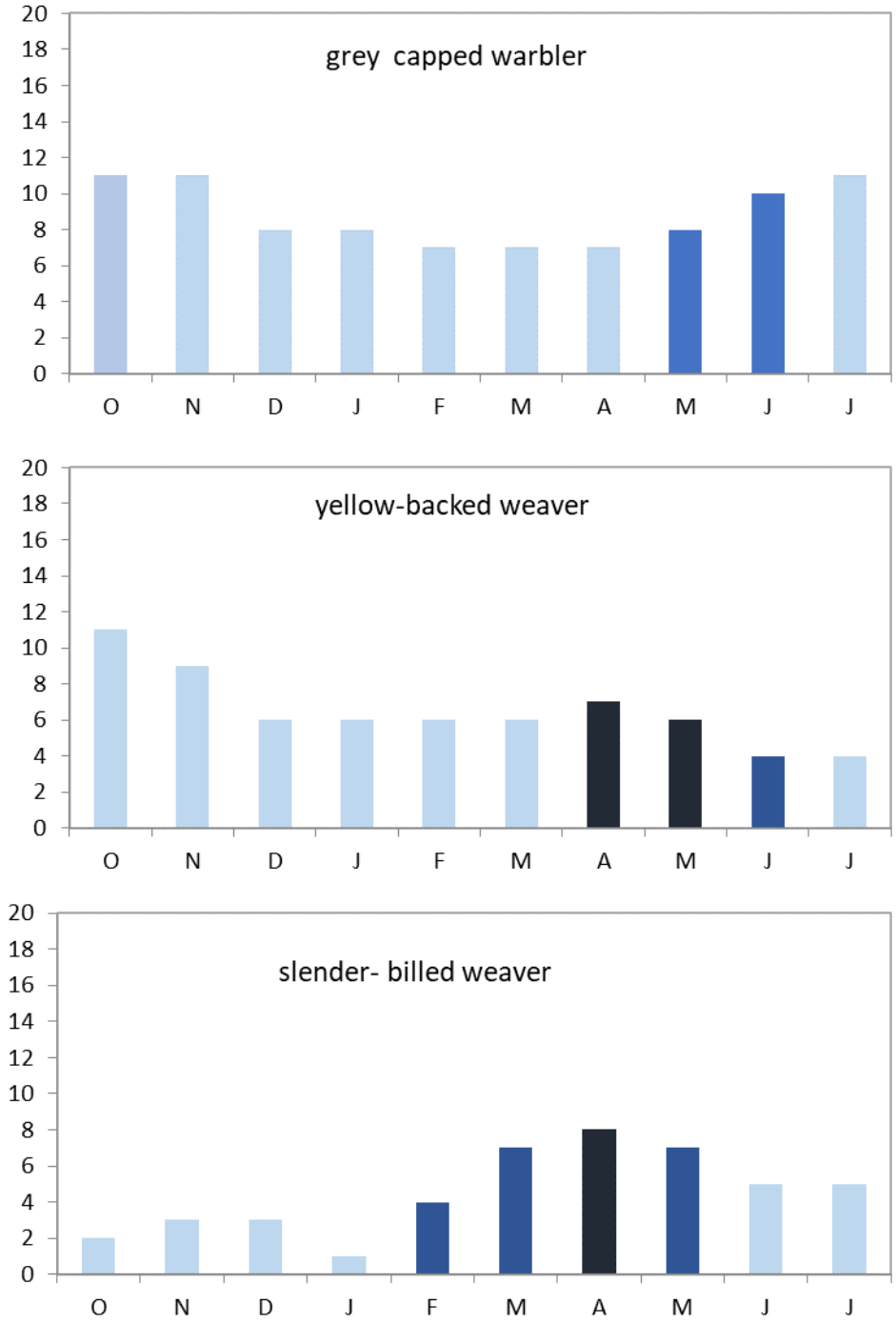

Figure 10. The numbers of count sites with records of swamp opportunist species (out of possible 20). Data are three point running means. The main egg-laying months from our data (unpubl) are shown in dark blue with additional data from Brown & Britton (1980) in mid-blue.

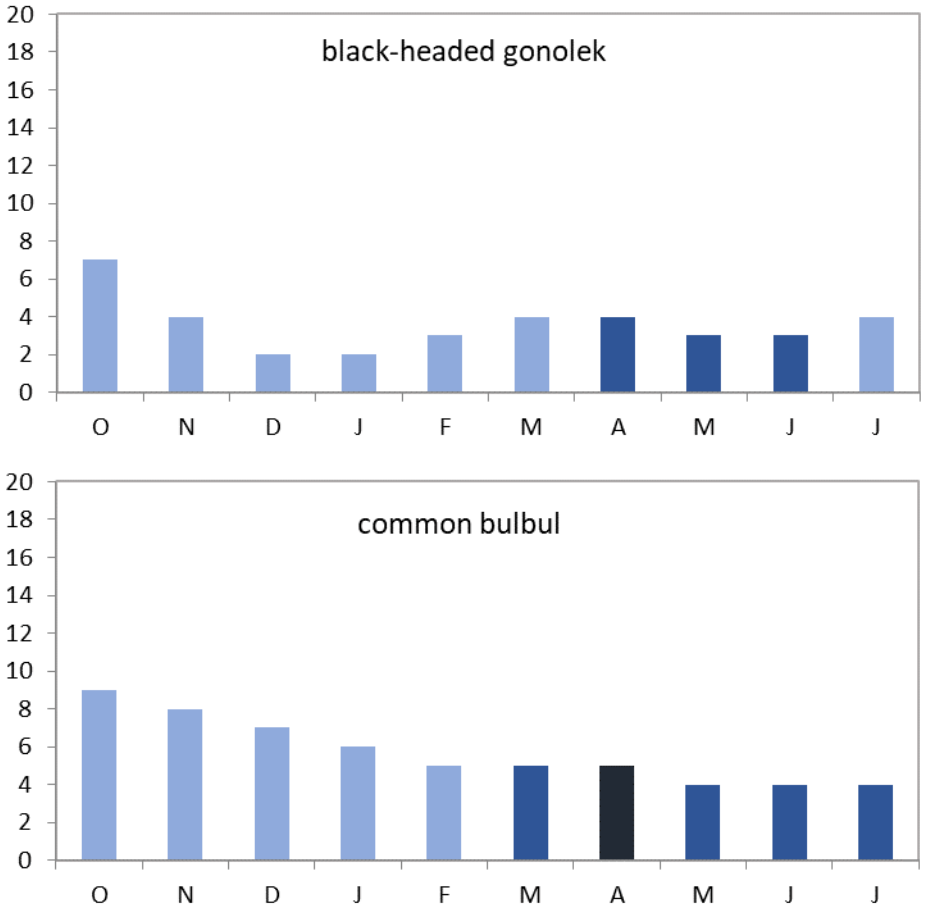

Figure 11. The numbers of sites with records of Generalist species (out of possible 20). Data are three point running means. The main egg-laying months from our data (unpubl.) are shown in dark blue with additional data from Brown & Britton (1980) in mid-blue.

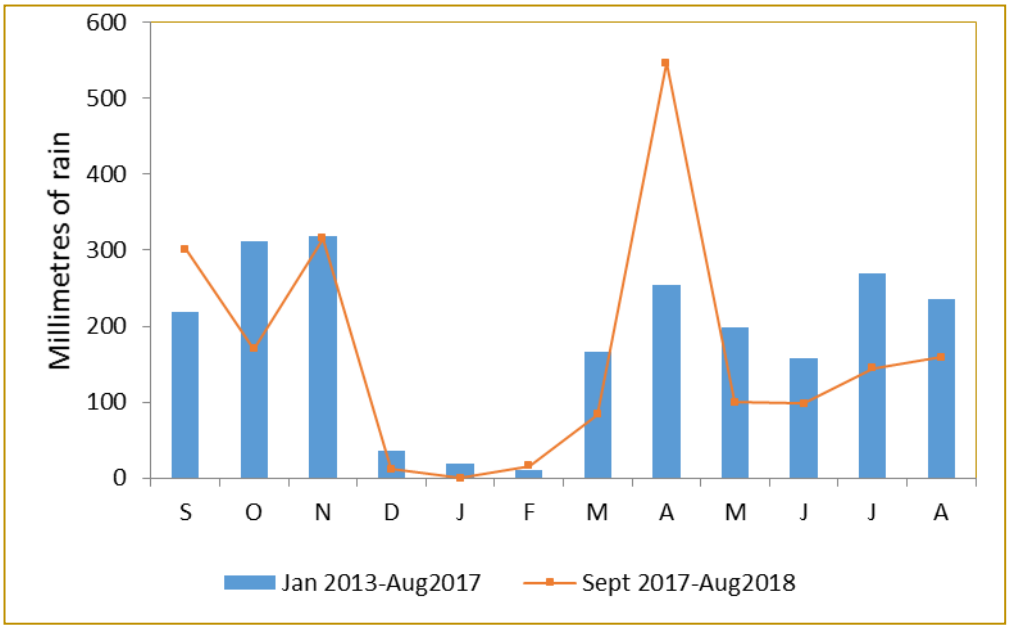

Figure 12. Monthly average rainfall at MFNP (Park Headquarters) from January 2013 to August 2017, and actual monthly rainfall for September 2017 to August 2018, which is seen to follow a similar pattern.

DISCUSSION

The Nile delta section of this Ramsar site clearly supports large numbers of birds, although with relatively few species confined to the papyrus. However, we recorded 134 species in the overall area of the delta, as shown in table 1 and appendix 2, which includes birds flying over if they were thought, at times, to use the papyrus, or, as with hirundines, were feeding above it. Whilst a number of species are either confined to papyrus swamps, or are characteristic of them, we were surprised at the numbers and prevalence of more generalist species, often five or more kilometres from dry land, adding to the species richness of the swamps.

Encounter rates are obviously affected by detectability, and the abundances of birds will almost certainly have been under-estimated for those species recorded mainly by calls, particularly those that do not duet. Further, some species will have occurred in lower numbers towards the edge of the papyrus, as found, for example, by Maclean *et al.* (2011b) for the papyrus gonolek.

Nevertheless, the counts reported here provide robust baseline data with which future counts can be compared for monitoring purposes, provided that those counts follow similar times of year and times of day and should also reflect any major changes that have taken place in the environment. It is therefore desirable to monitor key environmental factors, such as water levels and water quality, as well as the birds. And for the birds, it will be worth considering passive acoustic monitoring (Perez-Granados & Traba, 2021), which would allow more frequent sampling, and possibly also sampling from within the papyrus. The latter would allow population densities to be estimated. Encounter rates, as described here, are however a simple and effective method where counts can only be made from the edge.

The virtual absence of papyrus yellow warbler and low numbers of white-winged warbler are mainly a result of the comparatively low altitude (Lake Albert is at 619 m). The altitudinal range of the former in Uganda is given by Carswell *et al.* (2005) as 1000-2000 m. The global range of the white-winged warbler is small, Uganda and nearby parts of neighbouring countries, where it has mainly been recorded at altitudes above 1000 m (Urban *et al.,* 1997). The range extension of these species is therefore both geographical and altitudinal, since, in Uganda they had previously only been recorded further south (Carswell *et al.*, 2005).

The outer part of the delta is outside the National Park (figure 1) and is heavily fished. The outer edge is only partly fringed by papyrus, other sections having much shorter swamp plants, and these areas have large numbers of species such as African open-billed storks *Anastomus lamelligerus* Temminck, 1823, various herons and waders, with smaller numbers of lesser jacanas, *Microparra capensis* (Smith, 1839), shoebills and others. We have therefore recommended to the Uganda Wildlife Authority, that they consider extending the park boundary to include these areas, and they have agreed to consider this, subject to approval by all parties concerned. One important feature of this site is its large size; however, the fact that any particular site could be the subject of harmful changes means that a regional approach to the conservation of these species is important (Gaston, 2003, p174). In other words, efforts should be made to conserve more, geographically spread, areas of papyrus, such as those around Lake Kyoga.

The Ramsar Convention encourages ‘wise use’ of wetlands, and their sustainable management has been widely considered (*e.g.* Denny, 1985; van Dam *et al.*, 2011). Zsuffa *et al.,* (2014) described an interesting procedure for integrated management of papyrus wetlands in Uganda, but this has yet to be adopted by government. In the case of the extensive papyrus swamp of the Nile delta, in the part that is outside the park, some papyrus is cut to make fences and for craft use; its fringes are also heavily fished. If, as proposed, the outer part is incorporated into the park, some cutting might still be permitted, but extensive damage is not good for the papyrus birds (Donaldson *et al.,* 2018; Maclean *et al.,* 2006). Non-consumptive use—for conservation and tourism—would be best; there are other papyrus areas along Lake Albert where the sedge could be harvested, sustainably if possible. Future monitoring counts will show whether the bird populations in this Ramsar site are indeed being sustained. However, it will also be necessary to consider environmental changes. Rainfall has been increasing for some years (Diem *et al.*, 2019) and this can affect water levels which, in turn affect papyrus growth. Temperatures are also rising, as is the frequency of heat waves (Engdaw *et al.*, 2022), and that can increase stress on both plants and animals.

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Appendix 1: the papyrus habitat

Because of its importance as a specialised habitat through much of tropical Africa, and along the Nile into Egypt, we here describe this habitat in more detail, mainly based upon the classic work of Thompson *et al.* (1979) and Thompson (1985). Papyrus swamps are close to being a monoculture, with stems (culms) occurring at a high density—up to 10-12 mature culms per m^2, each with a spreading terminal umbel of bracts and flowers, providing almost complete canopy closure. Because of the high density of stems, most papyrus-dwelling birds communicate by sound rather than sight. A papyrus swamp can have a dry weight biomass of 30-50 $t.ha^{-1}$, of which 10-30 t is photosynthesising culms and umbels. For comparison, tropical forest has on average about 10 $t.ha^{-1}$ of photosynthesising leaves. Thus, papyrus provides an important ecosystem service by sequestering large amounts of carbon, which it is released when it is burnt. In the case of the delta, the slow flow of water beneath the papyrus may lead to an improvement of the quality of water entering the lake.

Papyrus also has the advantage of C4 metabolism—a high-capacity photosynthetic mechanism with a temperature optimum at 24 degrees Celsius. Forest trees only have conventional photosynthesis. And papyrus never has a water deficit. On comparative productivities, maize can produce 20 $t.ha^{-1}$ and even ryegrass can approach that, whilst tropical forest can produce 10-20 $t.ha^{-1}.yr^{-1}$, so it is not surprising that papyrus, with more green tissue, not structural material like trunks to support, and a more efficient photosynthetic system, can produce 30-50 $t.\ ha^{-1}.yr^{-1}$ (Thompson *et al.,* 1979).

The swamps of Uganda have been reported on for many years (Brown, 1905; Eggeling, 1935; Carter, 1956). Because papyrus has such a remarkably high productivity, reflected in rapid growth (Thompson, 1976), and unsurprisingly, as there are so many papyrus swamps in Uganda, they vary in their composition. For example, in some *Miscanthus violaceus* is characteristic of the swamp interior (Eggeling, 1935), but it has not been recorded in our study. One of the significant features of many papyrus swamps, including those of the Nile delta, are the clumps of a swamp fig tree *Ficus trichopoda* (synonym *F. congensis*) whose presence is important for a number of the bird species recorded, such as doves and bulbuls.

As well as its relevance as a study of the birds of such an extensive papyrus habitat, in this paper we have confirmed the importance of the delta as part of a Ramsar site, and one lying within an area of industrial development (particularly for oil and gas production). We also consider its potential for wise use, notably ecotourism.

Appendix 2. *The mean monthly totals of the less common species (those not shown in Table 2), totalled across the 20 delta sites (B1-20); 'w' indicates the main species of open waters.*

2016 No	COMMON NAME Scientific Name		Monthly	
			Mean	SD
2	White-faced whistling duck *Dendrocygna viduata* (Linnaeus, 1766)	w	5.58	8.47
6	Egyptian goose *Alopochen aegyptiaca* (Linnaeus, 1766)	w	2.33	6.54
7	Spur-winged goose *Plectropterus gambensis* (Linnaeus, 1766)	w	0.50	1.73
8	Knob-billed duck S*arkidiornis melanotos* (Pennant, 1769)		1.08	2.75
62	Red-eyed dove S*treptopelia semitorquata* (Ruppell, 1837)		0.08	0.29
68	Black-billed wood dove *Turtur abyssinicus* (Sharpe, 1902)		0.08	0.29
69	Blue-spotted wood dove *Turtur afer* (Linnaeus, 1766)		1.33	1.30
91	African palm swift *Cypsiurus parvus* (Lichenstein, 1823)		32.75	88.76
94	White-rumped swift *Apus caffer* (Lichtenstein, 1823)		0.33	1.15
100	Common swift *Apus apus* (Linnaeus, 1758)		0.08	0.29
107	Jacobin cuckoo *Clamator jacobinus* (Boddaert, 1783)		0.08	0.29
118	Red-chested cuckoo C*uculus solitarius* Stephens, 1815		0.17	0.58
125	Eastern grey plantain-eater C*rinifer zonurus* (Ruppell, 1833)		0.92	1.31
131	White-crested turaco *Tauraco leucolophus* (Heuglin, 1855)		0.08	0.29
139	Black crake *Zapornia flavirostra* (Swainson, 1837)		9.58	2.68
152	Grey crowned crane B*alearica regulorum* Bennett, 1833	w	2.08	2.43
161	Marabou stork *Leptoptilos crumenifer* (Lesson, 1831)		0.33	0.89
163	African open-bill stork *Anastomus lamelligerus* Temminck, 1823	w	1.83	1.95
168	Saddle-billed stork *Ephippiorhynchus senegalensis* (Shaw, 1800)	w	0.83	1.11
170	Pink-backed pelican *Pelecanus rufescens* Gmelin, 1879	w	1.33	3.73
171	Hamerkop *Scopus umbretta* Gmelin, 1879 *,w*		0.08	0.29
174	Little bittern *Ixobrychus minutus* (Linnaeus, 1766)		1.67	1.83
175	Dwarf bittern *Ixobrychus sturmii* (Wagler, 1827)		0.08	0.29
177	Black-crowned night heron *Nycticorax nycticorax* (Linnaeus, 1758)	w	0.17	0.39
178	Striated heron *Butorides striata* (Linnaeus, 1758)	w	0.42	0.90
179	Squacco heron *Ardeola ralloides* (Scopoli, 1769)		3.83	3.24
182	Cattle egret *Bubulcus ibis* (Linnaeus, 1758)		106.08	104.81
183	Grey heron *Ardea cinerea* Linnaeus, 1758	w	1.75	2.26
184	Black-headed heron *Ardea melanocephala* Vigors & Children, 1826		1.25	1.91
185	Goliath heron *Ardea goliath* Cretzchmar, 1827	w	2.42	1.51
186	Purple heron *Ardea purpurea* Linnaeus, 1756	w	5.42	2.39
187	Great white egret *Ardea alba* Linnaeus, 1758	w	0.08	0.29
188	Intermediate egret *Ardea intermedia* (Wagler, 1829)	w	0.42	0.67
190	Little egret *Egretta garzetta* Linnaeus, 1766	w	0.75	1.22
191	Sacred ibis *Threskiornis aethiopicus* (Latham, 1790)	w	1.83	3.49
196	Hadada ibis *Bostrychia hagedash* (Latham, 1790)		5.58	4.27
197	Glossy ibis *Plegadis falcinellus* (Linnaeus, 1766)	w	0.17	0.58
198	Long-tailed cormorant *Microcarbo africanus* (Gmelin, 1789)	w	41.42	92.21
199	Greater cormorant *Phalacrocorax carbo* (Linnaeus, 1758)	w	2.17	2.62
200	African darter *Anhinga rufa* Pennant, 1759	w	9.08	3.37
202	Senegal thick-knee *Burhinus senegalensis* (Swainson, 1837)		0.67	1.78
203	Water thick-knee *Burhinus vermiculatus* (Cabanis, 1868)		0.75	1.36

2016 No	COMMON NAME Scientific Name		Monthly	
			Mean	SD
221	Long-toed lapwing *Vanellus crassirostris* (Hartlaub, 1885)	w	7.00	4.16
222	Spur-winged lapwing *Vanellus spinosus* (Linnaeus, 1758)	w	5.17	4.04
223	Black-headed lapwing *Vanellus tectus* (Boddaert, 1783)	w	0.33	1.15
225	Senegal lapwing *Vanellus lugubris* (Lesson, 1826)		0.50	1.73
227	African wattled lapwing *Vanellus senegallus* (Linnaeus, 1766)		6.00	8.15
230	Lesser jacana *Microparra capensis* (Smith, 1839)	w	0.25	0.87
231	African jacana *Actophilornis africana* (Gmelin, 1789)		11.33	15.13
246	Great snipe *Gallinago media* (Latham, 1787)		0.17	0.58
247	Common snipe *Gallinago gallinago* (Linnaeus, 1758)		0.25	0.62
250	Common sandpiper *Actitis hypoleucos* (Linnaeus, 1758)		2.42	2.75
254	Common redshank *Tringa totanus* (Linnaeus, 1758)		0.17	0.58
272	Grey-headed gull *Chroicocephalus cirrocephalus* Viellot, 1818	w	3.33	11.55
277	Gull-billed tern *Gelochelidon nilotica* (Gmelin, 1789)	w	0.83	1.59
280	White-winged black tern *Chlidonias leucopterus* (Temminck, 1815)	w	5.08	5.50
285	Osprey *Pandion haliaetus* (Linnaeus, 1758)		0.83	0.94
290	African harrier hawk *Polyboroides typus* A. Smith, 1829		0.25	0.45
291	Palm-nut vulture *Gypohierax angolensis* (Gmelin, 1788)		0.17	0.39
295	Bateleur *Terathopius ecaudatus* (Daudin, 1800)		0.17	0.39
299	Western banded snake eagle *Circaetus cinerascens* von Müller, 1851		0.08	0.29
322	Western marsh harrier *Circus aeruginosus* (Linnaeus, 1758)		1.25	1.42
323	African marsh harrier *Circus ranivorus* (Daudin, 1800)		0.75	0.75
324	Pallid harrier C*ircus macrourus* (Gmelin, 1770)		0.08	0.29
326	African goshawk *Accipiter tachiro* (Daudin, 1800)		0.08	0.29
336	African fish eagle *Haliaeetus vocifer* (Daudin, 1800)	w	5.08	2.35
337	Black kite *Milvus migrans* (Boddaert, 1783)		1.67	2.19
435	Black-billed barbet *Lybius guifsobalito* Hermann, 1783		0.08	0.29
441	White-throated bee-eater *Merops albicollis* Vieillot, 1817		0.33	1.15
446	Blue-cheeked bee-eater *Merops persicus* Pallas, 1773		0.92	1.44
447	European bee-eater *Merops apiaster* Linnaeus, 1758		1.33	4.62
450	Blue-breasted bee-eater *Merops variegatus* Vieillot, 1817		0.75	1.22
458	Broad-billed roller *Eurystomus glaucurus* (Muller, 1776)		0.25	0.45
462	Malachite kingfisher *Corythornis cristatus* Pallas, 1764		4.25	4.07
465	Pied kingfisher *Ceryle rudis* (Linnaeus, 1758)	w	29.67	6.36
477	Red-necked falcon *Falco chicquera* Daudin, 1800		0.25	0.62
540	Sulphur-breasted bush-shrike *Cholorophoneus sulfureopectus* (Lesson, 1831)		0.17	0.39
548	Black-headed gonolek *Laniarius erythrogaster* (Cretszchmar, 1829)		7.42	5.09
564	Piapiac *Ptilostomus afer* (Linnaeus, 1766)		0.17	0.39
566	Pied crow *Corvus albus* Müller, 1776		0.17	0.58
586	Scarlet-chested sunbird *Chalcomitra senegalensis* (Linnaeus, 1766)		0.25	0.62
592	Malachite sunbird *Nectarinia famosa* (Linnaeus, 1766)		0.17	0.39
599	Beautiful sunbird *Cinnyris pulchellus* (Linnaeus, 1766)		0.83	1.59
600	Marico sunbird *Cinnyris mariquensis* A. Smith, 1836		0.25	0.62
601	Red-chested sunbird *Cinnyris erythrocercus* (Hartlaub, 1857)		0.08	0.29
608	Copper sunbird *Cinnyris cupreus* (Shaw, 1811-1812)		0.33	1.15

2016 No	COMMON NAME Scientific Name	Monthly	
		Mean	SD
616	Grosbeak weaver *Amblyospiza albifrons* (Vigors, 1831)	2.25	2.01
618	Red-headed quelea *Quelea erythrops* (Hartlaub, 1848)	1.67	5.77
619	Red-billed quelea *Quelea quelea* (Linnaeus, 1758)	43.00	55.12
623	Northern red bishop *Euplectes franciscanus* (Isert, 1789)	0.17	0.39
629	Fan-tailed widowbird *Euplectes axillaris* (A. Smith, 1838)	0.08	0.29
640	Northern brown-throated weaver *Ploceus castanops* Shelley, 1888	1.25	2.05
643	Lesser masked weaver *Ploceus intermedius* Ruppell, 1845	1.17	3.46
646	Black-headed weaver *Ploceus cucullatus* (Müller, 1776)	0.92	2.31
665	Red-billed firefinch *Lagonosticta senegala* (Linnaeus, 1766)	0.58	1.00
676	Red-cheeked cordon-bleu *Uraeginthus bengalus* (Linnaeus, 1776)	0.08	0.29
681	Fawn-breasted waxbill *Estrilda paludicola* Heuglin, 1863	1.25	3.74
684	Black-rumped waxbill *Estrilda troglodytes* Lichenstein, 1832	1.33	3.55
686	Black-crowned waxbill *Estrilda nonnula* Hartlaub, 1883	0.50	1.00
705	Bronze mannikin *Spermestes cucullata* Swainson, 1837	7.75	7.99
706	Black-and-white mannikin *Spermestes bicolo*r (Fraser, 1843)	0.08	0.29
732	Western yellow wagtail *Motacilla flava* Linnaeus, 1758	1.17	2.29
791	Moustached grass warbler *Melocichla mentalis* (Fraser, 1843)	0.17	0.39
849	Little rush warbler *Bradypterus baboecala* (Vieillot, 1817)	0.08	0.29
868	Great reed warbler *Acrocephalus arundinaceus* (Linnaeus, 1758)	0.58	1.00
880	Barn swallow *Hirundo rustica* Linnaeus, 1758	28.33	48.08
882	Angola swallow *Hirundo angolensis* Bocage, 1868	0.17	0.58
884	Banded martin *Neophedina cincta* (Boddaert, 1783)	1.17	4.04
886	Common sand martin *Riparia riparia* (Linnaeus, 1758)	89.67	222.16
890	Yellow-throated greenbul *Atimastillas flavicollis* (Swainson, 1837)	1.25	2.01
958	Ruppell's starling *Lamprotornis purpuroptera* Ruppell, 1845	0.42	0.79
1003	Spotted palm-thrush *Cichladusa guttata* (Heuglin, 1862)	0.08	0.29
1023	Capped wheatear *Oenanthe pileata* (Gmelin, 1789)	0.08	0.29