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Effects of disturbance and habitat loss on papyrus-dwelling passerines

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ABSTRACT

Throughout the world, but particularly in tropical regions habitat loss and disturbance are considered detrimental to biodiversity. We examine the effects of disturbance by harvesting, burning and habitat fragmentation on six bird species associated with papyrus (*Cyperus papyrus*) swamps. The presence or absence of these species was verified in 93 wetlands in southern Uganda between June and August 2003. Disturbance was estimated directly by observation and indirectly from examining vegetation structure. Habitat fragmentation was quantified by delineating swamps on Landsat ETM images and applying 'Fragstats' to calculate relevant patch metrics. The occurrence of all six species was affected positively by increased swamp size, but birds were more likely to occur in small swamps at high altitude. The shape and proximity of swamps to neighbouring wetlands had little effect on occurrence. As altitude, habitat fragmentation and disturbance were correlated, determining avian responses to disturbance was problematic. However, the occurrence of all species was affected by disturbance, often showing unimodal responses, if disturbance was not considered in conjunction with habitat fragmentation. When the effects of habitat fragmentation and disturbance were analysed together, only the occurrences of papyrus yellow warbler and white-winged warbler were affected (positively) by disturbance. Results suggest that papyrus-dwelling passerines, except papyrus gonolek, are tolerant of low intensities of disturbance, a novel finding in the tropics. We recommend that policy-makers do not prohibit harvesting, thus generating good will and encouraging rural householders to comply with additional conservation policy.

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1. Introduction

Human alteration of natural landscapes is the root cause of many conservation problems (Perrings et al., 1992). The ability to determine how biodiversity is affected by habitat modification has become a major focus of ecology and biological conservation. Different species, even within a taxonomic group, may exhibit different responses to factors such as habitat destruction (Andrén, 1994; Turner, 1996; Bender et al., 1998)

and other forms of anthropogenic disturbance (Bengtsson et al., 2000), some species prospering in human altered landscapes (Saab, 1999).

The effects of disturbance on animals and plants are comparatively well studied. Both theory (Connell, 1978) and empirical evidence (Hobbs and Hueneke, 1992) suggest that in some cases natural disturbance can increase diversity, particularly at intermediate intensities and frequencies. Human disturbance can also benefit organisms, particularly in

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instances where activities have been carried out for long periods and are similar in nature to natural disturbances (Bengtsson et al., 2000). In nearly all cases, evidence of these benefits of human activity comes from temperate regions with long histories of landscape alteration. Often, the species that remain in such ecosystems are those that are able to tolerate human activities and may not be representative of natural habitats (Baldi, 1996; Foster et al., 1996).

In tropical regions, extensive areas of natural habitat remain, but are under continuing threat of destruction from human activities (Skole and Tucker, 1993; Turner, 1996). Studies, in which the effects of disturbance on tropical communities are examined, reveal that although in some instances species richness increases, additional species are often generalists of little conservation concern (Thiollay, 1992; Hammer et al., 1997; Barlow et al., 2002; Maclean et al., 2003a). Conversely, adverse effects on specialists have been documented for a range of taxonomic groups (e.g. Holloway et al., 1992; Hammer and Hill, 2000; Stephenson, 1993; Thiollay, 1999). However, most studies concerned with anthropogenic disturbances in the tropics have determined responses to modern activities, such as logging in tropical forests (e.g. Sekercioglu, 2002). The importance of human disturbance, ongoing for longer periods is less understood.

Areas disturbed by human activities are likely to be situated in regions in which extensive habitat loss has occurred. Similarly, smaller fragments of habitat may be more accessible and consequently more heavily disturbed (Turner, 1996). In both cases disturbance and fragmentation will be closely correlated. For this reason, the effects of habitat fragmentation and disturbance should be considered together. Island biogeography (MacArthur and Wilson, 1967) and metapopulation theories (Hanski and Gilpen, 1991) predict that probability of species occurrence is related to habitat fragment size and landscape connectivity. Empirical tests of these theories (see Andr n, 1994; Bender et al., 1998 for reviews) have been mostly in temperate regions with a strong bias towards forests and grasslands (Debinski and Holt, 2000). Despite the high proportion of biodiversity at lower latitudes, fewer tests of these theories have been in tropical regions, of those that have (e.g. Wethered and Lawes, 2003), few have addressed the effects of disturbance and fragmentation together.

The majority of such studies in the tropics have focused on the consequences of fragmenting contiguous habitats and not on naturally fragmented habitats such as wetlands. In East and Central Africa the most widespread type of wetland is papyrus (*Cyperus papyrus*) swamp (Thompson, 1976). These swamps have a long history of human disturbance and although naturally fragmented, are increasingly threatened by human activities (Crisman et al., 1996; Mafabi, 2000). Papyrus is often harvested intensively for handcrafts and thatching and these activities and drainage are increasing as a consequence of expanding human populations (Maclean et al., 2003c). Several species of bird are dependent mostly on papyrus swamps and are considered amongst the most threatened and least adequately protected of bird species in East Africa (Muriuki et al., 1997; Bennun and Njoroge, 1999; Byaruhanga et al., 2001). Studies on this group of species are limited (but see Britton, 1978; Vande weghe, 1981; Maclean et al., 2003a) and very little is known about

the effects of human landscape alteration on their populations.

In this paper, we develop logistic regression models, to predict the occurrence of the six species studied and their responses to both human disturbance and fragmentation. Landscape models using logistic regressions with presence-absence data have been used to examine the relationship between environmental conditions and the habitat requirements of a range of species (Schadt et al., 2002). Such models provide a means of determining the relative importance of variables that explain the suitability of papyrus swamp for the bird species studied, so that the impacts of disturbance and fragmentation can be quantified. We test two hypotheses. Firstly, that variables associated with habitat fragmentation will be significant predictors of bird occurrence. Secondly, that papyrus dwelling passerines are tolerant of moderate levels of traditional forms of human disturbance such as papyrus harvesting. These birds should be no less likely to occur in moderately disturbed swamps than in undisturbed swamps, although the relationship between occurrence and disturbance may depend on whether disturbance is considered alone or in combination with fragmentation.

2. Methods

2.1. Study species

The six species of bird included in this study were papyrus yellow warbler (*Chloropeta gracilirostris*), papyrus gonolek (*Laniarius mufumbiri*), white-winged warbler (*Bradypterus carpalis*), papyrus canary (*Serinus koliensis*), Carruthers's cisticola (*Cisticola carruthersi*) and greater swamp warbler (*Acrocephalus rufescens*). Papyrus yellow warbler is globally-threatened and vulnerable (BirdLife International, 2000) but some doubt exists over its taxonomy (Maclean et al., 2003b). Papyrus gonolek is considered near-threatened (BirdLife International, 2000). Carruthers's cisticola and papyrus canary are almost certainly vulnerable (Maclean, 2004), despite their current designation as non-threatened (BirdLife International, 2000).

Papyrus gonolek is restricted to papyrus and white-winged warbler and greater swamp warbler, race foxi, almost so: white-winged warbler has been recorded in elephant grass following recent drainage of papyrus (Vande weghe, 1981) and greater swamp warbler occasionally occupies sorghum (*Sorghum bicolor*) plantations immediately adjacent to swamps (personal observations). Other races of the species are not considered in this study, but are distributed widely throughout central Africa and inhabit a range of wetland vegetation types (Vande weghe, 1981; Urban et al., 1997). Papyrus canary is entirely dependent on papyrus in which it nests. However, it often forages in crops adjacent to swamps, particularly in sorghum (Britton, 1971). Papyrus yellow warbler and Carruthers's cisticola, are usually associated with papyrus swamps, particularly at lower altitudes (Vande weghe, 1981), but also inhabit swamps dominated by other sedges such as *Cyperus denudatus* and *Cyperus latifolius* and reeds such as *Miscanthus violaceum* and *Typha* species. Several other bird species utilise papyrus, particularly around the edges of swamps, but are not dependent on it and are not included in this study. For a comprehensive review of bird species

found in papyrus swamps, and their degree of dependence on this habitat see Vande weghe (1981) and Maclean et al. (2003a).

2.2. Study region

The study was conducted between June and August 2003 in 93 swamps in southern Uganda (Fig. 1). These swamps were selected using 1:50,000 topographical maps obtained from the Uganda Department of Lands and Surveys, Entebbe such that the full altitudinal and distributional ranges of papyrus-reliant species in the region were included. The swamps surveyed encompass c. half of the range of the species studied.

2.3. Field survey

In each swamp, visited between 07h00 and 09h30, the presence or absence of study species was established by searching extensively whilst intermittently playing vocal recordings obtained in the field prior to commencing the study. In most instances, birds found to be present in a swamp were located aurally within the first 5 min of a survey as papyrus-dwelling passerines have distinctive calls and sing frequently. The papyrus canary was on occasion more difficult to find, as it is highly mobile, often foraging outside the swamp and closely resembles African citril (*Serinus citrilinoides*). At higher altitudes, greater swamp warbler was sometimes less vocal early in the morning and was not located until after 08h30, when it became highly vocal.

To test detection efficiency 23 swamps dispersed throughout the study region, were surveyed more extensively for three-four days of continuous observation, at intermittent intervals between the beginning of June and the end of August 2003. In only one of the 23 sites, one species (papyrus yellow warbler) that was not recorded in the first 2½ hours was located subsequently (on the third day). All surveys were carried out during the main breeding season when this species is at its most vocal (Britton, 1978). However, as the vocalisation

period of papyrus yellow warbler is short and varies with altitude (Byaruhanga, A., personal communication) this one swamp, Nyarungu swamp, Lake Bunyonyi, which was surveyed on the 3rd June 2003, may have been visited just outside the main breeding period of June to August (Britton, 1978; Byaruhanga, A., personal communication).

Swamp disturbance was estimated in two ways. Recent disturbance was assessed by mapping the proportions of each swamp that had been burnt and/or cut and partially re-grown (after burning and/or cutting). Longer-term disturbance was estimated by examining vegetation structure since heavily disturbed swamps have a higher culm density dominated by short thin papyrus (Muthuri et al., 1989). Twenty 1 m × 1 m quadrats were placed randomly 10–20 m from the edge of every swamp. Initial observations of swamp vegetation revealed that although the structure of vegetation differed close to the edge of some swamps, at distances of >10 m from the edge such differences were not observable. Complete random sampling was impractical as some swamps were several km² in size and only penetrable by cutting a pathway, which is highly labour intensive. In each quadrat, all culms were cut and the number of culms, the height, base width and age category of each culm were recorded. The width of culms was measured on the broadest side approximately 8 cm from the root, the height at which vegetation can be cut easily. Culms were aged by categorising them as juvenile, immature, flowering, adult and senescing (Sutton and Hudson, 1981). The number of dead culms with umbels was also recorded.

2.4. Estimating habitat fragmentation variables

At each of the swamps, GPS readings were taken and a ground map drawn to delineate the boundaries of papyrus swamps and other types of wetland dominated by emergent macrophytes, used by papyrus yellow warbler and Carruthers's cisticola. Surrounding land-use was also recorded. These ground maps were compared and adjusted using 1:50,000 topographical maps to enhance the accuracy of feature boundaries. Recent (1999–2001), relatively cloud free Landsat ETM satellite images (30 × 30 m resolution) of the study area were obtained from the University of Maryland's Global Land Cover Facility (Fig. 1). Using these images, false colour composites of Bands 2, 3 and 4, Bands 3, 4 and 5 and Bands 3, 4 and 7 (all in the order blue, green and red) were created, since these are regarded widely as the best for distinguishing different vegetation types (Lillesand et al., 2004). Band 2 corresponds to green (0.52–0.60 μm), Band 3 to Red (0.63–0.69 μm), Band 4 to Near IR (0.76–0.90 μm), Band 5 to Mid IR (1.55–1.75 μm) and Band 7 to Mid IR (2.08–2.35 μm). Swamps in which bird surveys were conducted were identified on each set of images and other pixels with similar reflectance values found using a parallelepiped classifier available in the ArcView Image Analysis extension (ESRI, Redland, CA, USA). All three false colour composites were used, as no single composite image distinguished clearly swamps from other vegetation types. In almost all cases, surveyed swamps were situated in cloud-free parts of the satellite images.

As swamps are more likely to be situated in wetter areas, water flow accumulation, i.e. the total number of other cells contributing water to each focal cell, was calculated to

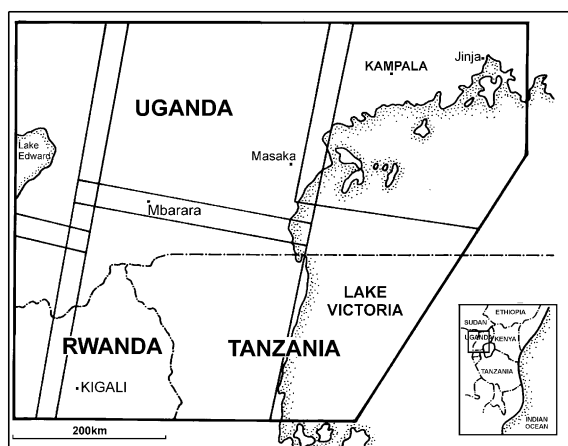


Fig. 1 – The study area showing the location of satellite images used to map wetlands. Dates images were created were as follows: (1) 11/12/01; (2) 31/12/99; (3) 27/11/01; (4) 15/06/01; (5) 08/07/99.

improve the accuracy of the swamp classification process. One km² digital elevation data were obtained from the USGS Distributed Active Archive Centre and the flow direction of each pixel was determined by examining which neighbouring pixel had the lowest elevation. Flow accumulation was then calculated using an Avenue Script available from the ESRI support centre. The resulting data were interpolated to a grid of 30 × 30 m resolution to ensure compatibility with remotely sensed data, using ArcView.

Each pixel was given a weighting dependent upon both the number of times it had been distinguished as papyrus or as wetland by image analysis and by flow accumulation. Resulting grids were smoothed to reduce speckle by averaging pixel values within a 90 m radius of each pixel (Lillesand et al., 2004). All pixels above a cut-off weighting were classified as 'papyrus' or 'wetland' (i.e. types containing mixed emergent vegetation and papyrus). The cut-off weighting was chosen on each image derived grid by experimenting with different values until the boundaries of the study swamps corresponded closely with maps drawn on location. To assess the accuracy of this classification process, the locations of 50 papyrus swamps and 50 swamps containing mixed emergent macrophytes were determined during field survey using a GPS, but were not included in the image classification process. It was necessary to accommodate small geometric mis-registration of the map and check data. For example, there are known residual errors averaging about 15 m on the images (Fuller et al., 1998). Obtaining good satellite coverage in the middle of papyrus swamp was sometimes problematic, and error estimates given by the GPS were sometimes as high as 50 m. Although readings were always taken more than 25 m from the edge of swamps, to compensate for these spatial inaccuracies, the scoring of image classification was carried out within a 25 m buffer zone drawn around each GPS location.

Three habitat patch parameters were considered: swamp size, the relative proportion of edge habitat and the proximity of swamps to neighbouring swamps. "Related Circumscribed Circle" (McGarigal, 2004), which measures how circular habitat patches are, was used instead of edge to area ratio to indicate relative proportions of edge habitat. The edge to area ratio of swamps was highly correlated with area, so it is not suitable to use at the same time as area in regression analyses. Proximity was measured by using an index developed by Gustafson and Parker (1994). Using this index, the size and proximity of all habitat patches with edges within a specified search radius of a focal patch were calculated and the patch area of each of these neighbouring patches was then summed and the total divided by the square of nearest edge-to-edge distances from each patch to the focal patch. A 10 km radius was specified as mark-recapture work carried out in western Kenya indicates that this distance corresponds to the maximal distance over which papyrus dwelling passerines disperse readily (Nasirwa, O., personal communication). The three patch metrics were calculated by coupling the ArcView grids of swamp coverage to Fragstats software (Landscape Ecology Programme, University of Massachusetts, Amherst, MA, USA). This exercise was first conducted using pure papyrus swamps only. As both papyrus swamps and swamps containing other emergent macrophytes are used

by Carruthers's cisticola and papyrus yellow warbler, the exercise was then repeated drawing no distinction between these two habitat types. In some instances, where boundaries of swamps did not correspond well to ground maps, or in cases where surveyed swamps were too small to be accurately displayed at 30 × 30 m resolution, the ground maps were used to adjust the measures of swamp size and shape obtained using Fragstats.

2.5. Data analysis

Measures of disturbance, habitat fragmentation, surrounding land-use within 500 m of the perimeter of swamps and the elevation of each swamp were considered predictor variables in regression models. Due to a high degree of multicollinearity between the different variables collected to indicate disturbance, principal components analysis (PCA) was performed on disturbance data. Two PCAs were conducted, one on the direct measurements of disturbance and one on vegetation structure. In both cases, varimax rotation was applied in order to maximise the variance of factor loadings thus equalising the effects of each variable on principal components (Tabachnick and Fidell, 2001). The sample scores of the first two axis were plotted to verify the absence of unimodal relationships, which would invalidate the use of principal components analysis (Jongman et al., 1995).

Bird occurrence was often concentrated in certain geographical areas, thus data share common attributes. Consequently, two dummy variables, 'eastings' and 'northings' were included in the analysis, to avoid pseudo-replication. Continuous rather than categorical location variables were used as clear distinctions by region were deemed unrealistic and because for no species were high incidences of occurrences clustered in more than one region. Several interaction terms were also included as dummy variables. The first, 'altitude × log_e (swamp area)' was included as previous work suggests that the occurrence of papyrus endemics may be restricted at lower altitudes due to interspecific competition (Vande weghe, 1981). The second, 'log_e (swamp area) × proximity index' was included as it was strongly suspected that isolation would be more important for birds in smaller swamps. Square-root transformations of these dummy variables were also compared.

First, each variable was entered independently into a logistic regression (logit link and binomial error using SPLUS, Insightful Corporation, Seattle, WA, USA). The strength of dependence between bird occurrence and each predictor variable was then determined by computing log-likelihood ratios and using χ^2 for determining levels of significance (Tabachnick and Fidell, 2001). Potential Gaussian relationships were also investigated by including a squared term for each variable (Jongman et al., 1995). All remaining terms were then added sequentially into multiple logistic regression models, starting with dummy variables 'eastings' and 'northings' (if significant independently) to avoid pseudo-replication and then with the predictor variables that had the greatest influence on the dependent variable. To avoid strong multicollinearity between explanatory variables, the variable that had the least effect on occurrence, was excluded from regression models. Two independent variables were considered to be

strongly correlated when $r > 0.7$, determined by the correlation matrix of the predictors (Spearman- ρ , two-tailed). The absence of multivariate collinearity was established by verifying the absence of variance inflation (Tabachnick and Fidell, 2001). Potential models were then compared and terms included if they significantly ($p < 0.05$) improved the difference in loglikelihoods.

Two of the PCA variables, one derived from recent disturbance evidence and one derived from vegetation structure were regressed individually against bird occurrence data. Thus, relationships revealed between bird occurrence and disturbance considered alone could be compared to relationships revealed when disturbance was considered at the same time as other variables. As disturbance can benefit species at intermediate intensities and frequencies, both Gaussian and sigmoidal models were tested.

3. Results

3.1. Image classification

In total, 5781 km² were classified as wetland types containing mixed emergent vegetation and papyrus, including 2169 km² of pure papyrus swamps. The former, broader wetland category represents the habitat types used by papyrus yellow warbler and Carruthers's cisticola. Wetlands could in most instances be differentiated from other vegetation (Table 1).

3.2. Principal component analyses and disturbance

Three components extracted from direct measurements of disturbance and four from vegetation structure measurements had eigenvalues over 1. In both cases, only the components with the highest eigenvalues were significant predictors of bird occurrence and are shown in Table 2.

The component with the highest eigenvalue derived from direct measurements of disturbance was positively correlated with increased cutting and recent burning and negatively with less recent burning. The component with the highest eigenvalue derived from vegetation structure, was negatively correlated with the number of older culms, average culm width and height, but positively with the number younger culms and culm density. When these two components were regressed individually against bird occurrence data, all spe-

Table 1 – Correspondence between 50 points known to be covered by papyrus and 50 known to be covered by other wetlands and predicted coverage from analyses of satellite imagery

Image classification	Survey validation	
	Papyrus	Other wetland
Papyrus	39 (78%)	4 (8%)
Other wetland	7 (14%)	35 (70%)
Classified as neither	4 (8%)	11 (22%)

Figures refer to the number of swamps visited that were classified as papyrus, other wetland or non-swamp in the image classification process.

Table 2 – Disturbance data and vegetation structure and their correlation with principal components

Disturbance variable	
PCA 1: Direct disturbance component (eigenvalue: 1.76; percentage variance explained: 43.9)	
Percentage of swamp recently burnt	0.434**
Percentage of swamp burnt and re-grown	-0.210*
Percentage of swamp recently cut	0.896**
Percentage of swamp cut and re-grown	0.850**
PCA 2: Vegetation structure component (eigenvalue: 2.15; percentage variance explained: 38.2)	
Number of juvenile culms m ⁻²	0.600**
Number of immature culms m ⁻²	0.603**
Number of flowering culms m ⁻²	-0.140
Number of adult culms m ⁻²	-0.500**
Number of senescing culms m ⁻²	-0.192
Number of dead culms m ⁻²	-0.458**
Mean height of culms	-0.753**
Mean diameter at base of culms	-0.556**
Mean culm density m ⁻²	0.606**

* $P < 0.05$.
** $P < 0.001$.

cies showed a significant relationship with at least one of the PCA variables. Both sigmoidal and Gaussian relationships were examined (Table 3) and significant relationships are shown in Fig. 2a and b.

3.3. Logistic models

The occurrence of each of the study species in different swamp types and at different altitudes is shown in Table 4. All of the models used to predict which swamps contained the study species were significant ($p < 0.001$). The variables used to predict occurrences are shown in Table 5. In all instances, only sigmoidal relationships were significant. Prob-

Table 3 – Relationship between bird occurrence and the principal components extracted from direct measurements of disturbance (PCA 1) and from vegetation structure data (PCA 2)

	PCA 1		PCA 2	
	Relationship	χ^2	Relationship	χ^2
Papyrus yellow warbler	Gaussian	10.84**	Gaussian	10.02**
Papyrus gonolek	n.s.		Sigmoidal	29.99***
Papyrus canary	Gaussian	9.61**	n.s.	
White-winged warbler	Gaussian	12.25**	Sigmoidal	17.55***
Carruthers's cisticola	Gaussian	8.14*	Sigmoidal	9.43**
Greater swamp warbler	Gaussian	9.56**	n.s.	

χ^2 was used to determine levels of significance.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

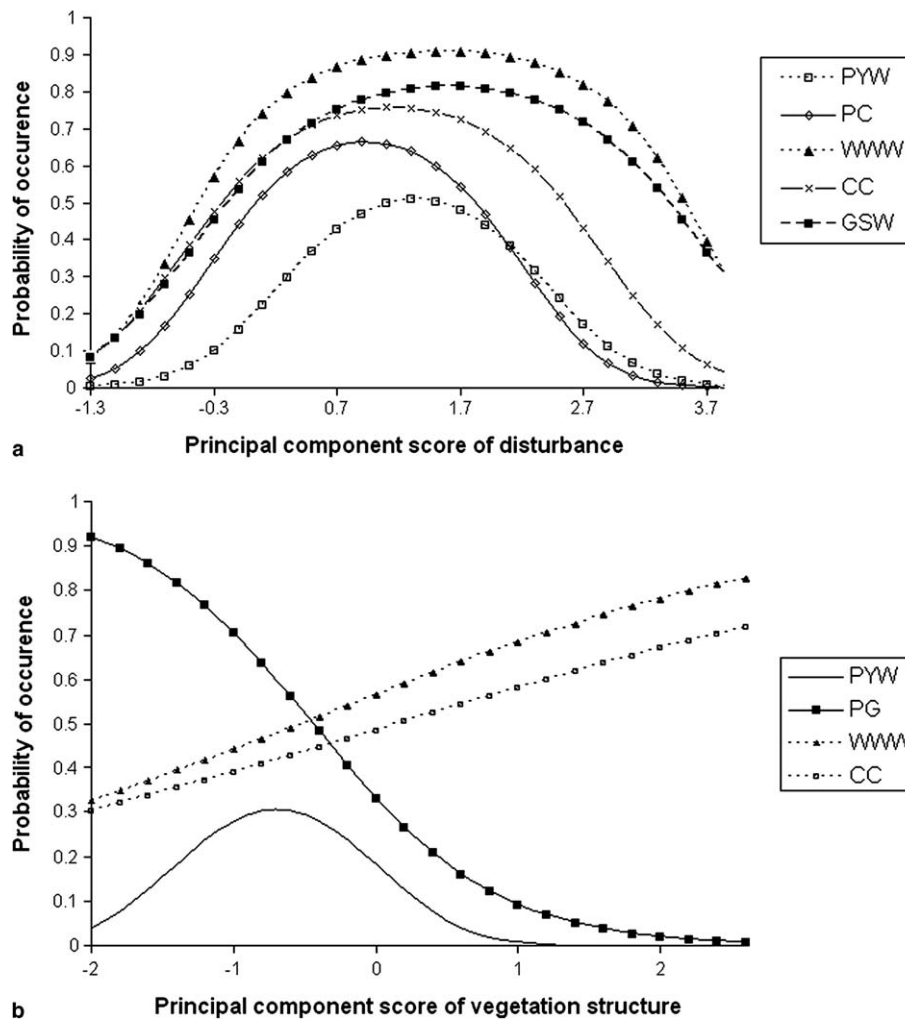


Fig. 2 – Relationship between the probability of occurrence of each of the study species and (a) PCA 1, extracted from direct measurements of disturbance and (b) PCA 2, extracted from vegetation structure data. PYW = papyrus yellow warbler; PC = papyrus canary; WWW = white-winged warbler; CC = Carruthers's cisticola; GSW = greater swamp warbler.

ability of occurrence of all species increased as the interaction term between altitude and swamps size increased. Papyrus yellow warbler occurrence increased towards the west of the study area. Papyrus gonolek preferred swamps towards the west and north of the study area and at lower altitude. Papyrus canary preferred swamps towards the west of the study area and with neighbouring sorghum. Carruthers's cisticola was more likely to occur in swamps in the south and east of the study area and was affected (positively) by both altitude alone and by altitude \times log_e (wetland area). Greater

swamp warblers were more likely to occur in swamps towards the south and east of the study area.

Considering all variables together, both the principal component extracted from vegetation structure data and the principal component extracted from estimations of cutting and burning had a negative effect on the occupancy of papyrus gonolek, but a positive effect on the occupancy of all other species, although in most instances this relationship was insignificant. Only white-winged warbler and papyrus yellow warbler were significantly affected by disturbance: white-

Table 4 – Occurrence of papyrus-dwelling passerines in different swamp-types

	Pure papyrus (<1500 m.a.s.l)	Pure papyrus (>1500 m.a.s.l)	Mixed wetland (<1500 m.a.s.l)	Mixed wetland (>1500 m.a.s.l)
Papyrus yellow warbler	0	5	0	7
Papyrus gonolek	31	5	0	0
Papyrus canary	7	23	0	0
White-winged warbler	25	27	0	0
Carruthers's cisticola	5	14	8	18
Greater swamp warbler	13	30	0	0

Table 5 – Variable parameter values used in logistic regressions for each study species

Model parameters	Predictor					
	Papyrus yellow warbler	Papyrus gonolek	Papyrus canary	White-winged warbler	Carruthers's cisticola	Greater swamp warbler
Constant	-4.02***	31.2***	-5.15***	-7.58***	-19.0***	-7.48***
Eastings	$-6.48 \times 10^{-2***}$	$-3.15 \times 10^{-2***}$	$-6.00 \times 10^{-3*}$	n.s.	$1.50 \times 10^{-2*}$	$8.54 \times 10^{-3*}$
Northings	n.s.	$1.39 \times 10^{-2***}$	n.s.	n.s.	n.s.	$-2.71 \times 10^{-2***}$
Altitude	n.s.	$-2.32 \times 10^{-2***}$	n.s.	n.s.	$1.05 \times 10^{-2***}$	n.s.
Altwarea	$5.64 \times 10^{-4***}$	n.s.	n.s.	n.s.	$4.10 \times 10^{-4***}$	n.s.
Altparea	n.s.	$7.35 \times 10^{-4***}$	$4.76 \times 10^{-4***}$	$1.14 \times 10^{-3***}$	n.s.	$6.67 \times 10^{-4***}$
PCA 1	1.27**	n.s.	n.s.	n.s.	n.s.	n.s.
PCA 2	n.s.	n.s.	n.s.	1.57***	n.s.	n.s.
Sorghum	n.s.	n.s.	1.98***	n.s.	n.s.	n.s.
Overall model (χ^2)	39.7***	95.2***	40.7***	79.3***	77.0***	61.5***
df	3	4	3	2	4	3

Further details of principal components are given in Table 3. Only sigmoidal relationships were found to be significant. Eastings = longitudinal distance (km) measured from 30°00'00" E; Northings = latitudinal distance (km) measured from the equator; Altitude = mean altitude (m) above sea level; Altwarea = altitude × log_e (wetland area in hectares); Altparea = altitude × log_e (papyrus area in hectares); Sorghum = presence or absence of sorghum fields neighbouring swamps (1 = presence, 0 = absence).

* P < 0.05.
 ** P < 0.01.
 *** P < 0.001.

winged warbler by one of the components extracted from vegetation structure data and papyrus yellow warbler by one of the components extracted from estimations of cutting and burning (Table 6).

The proximity of swamps to other swamps, and the circularity of swamps had no effect on the occurrences of any of the study species. In most cases, using a predicted probability of occurrence of 50% as a decision point, models predicted accurately which birds would occur in swamps. The correspondence between predicted and observed swamp occupancy is shown in Table 6.

4. Discussion

4.1. Habitat fragmentation and altitude

The theories of island biogeography (MacArthur and Wilson, 1967) and metapopulations (Hanski and Gilpen, 1991) predict that smaller and more isolated units of habitat will have a lower probability of containing species associated with that habitat. In this study, swamp size alone was a less significant predictor of bird occurrence than the interaction between altitude and swamp size. This interaction was retained consis-

tently in regression models instead of swamp size and had an effect on all study species. The value of the interaction term for a small swamp at high altitude is similar to that of a large swamp at low altitude. This would suggest therefore, that birds are more tolerant of small swamps at higher altitudes.

The reason for this relationship is not clear, but the effects of interspecific competition between swamp specialists and other species provides the most likely explanation. The effects of altitude on papyrus avifauna were studied in Rwanda and Burundi by Vande weghe (1981). He found that papyrus-dwelling passerines, notably Carruthers's cisticola and papyrus yellow warbler have more specialist habitat requirements at lower altitudes. He suggested that this is due to competition between papyrus specialists and other wetland birds such as African reed warbler (*Acrocephalus baeticatus*) and winding cisticola (*Cisticola gracilirostris*). These later two species are not found at higher elevations. Moreover, the density of papyrus endemics is lower near the edge of swamps where the abundance of potential competitors is higher (Vande weghe, 1981; Maclean et al., 2003a). Thus, birds at higher altitudes are perhaps able to utilise the edges of swamps more frequently and consequently inhabit smaller

Table 6 – Correspondence between predicted and observed swamp occupancy of study species

	Occupied			Unoccupied		
	Observed	Correctly predicted	% Correct	Observed	Correctly predicted	% Correct
Papyrus yellow warbler	12	7	58	81	78	96
Papyrus gonolek	36	33	92	57	53	93
Papyrus canary	30	20	67	63	56	89
White-winged warbler	52	48	92	41	34	83
Carruthers's cisticola	45	35	78	48	43	90
Greater swamp warbler	43	36	84	50	50	100

If predicted probability of occurrence was greater than 50%, the swamp was predicted to be occupied, if less than 50% then unoccupied.

swamps. Swamp shape appeared not to significantly affect occurrence of study species. This may have been due to the inherent difficulty of determining how circular a habitat is using 30×30 m square pixels, but requires further investigation.

Several of the study species were affected by altitude. Notably, papyrus gonolek was absent from any swamps over 1680 m.a.s.l. This is consistent with its altitudinal distribution in Rwanda and Burundi being restricted to below 1600 m.a.s.l. (Vande weghe, 1981). Conversely, Carruthers's cisticola appeared to prefer swamps at higher altitude. In Rwanda and Burundi, this species is parapatric with winding cisticola, which is absent at altitudes over 1650 m.a.s.l. Where both species are present, Carruthers's cisticola is confined to large stands of pure papyrus (Vande weghe, 1981). Although in this study, Carruthers's cisticola was found to coexist with winding cisticola in swamps fringing Lake Victoria (1133 m.a.s.l.), these swamps were very large and Carruthers's cisticola was less common in those swamps than at higher altitudes and could be excluded to some degree (Maclean, 2004). It is possible, therefore, that at high altitudes, where in winding cisticola is absent, Carruthers's cisticola is able to occupy less favourable habitats and therefore occupies more swamps.

The degree to which habitat isolation affects the occurrence of papyrus aviflora is not readily apparent. Whilst empirical studies for a wide range of organisms, show that incidences of occupancy typically decrease with increased isolation (Hanski, 1994), in this study, the area of habitat within a 10 km radius of surveyed habitat patches, the distance over which the study species will disperse readily (Nasirwa, O., personal communication), had no significant bearing on probability of occurrence. However, one of the assumptions of metapopulation theory is that habitat patches are situated within dispersal range of occupied patches. Lower probability of occupancy in more isolated patches is predicted to result from slower recolonisation following stochastic extinctions (Hanski and Gilpen, 1991). The distributions of papyrus specialists, with the exception of white-winged warbler were spatially aggregated and strong relationships between geographic location and predicted probabilities of occurrence were revealed, suggesting that a higher proportion of swamps may be occupied if situated close to core populations. Consequently, a significant proportion of swamps were situated outside the usual dispersal range of study species and one would therefore not necessarily expect habitat isolation to be a predictor of bird occurrence over the entire study region. Instead, bird occurrence would be concentrated around key source populations, such as those around Lake Bunyonyi in the south-west of Uganda, as was indeed the case. Although the existence of aggregated occupied swamps may in part have been due to these swamps sharing common attributes such as altitude and human disturbance history, metapopulation dynamic processes could have been operating in specific localities.

4.2. Disturbance

Both the principal components used in logistic regression models appear to have been good indicators of disturbance. The first, extracted from direct estimations of cutting was pos-

itively correlated with increased cutting and recent burning. Only evidence of less recent burning was negatively correlated, but this relationship was weak. The second component, extracted from vegetation structure data, was negatively correlated with the number of adult and senescing culms and culm height, but positively with young culms and culm density. The relationship between bird occurrence and both vegetation structure and recent disturbance varied, dependent on whether components were considered alone or in conjunction with other predictor variables. When regressed alone, at least one of the components had a significant bearing on all of the species considered in this study. All species except papyrus gonolek were more likely to occur in swamps in which intermediate proportions of papyrus had been cut and burnt recently. Vegetation structure associated with repeated cutting (Muthuri et al., 1989) appeared to have a beneficial effect on Carruthers's cisticola and white-winged warbler and at low intensities or frequencies on papyrus yellow warbler, which exhibited a Gaussian response. Conversely, papyrus gonoleks were negatively associated with vegetation structure that indicated intensive cutting. When disturbance was considered together with other variables, the occurrence of only two species was significantly related to components extracted from disturbance data. Papyrus yellow warbler was more likely to occur in swamps in which a high proportion had been disturbed by cutting and recent burning. White-winged warbler also showed a positive response to disturbance as it was more likely to occur in swamps with vegetation structures indicative of frequent cutting.

Although not correlated closely, smaller wetlands and swamps at higher elevations, where agriculture is the predominant land use (Byaruhanga et al., 2001) were often more disturbed. Consequently, separating the effects of disturbance from altitude and swamp size is problematic. Nevertheless, although not significant in all cases, the occurrence of all the species considered in this study with the exception of papyrus gonolek was positively or unimodally related to components of disturbance even when other variables were also considered. The results of this study would suggest therefore, that although papyrus-dwelling passerines did not necessarily benefit significantly from disturbance, they were not adversely affected by it. All, except perhaps papyrus gonolek, could be considered at least tolerant of disturbance, if the intensity of disturbance was not too high. These findings were not as previously predicted from studies of heavily disturbed sites (Maclean et al., 2003a), which suggest that the diversity and density of papyrus specialists is lower in stands of papyrus disturbed heavily by herbivores, burning and pollution. This may be accounted for by the swamps surveyed in this study being considerably less intensely disturbed than those studied previously.

It has long been recognised that disturbance, particularly at intermediate intensities and frequencies can benefit many species and enhance species richness (Connell, 1978; Hobbs and Huenekke, 1992). In tropical regions however, species that profit from disturbance are often widespread habitat generalists of little conservation concern. Disturbance does not generally favour specialist species confined to one habitat type (Thiollay, 1992; Hammer et al., 1997; Hammer and Hill, 2000; Barlow et al., 2002). In temperate regions, it is well known that

many species persist in habitats that have a long history of human alteration (Sutherland and Hill, 1995; Bengtsson et al., 2000). Indeed specialist species of conservation concern in habitats such as heathland are often reliant on anthropogenic disturbance (Sutherland and Hill, 1995). The importance of traditional human activities in maintaining biodiversity in tropical ecosystems has received less attention. Nevertheless, increasingly, ecologists and palaeontologists are recognising that human disturbance has played an important role in the history of tropical ecosystems (Bird and Cali, 1998; Foster et al., 1999; van Gemerden et al., 2003), although to date little work has examined faunal responses to these types of disturbance.

The history of human activities in papyrus swamps is poorly studied. Papyrus is usually cut to provide material to thatch roofs, build fences and to make handcrafts such as mats and trays, which are used to dry sorghum and beans (Maclean et al., 2003c). Burning is either started accidentally, often in attempting to smoke bees out of hives, or a deliberately in order to help capture game such as sitatunga (*Tragelaphus speki*) by confining them into small areas. It is likely that swamps have been subjected to these types of disturbance since the region was first settled by agriculturalists, albeit at lower intensities when human population densities were lower. In addition to human disturbances, natural disturbances may have also been important in historic times. Prior to intensive hunting, large herbivores such as elephants (*Loxodonta africana*) and Hippopotami (*Hippopotamus amphibius*) had an important effect on Paleotropical ecosystems (Cristoffer and Peres, 2003) and wetlands prior to the fragmentation influence of drainage are susceptible to natural fires during the dry season (Beadle, 1981). Thus two mechanisms could explain the tolerance of papyrus-dwelling passerines to disturbance. It is possible that these species have evolved under a regime of natural disturbance, however an alternative explanation for this response could be that an extinction filter has been applied to papyrus avian communities by human activity such that only those species tolerant of disturbance remain. Whilst one can only speculate as to the relative importance of these mechanisms, it is interesting to note the apparent parallels with certain temperate communities in which pre-historic disturbance by megaherbivores played an important role in shaping community structure, the effects of which were often later mimicked by traditional human activities (Bengtsson et al., 2000). It is noteworthy that the papyrus yellow warbler, considered the most endangered of the papyrus endemics (BirdLife International, 2000) also appears also to be amongst the most dependent on disturbance. This species has its stronghold in higher altitude swamps in south-west Uganda and northern Rwanda (Maclean et al., 2003b). This region of East Africa has been settled by humans at least since the early first millennium B.C. (Ehret, 1998) and is amongst the most densely populated rural regions of Africa (Lindblade et al., 1998; Carswell, 2002).

4.3. Conclusions

The results of this study have important implications for the conservation management of Ugandan wetlands. To date, conservationists have regarded harvesting as detrimental to

papyrus avifauna (Bennun and Njoroge, 1999; Byaruhanga et al., 2001) and government legislation prohibits harvesting for this reason (Wetlands Inspectorate Division, 2001). Although this legislation is largely ignored by local people (Maclean et al., 2003c), attempts to enforce these rules are in progress (Wetlands Inspectorate Division, 2001). Furthermore, several papyrus swamps in the region have been designated as Important Bird Areas and Ramsar sites with the intention of enhancing their protected status (Byaruhanga et al., 2001). However, people living around wetlands in East Africa often exercise more power than governments over the local use of wetland resources and their goodwill is needed if conservation initiatives are to work (Gichuki, 2000). Regulated harvest quotas could contribute to achieving this, and therefore contribute to the success of such initiatives without detriment to papyrus-dwelling passerines.

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