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Effects of habitat degradation on avian guilds in East African papyrus *Cyperus papyrus* swamps

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Summary

The density and species richness of bird communities in disturbed and undisturbed stands of papyrus *Cyperus papyrus* were compared. Point counts, corrected for different probabilities of detection in different swamps, suggested that the species richness of bird communities in stands of papyrus disturbed by burning, grazing or pollution was higher than in nearby stands that were not disturbed. However, there were fewer species and individuals of highly specialized birds or species characteristic of papyrus, in disturbed stands than in undisturbed swamps. At < 1 ha^{-1}, the density of Papyrus Gonolek *Laniarius mufumbiri* in Ugandan swamps was, for example, significantly lower in polluted and burnt sites than in undisturbed papyrus where up to 13 ha^{-1} were recorded in the centre of swamps. White-winged Swamp Warbler *Bradypterus carpalis* was only recorded in undisturbed papyrus. In the papyrus that fringes Lake Naivasha in Kenya, outside the geographical range of species restricted to papyrus, disturbance in the form of grazing selects against species classified as swamp-reliant. Species classified as generalist users of papyrus were much less sensitive to disturbance than specialists. The density of swamp specialists was also lower near the edge of swamps, where total species richness was higher. These results are discussed in relation to conservation management of papyrus swamps in East Africa.

Introduction

Papyrus *Cyperus papyrus* bird communities are thought to be amongst the least well protected birds in East Africa (Muriuki *et al.* 1997, Bennun and Njoroge 1999) and, in many places, their habitat is under immediate threat of degradation or loss (Britton 1978, Vande weghe 1981, Muriuki *et al.* 1997, Boar *et al.* 1999). Several East African species are entirely, or almost entirely, restricted to papyrus (Britton 1978, Vande weghe 1981). One of these, Papyrus Yellow Warbler *Chloropeta gracilirostris* is threatened globally and is classed as Vulnerable. Papyrus Gonolek *Laniarius mufumbiri* is considered Near Threatened (BirdLife International 2000). Several other species utilize papyrus, particularly around the edges of swamps. Although these birds may benefit from the presence of papyrus, they are not entirely reliant on this habitat.

In addition to clearance for agriculture and papyrus harvesting, swamps are particularly prone to three forms of habitat degradation: herbivore grazing and trampling, burning, and pollution (Vande weghe 1981, Mafabi 2000). Due to the current status of papyrus avian communities and continued stress on their habitat as a result of human activities, there is an urgent need to determine the impact of these forms of degradation on papyrus avian communities. These forms of degradation are unlikely to affect all species uniformly. In this study we therefore used avian guilds to draw comparisons between degraded and undegraded stands of papyrus.

Few studies of the birds of papyrus swamps have been conducted. Britton (1978) used mark-release-recapture to examine the seasonality, density and diversity of birds in a papyrus swamp near Lake Kanyaboli in western Kenya and Nasirwa (unpubl. data) examined the effects of vegetation structure on mist-net capture rates. Vande weghe (1981) proposed that altitude and rainfall were major influences on papyrus-associated birds in Rwanda and Burundi. In none of these studies were any quantitative comparisons between sites included. In this study we use point counts for estimating density and species richness in papyrus and develop a technique for comparing the species richness of sites with different probabilities of detecting birds.

Method

Study areas and sampling sites

Three types of degraded swamp were selected for study and compared with undegraded stands of papyrus in Uganda and Kenya (Figure 1). Sites were chosen where papyrus was influenced heavily by grazing at Lake Naivasha, Kenya (1,890 m), by burning on the north shores of Lake Victoria, Uganda (1,135 m) and by organic and industrial pollution at Kinawataka, south-east of Kampala, Uganda (1,185 m). Each of these three swamps showed symptoms of only one type of habitat degradation. In the Lake Naivasha and Kinawataka swamps, stands of apparently undegraded swamp within 5 km of the disturbed sites were also selected. For Kinawataka swamp, a valley-bottom swamp in south-western Uganda (0°24′ N, 30°24′ E, 1,190 m) with similar rainfall to Kampala (*c.* 1,400 mm) was selected for comparison. At the time of sampling, none of the swamps selected as controls showed any symptoms of current or recent degradation. All the undisturbed swamps were of similar size, shape and isolation to the swamps to which they were compared. Moreover, the surrounding topography and edge habitat were also similar between pairs of disturbed and undisturbed sites. Lake Naivasha differed from other sampling areas in that it was outside the geographical range of birds restricted to papyrus. Swamps subjected to pollution, burning or grazing can all be viewed as disturbed, if disturbance is taken to mean ''any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability or the physical environment'' (White and Pickett 1985).

Species richness estimates

In each swamp between 10 and 23 randomly located point counts were made, to calculate the mean species richness per point count in each swamp. All counts were conducted by the same observer between July and August 2001. The rar-

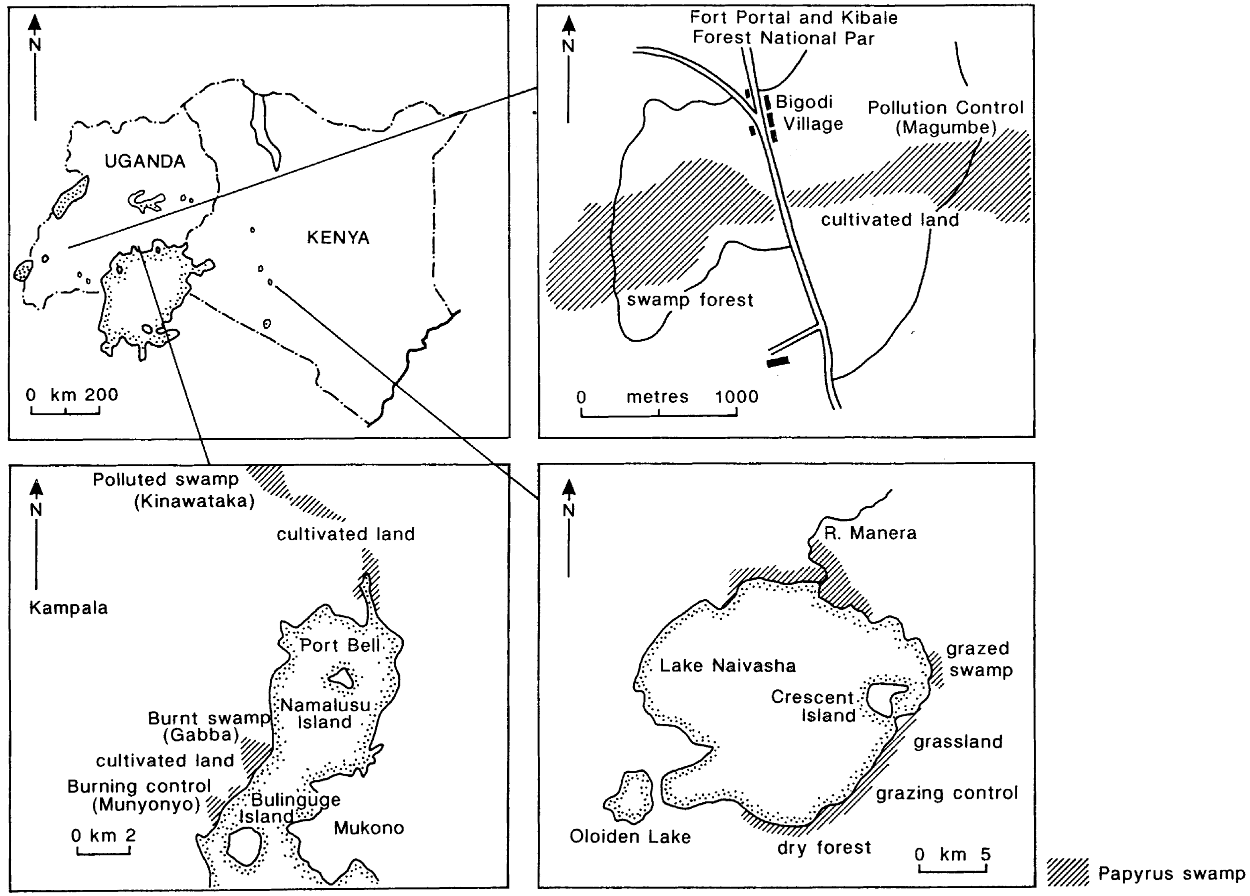

Figure 1. Map of East Africa showing the location of study areas. Areas of swamp and the type of habitat adjacent to the swamp are indicated.

efaction method (Hurlbert 1971) was also used to estimate the expected species richness of a sample of 30 individuals in each swamp. Between 06h00 and 10h00, birds were located either aurally or visually, identified, and their distance to the observer estimated. Distance of the sampling point to the landward edge of the swamp was measured directly or estimated from GPS readings. A sketch map was drawn to indicate the proportion of each sampling site that was covered by papyrus. The structure of the plant community that dominated the landward edge of each sampling site was recorded. Plant communities were classified as cultivated, grassland, dry forest or swamp forest.

In the smaller swamps, much of the area within which birds were detectable lay outside the swamp. Consequently, the area sampled by each point count differed. Moreover, probability of detection varied between disturbed and undisturbed stands because of very large differences in density of papyrus stems. For this reason, DISTANCE 3.5 software (Thomas *et al.* 1998) was used to calculate probability of detection functions for all species combined. First, data were grouped into 10 m distance intervals and evaluated for goodness of fit with detection probability function models. We evaluated uniform, half-normal and hazard-rate functions, selecting functions using lowest Aikake's Information Criterion (Buckland *et al.* 1993). An area/detectability product was then determined (area of swamp sampled multiplied by the probability of detection of a bird) and was held constant in analyses of data collected from each point where counts were made. This was achieved by calculating cut-off distances beyond which all birds located were ignored. Details of how cut-off distances were calculated are given in Appendix 1.

Density estimates

The density of birds in each swamp was estimated by dividing the number of birds recorded in each swamp by the area of swamp sampled and their probability of detection using DISTANCE. As some of the point counts were conducted near the edge of the swamp, and thus part of the area sampled within the cut-off distance lay outside the swamp, the area of swamp was estimated to the nearest 5 m^2 from sketch maps. Data were grouped into 10 m intervals and uniform, half-normal and hazard-rate models with cosine adjustments of order, evaluated for goodness of fit again using lowest Aikake's Information Criterion. Comparisons were made between the density of birds in the interior (> 25 m) of swamps with those near the edges (< 25 m). Densities were calculated using the same probability of detection function for both categories, and estimating the total area of papyrus sampled by point counts, using the sketch maps.

Species guilds

Each species encountered during the study was assigned to one of the following guilds depending upon the strength of its association with papyrus swamp. Notes on habitat use are taken from Mackworth-Praed and Grant (1960) and Fry *et al.* (2000).

Table 1. Estimated species richness of 30 individual birds in pairs of disturbed and undisturbed papyrus swamp in East Africa. Estimates were made using the rarefaction method (Hurlbert 1971).

Form of disturbance	Species richness in disturbed	Species richness in control
Pollution	11.83	11.41
Burning	12.59	8.65
Grazing	10.06	5.32

Papyrus-restricted species. Papyrus Gonolek, Papyrus Canary *Serinus koliensis* and White-winged Swamp Warbler are entirely restricted to papyrus (Vande weghe 1981). Carruthers's Cisticola *Cisticola carruthersi*, Greater Swamp Warbler *Acrocephalus rufescens* and Papyrus Yellow Warbler are restricted locally to papyrus (Britton 1978, Vande weghe 1981, Fry *et al.* 2000).

Swamp-reliant species. These are reliant on tall emergent swamp vegetation, but, in many cases, not papyrus. Where papyrus-restricted species are present, several species of warblers may, for example, be restricted to other swamp vegetation or to the edges of papyrus swamp, e.g. Lesser Swamp Warbler *Acrocephalus gracilirostris*.

Swamp-opportunist species. These birds are usually found in swampy areas, but are not reliant on tall emergent swamp vegetation and may be found far from a swamp, e.g. Winding Cisticola *Cisticola galactotes*.

Open water associated species. These birds are often found in swamps and forage in or around open water. Most are piscivorous, such as kingfishers, and will use emergent vegetation fringing open water for roosting or as hunting perches. The category includes birds such as jacanas, which are reliant on water lilies and floating vegetation fringing lakeside swamps.

Generalist species. These are not typical of lakeside or swamp habitats, and are found in a wide variety of habitats. All birds not assigned to one of the other categories were assigned here. Some swamp forest or other edge habitat specialists were included.

Results

In total, 56 species were recorded in the study (Appendix 2). Six of these were classed as papyrus-restricted, three as reliant upon swamp habitat, 11 species as swamp-opportunists with four species associated with open water. Of the species found 32 (57 %) were habitat generalists.

The species richness of 30 individuals, estimated using the rarefaction method, ranged from 5.3 to 12.6 species (Table 1). Mean species richness per point count in the grazed swamp was significantly greater than in the nearby undisturbed swamp (t_{21} = 3.48, P = 0.002), although other differences in species richness between swamps were insignificant (Figure 2).

The overall trend appears to be that disturbance results in a decrease in special-

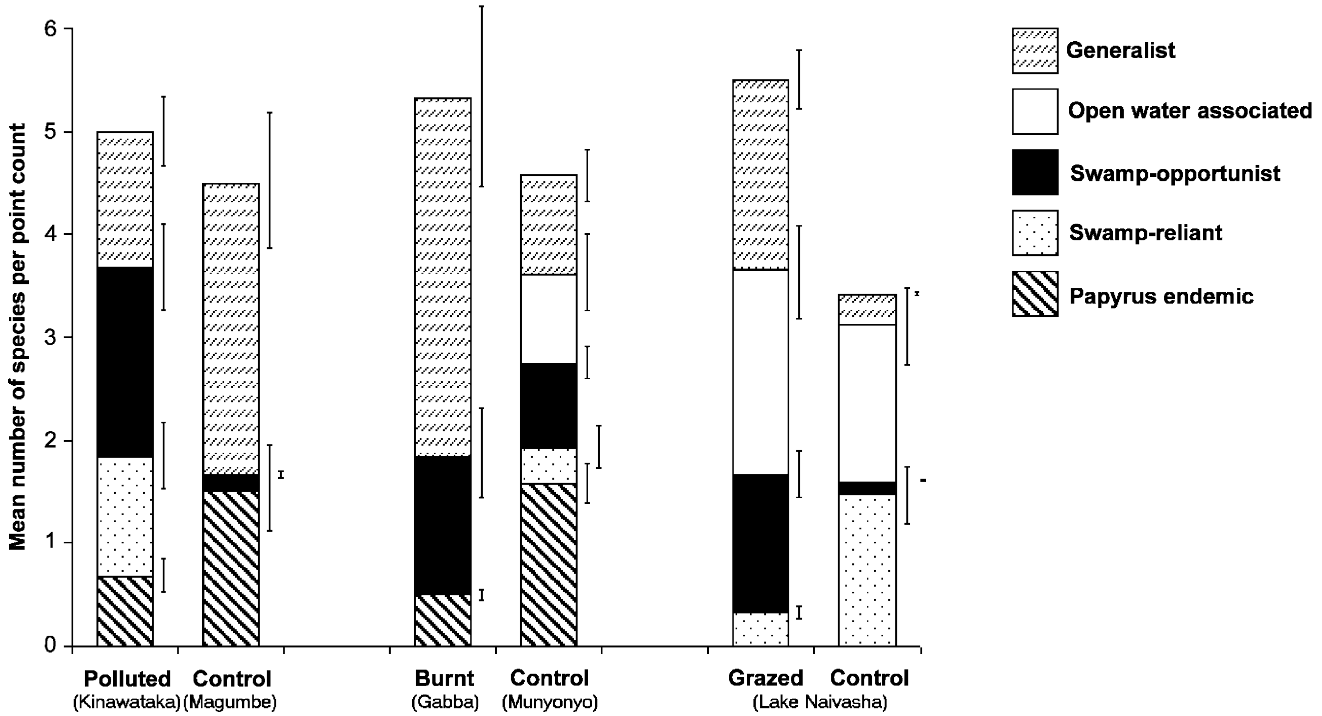

Figure 2. The mean number of bird species (± 1 S.E.) in each guild recorded by point counting in papyrus swamps in Kenya and Uganda during August 2000.

Table 2. Student (*t*) values, degrees of freedom (*df*) and levels of significance (*P*), indicating the differences in the number of bird species belonging to each guild, between disturbed and control swamps as shown in Figure 2.

	Polluted vs. control			Burnt vs. control			Grazed vs. control		
	t	*df*	*P*	*t*	*df*	*P*	*t*	*df.*	*P*
Generalist	1.98	22	0.061	2.75	27	0.011	5.32	21	<0.001
Open water associated	–	–	–	2.29	27	0.030	0.79	21	0.436
Swamp-opportunist	3.79	22	0.001	1.08	27	0.289	5.39	21	<0.001
Swamp-reliant	3.51	22	0.002	1.67	27	0.106	3.99	21	0.001
Papyrus-restricted	1.84	22	0.079	5.36	27	<0.000	–	–	–

ist species, but an increase in generalist species. For example, the number of papyrus-restricted species recorded in undisturbed swamps was more than in disturbed swamps, where in total, only two of the papyrus-restricted species (Papyrus Gonolek and Carruthers's Cisticola) were recorded. The species richness of generalists was greater in both the swamps disturbed by grazing and burning, although pollution made no difference to the number of generalist species (Figure 2, Table 2).

The mean number of open water associated species was lower in burnt than unburnt swamp, although this can be explained by the distance from open water at which burnt swamps were sampled as the burnt swamp was sampled more than 100 m from the waters edge. No differences in open water associated species between other pairs of disturbed and undisturbed swamp were found (Figure 2, Table 2). More swamp-opportunist species were supported by grazed and polluted papyrus than the corresponding undisturbed swamps, but there was no difference in the richness of swamp-opportunists between the burnt and unburnt papyrus (Figure 2, Table 2). There were fewer swamp-reliant species in grazed swamp but more in polluted papyrus than in the corresponding undisturbed swamps. Burning had a significant impact on the mean richness of papyrus-restricted species, whereas pollution appeared to make little difference (Figure 2, Table 2). There is no open water at Magumbe swamp and Kinawataka swamp and consequently no open water associated species were recorded at these swamps.

In two of the three control swamps, distance from the edge of the swamp appeared to make a difference to total species richness, with the edges of undisturbed swamps supporting similar avian communities to disturbed swamps (Figure 3). Mean species richness of birds in the centre (> 25 m from the edge) of control swamps was compared with that near the landward edges (< 25 m from the edge). Both the pollution control swamp, Magumbe, in western Uganda and also the burning control swamp, Munyonyo, on the shores of Lake Victoria had a greater species richness near the edge (Figure 3; at Magumbe: $t_{16} = 2.42$, $P = 0.028$; at Munyonyo: $t_{21} = 2.36$, $P = 0.028$). However, this is primarily due to the number of generalist species, as the richness of generalists was higher near the edges at both these sites (Figure 3, Table 3). Conversely, the richness of papyrus-restricted species was higher in the centre of swamps at both these sites (Figure 3, Table 3).

At Lake Naivasha, in Kenya, where the undisturbed swamp was surrounded by grassland, the overall species richness in the centre of the swamp did not

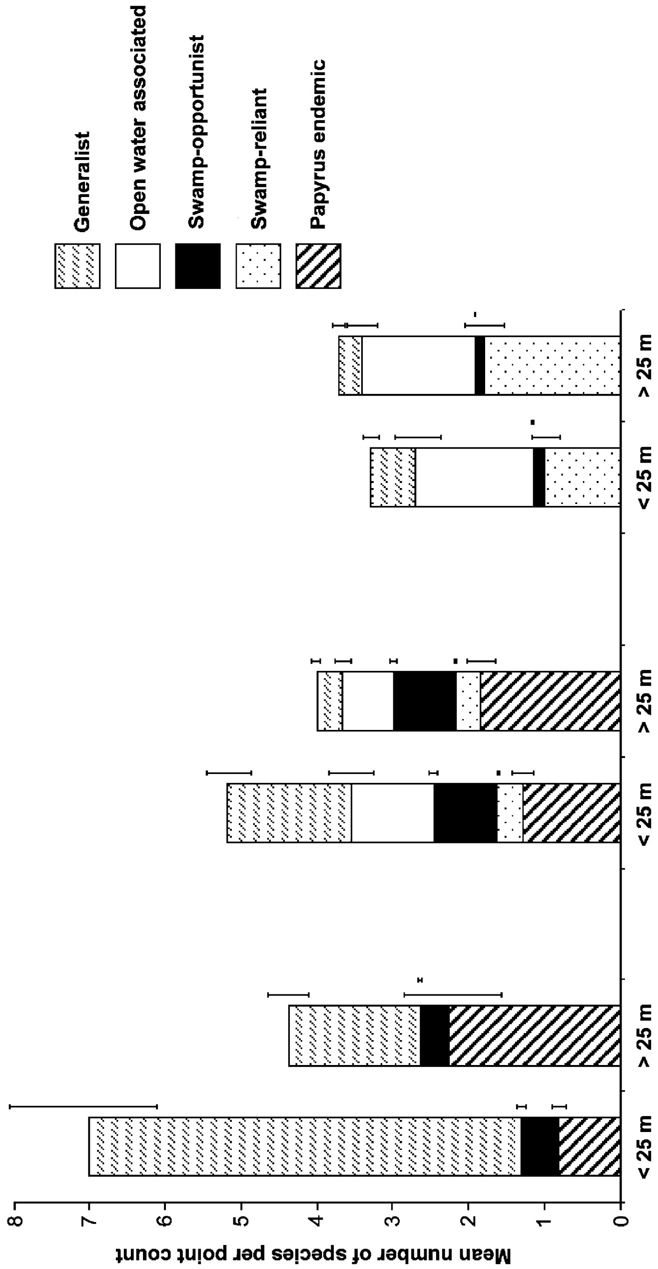

Figure 3. The mean number of bird species (± 1 S.E.) in each guild, recorded by point counts conducted near the edge (< 25 m) or in the interior (> 25 m) of swamps.

Table 3. Student *t* values, degrees of freedom (*df*) and levels of significance (*P*), indicating the differences in the number of bird species belonging to each guild, between the edge and centre of control swamps as shown in Figure 3.

	Pollution control centre vs. edge			Burning control centre vs. edge			Grazing control centre vs. edge		
	t	*df*	*P*	t	*df*	*P*	t	*df*	*P*
Generalist	3.92	16	0.001	3.68	21	0.001	1.86	15	0.083
Open water associated	–	–	–	1.36	21	0.187	0.19	15	0.849
Swamp-opportunist	1.71	16	0.106	0.13	21	0.898	1.68	15	0.113
Swamp-reliant	–	–	–	1.20	21	0.245	2.58	15	0.021
Papyrus-restricted	2.42	16	0.028	2.36	21	0.028	–	–	–

differ significantly from that near the edge (Figure 3). Nevertheless, the richness of swamp-reliant species was lower near the edge (Figure 3, Table 3). However, undisturbed papyrus at Lake Naivasha, bordered by dry woodland had a higher species richness than swamp bordered by grassland and a higher number of generalist and swamp-opportunist species (Table 4).

Because of the potential significance of papyrus-restricted species in the overall bird communities of the study sites, densities of the papyrus-restricted White-winged Swamp Warbler and Papyrus Gonolek were calculated. These species were chosen for density calculations as both were sufficiently abundant for reliable estimates to be made. Neither of these species were recorded at Lake Naivasha. Papyrus Gonolek occurred at lower densities in both the polluted swamp and burnt swamp, than in corresponding controls (Table 5). White-winged

Table 4. Point count bird species richness (mean ± S.E), indicating the differences in the number of species belonging to each guild, in papyrus surrounded by dry forest and papyrus surrounded by grassland at Lake Naivasha in Kenya.

Guild	Dry forest (± S.E.)	Grassland (± S.E.)	*df*	*t*	*P*
Generalist	3.17 ± 0.87	0.29 ± 0.14	21	3.27	0.004
Open water associated	1.67 ± 0.33	1.53 ± 0.23	21	0.35	0.730
Swamp-opportunist	0.83 ± 0.17	0.12 ± 0.08	21	3.78	0.001
Swamp-reliant	1.00 ± 0.37	1.47 ± 0.15	21	1.17	0.255
Total	6.67 ± 0.56	3.41 ± 0.32	21	2.14	0.044

Table 5. Density estimates (mean ha^{-1} ± S.E.) of White-winged Swamp Warbler, Papyrus Gonolek, Lesser Swamp Warbler and Little Rush Warbler in disturbed and control swamps.

	Disturbed site (± S.E.)	Control site (± S.E.)	*df*	*t*	*P*
Pollution					
White-winged Swamp Warbler	0.00 ± 0.00	10.29 ± 2.77	16	3.71	0.002
Papyrus Gonolek	0.16 ± 0.17	6.11 ± 1.34	16	4.40	<0.001
Burning					
White-winged Swamp Warbler	0.00 ± 0.00	7.10 ± 2.20	27	3.23	0.003
Papyrus Gonolek	0.32 ± 0.55	9.06 ± 3.34	27	2.58	0.016
Grazing					
Lesser Swamp Warbler	1.02 ± 0.47	29.52 ± 7.23	21	3.93	0.001
Little Rush Warbler	0.00 ± 0.00	6.43 ± 1.25	21	5.14	<0.001

Table 6. Density estimates (mean ± S.E. ha^{-1}) of White-winged Swamp Warbler, Papyrus Gonolek, Lesser Swamp Warbler and Little Rush Warbler in the edge and centre of control swamps.

	Edge (± S.E.)	Centre (± S.E)	*df*	*t*	*P*
Pollution control (Magumbe)					
White-winged Swamp Warbler	4.78 ± 1.85	12.93 ± 2.03	16	2.97	0.009
Papyrus Gonolek	3.67 ± 1.12	9.17 ± 1.55	16	2.88	0.011
Burning control (Munyonyo)					
White-winged Swamp Warbler	3.41 ± 1.76	10.48 ± 2.56	21	2.28	0.033
Papyrus Gonolek	4.70 ± 0.99	13.06 ± 3.34	21	2.27	0.034
Grazing control (Lake Naivasha)					
Lesser Swamp Warbler	23.07 ± 5.85	35.28 ± 6.25	15	1.86	0.167
Little Rush Warbler	4.46 ± 1.08	8.09 ± 1.55	15	3.28	0.005

Swamp Warbler was not found in disturbed sites, but occurred at densities significantly greater than zero in corresponding control sites. The densities of the swamp-reliant Lesser Swamp Warbler and Little Rush Warbler *Bradypterus baboecala* at Lake Naivasha were also calculated. A substantially lower density of Lesser Swamp Warblers occurred in papyrus disturbed by grazing than in the corresponding control, and no Little Rush Warblers occurred in this disturbed swamp (Table 5).

In addition to an overall reduction in the number of specialist species, the density of those specialist species most commonly recorded was also lower near the edges than in the centre of control swamps (Table 6). The densities of Papyrus Gonolek and White-winged Swamp Warbler were significantly lower near the edges of control swamps in which they were found, as was the density of Little Rush Warbler near the edge of the swamp at Lake Naivasha. However, Lesser Swamp Warblers showed no such significant difference at Lake Naivasha (Table 6).

Discussion

At between 7 to 10 ha^{-1} and 6 to 10 ha^{-1} respectively, the average densities of White-winged Swamp Warbler and Papyrus Gonolek recorded in undisturbed papyrus were lower than the estimates made by Britton (1978) using mark-release-recapture in western Kenya (21 ha^{-1} and 9 ha^{-1}). To our knowledge, estimates of density of Lesser Swamp Warblers and Little Rush Warblers have not been made previously. At approximately 30 Lesser Swamp Warblers ha^{-1} and 7 Little Rush-Warblers ha^{-1}, the results were again slightly lower than Britton's density estimates of other swamp species. Britton found 33 Greater Swamp Warblers ha^{-1}. Although our density estimates are lower than those made by Britton, we agree that the overall density of birds in papyrus is very high. In Magumbe swamp, densities of over 60 birds ha^{-1} were recorded. Under ideal conditions, papyrus can sustain extremely high growth rates (Muthuri *et al.* 1989) and such high densities may be a result of the high productivity of papyrus. The lower density of individual species, however, may be due to edge effects. Because of potential interspecific competition between the papyrus-restricted species and generalists from surrounding habitats, predation or edge disturbances, density estimates of species restricted to papyrus were likely to be smaller near the edge of swamps. Furthermore, smaller swamps have a higher edge to area ratio, of relevance here because the swamps used in this study were less than 200 ha in size, considerably smaller than that studied by Britton, which formed part of an extensive swamp network 160 km^2 in size. Density estimates from the interior of swamps would appear to confirm this theory. At approximately 13 ha^{-1}, the density of White-winged Swamp Warblers in the interior of Magumbe swamp, in western Uganda, for example, was closer to Britton's estimate.

Although the densities of swamp-reliant and papyrus-restricted species are lower near the edge of swamps, edge habitat appeared to have a greater influence on the richness of generalists and swamp associates than on the richness of swamp-reliant or papyrus-restricted species. Total species richness was highest close to the edge. This was observed also by Vande weghe (1981) who recorded higher richness of non-swamp species at swamp margins in the Akagera basin in Rwanda. At Magumbe and Munyonyo in Uganda, the species richness of generalists was higher near the edge of swamps. At Lake Naivasha this was not the case, possibly because the short-grazed grassland adjacent to this swamp contained few species of bird. The higher number of species, particularly generalists, found in the swamp surrounded by dry forest would appear to confirm this. It appears that the interface between papyrus and edge habitats, although often physically distinct, is less distinct in terms of its avian community. The avian community near the edge of undisturbed papyrus swamps was similar to that in disturbed swamps.

The intermediate disturbance hypothesis predicts that disturbance, particularly at intermediate intensity or frequency, increases species richness (Connell 1978). The results of this study lend support to these predictions in that species richness in this study was highest in papyrus swamps that had been disturbed. However, species least dependent upon papyrus were less likely to be recorded in disturbed swamps. Habitat generalists and swamp-opportunists favoured disturbance much more than swamp-reliant or papyrus-restricted species. Generalists were better represented in grazed and burnt swamps and opportunists in grazed and polluted swamps than in stands that were apparently undisturbed. Clearly, disturbance, particularly by burning and grazing, reduced the abundance of papyrus-reliant species. The density of Papyrus Gonolek was lower in polluted and burnt sites and White-winged Swamp Warblers were absent from both. At Lake Naivasha, outside the geographical range of papyrus-restricted species, disturbance appears to select against swamp-reliant species.

These findings parallel the case of forest bird communities, where disturbance by human activities does not favour specialist species, which as a group are of high conservation concern (O'Connell *et al.* 1998, Barlow *et al.* 2002) and several studies on Lepidoptera suggest these findings are not unique to birds (Brown and Hutchings 1997, Hamer *et al.* 1997). Specialist species may persist at high density, but if they are restricted to one habitat, the risk of their extinction through habitat loss or degradation is much greater than for species that occur also in less threatened habitats (Muriuki *et al.* 1997). We conclude therefore that species richness should not be used as a parameter to target conservation resources if no consideration is given to the extent to which species are specialists.

Acknowledgements

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Appendix 1. Calculating cut-off distances.

An arbitrary cut-off distance of 50 m was chosen for a point count conducted near the edge of the swamp with the lowest probability of detecting birds. The probability of detecting birds beyond this distance is very low. The area sampled (a_s) was estimated from ground maps using the following formula:

$$a_s = \frac{\pi}{12} \sum_{n=1}^{12} y_n^2 \quad (1)$$

where: y_1 to y_{12} are distances beyond which all birds located were ignored, taken at 30° intervals as shown in Figure 4. Their length is either the cut-off distance or the distance to the edge of the swamp, which ever is less.

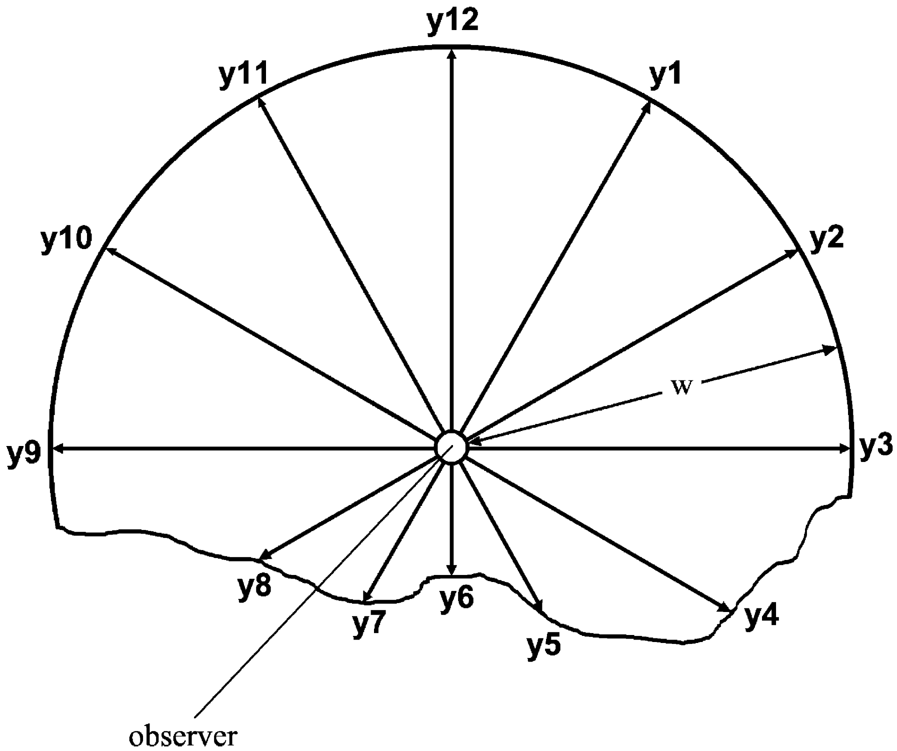

Figure 4. Diagrammatic representation of a point count conducted near to the edge of a swamp with an effective cut-off radial distance. Ground maps were used to mark the boundary of the swamp.

The average probability of detecting birds (P_a) within any given distance, w is given by the following equation (see Buckland *et al.* 1993 for details):

$$P_a = \frac{2\int_0^w r.g(r)\,dr}{w^2} \tag{2}$$

where: r is the distance from the observer.
g(r) is the probability of detection function – function that describes the probability that an object at distance, r from the observer will be detected, scaled such that $g(0) = 1$.

From (2), the mean probability of detection is thus given by:

$$P_a = \frac{1}{12}\sum_{n=1}^{12}\frac{2\int_0^{y_n} r.g(r)\,dr}{y_n^2} \tag{3}$$

and combining (1) and (3) gives the area/detectability product (a_sP_a):

$$a_sP_a = \frac{\pi}{12}\sum_{n=1}^{12} y_n^2 \cdot \frac{1}{12}\sum_{n=1}^{12}\frac{2\int_0^{y_n} r.g(r)\,dr}{y_n^2} \tag{4}$$

Probability of detection functions were integrated numerically using the Newton–Cotes rule (see Keast and Fairweather 1987) as there is no general solution to their integral. Cut-off distances were then estimated for all other point counts using the above formula to give an equal detection/area product value. This entailed using ground maps to estimate y values and selectively trying out different cut-off distance values until the correct detection/area product value was obtained. A simple programme using MAPLE V release 4 for Windows was written to do these calculations.

Appendix 2. Species list of birds recorded by point counts in six swamps in Uganda and Kenya (July–August 2001) and the guilds to which they have been allocated.

Hamerkop *Scopus umbretta*	Swamp-opportunist
Hadada *Bostrychia hagedash*	Generalist
White-spotted Flufftail *Sarothrura pulchra*	Generalist
Black Crake *Amaurornis flavirostris*	Swamp-opportunist
Purple Swamphen *Porphyrio porphyrio*	Swamp-opportunist
African Jacana *Actophilornis africana*	Open water associated
African Green Pigeon *Treron calva*	Generalist
Red-eyed Dove *Streptopelia semitorquata*	Generalist
Ring-necked Dove *Streptopelia capicola*	Generalist
Great Blue Turaco *Corythaeola cristata*	Generalist
Eastern Grey Plantain-eater *Crinifer zonurus*	Generalist
Red-chested Cuckoo *Cuculus solitarius*	Generalist
Dusky Long-tailed Cuckoo *Cercococcyx mechowi*	Generalist
Klaas's Cuckoo *Chrysococcyx klaas*	Generalist
Blue-headed Coucal *Centropus monachus*	Swamp-opportunist
African Pygmy Kingfisher *Ceyx picta*	Generalist
Malachite Kingfisher *Corythornis cristata*	Open water associated
Pied Kingfisher *Ceryle rudis*	Open water associated
Little Greenbul *Andropadus virens*	Generalist
Common Bulbul *Pycnonotus barbatus*	Generalist
Snowy-crowned Robin-Chat *Cossypha niveicapilla*	Generalist
Little Rush Warbler *Bradypterus baboecala*	Swamp-reliant
White-winged Swamp Warbler *Bradypterus carpalis*	Papyrus-restricted
African Reed Warbler *Acrocephalus baeticatus*	Swamp-reliant
Greater Swamp Warbler *Acrocephalus rufescens*	Papyrus-restricted
Lesser Swamp Warbler *Acrocephalus gracilirostris*	Swamp-reliant
Papyrus Yellow Warbler *Chloropeta gracilirostris*	Papyrus-restricted
Red-faced Cisticola *Cisticola erythrops*	Swamp-opportunist
Singing Cisticola *Cisticola cantans*	Generalist
Winding Cisticola *Cisticola galactotes*	Swamp-opportunist

Carruthers's Cisticola *Cisticola carruthersi*	Papyrus-restricted
White-chinned Prinia *Schistolais leucopogon*	Generalist
Bleating Warbler *Camaroptera brachyura*	Generalist
Grey-capped Warbler *Eminia lepida*	Generalist
Swamp Flycatcher *Muscicapa aquatica*	Swamp-opportunist
Arrow-marked Babbler *Turdoides jardineii*	Generalist
Western Olive Sunbird *Cyanomitra obscura*	Generalist
Red-chested Sunbird *Cinnyris erythrocerca*	Swamp-opportunist
Variable Sunbird *Cinnyris venusta*	Generalist
Tropical Boubou *Laniarius aethiopicus*	Generalist
Papyrus Gonolek *Laniarius mufumbiri*	Papyrus-restricted
Purple-headed Glossy Starling *Lamprotornis purpureiceps*	Generalist
African Citril *Serinus citrinelloides*	Generalist
Papyrus Canary *Serinus koliensis*	Papyrus-restricted
Streaky Seedeater *Serinus striolatus*	Generalist
Grey-headed Negrofinch *Nigrita canicapilla*	Generalist
White-collared Olive-back *Nesocharis ansorgei*	Generalist
Red-headed Bluebill *Spermophaga ruficapilla*	Generalist
Red-billed Firefinch *Lagonosticta senegala*	Generalist
Common Waxbill *Estrilda astrild*	Generalist
Black-headed Waxbill *Estrilda atricapilla*	Generalist
Slender-billed Weaver *Ploceus pelzelni*	Swamp-opportunist
Spectacled Weaver *Ploceus ocularis*	Generalist
Northern Brown-throated Weaver *Ploceus castanops*	Swamp-opportunist
Yellow-backed Weaver *Ploceus melanocephalus*	Swamp-opportunist
Grosbeak Weaver *Amblyospiza albifrons*	Generalist

Notes on habitat guild are taken from Mackworth-Praed and Grant (1960) from the African Citril to the Grosbeak Weaver and Fry *et al.* (2000) for all other species.

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