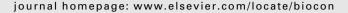


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Effects of disturbance and habitat loss on papyrus-dwelling passerines

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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 land-scapes (Saab, 1999).

The effects of disturbance on animals and plants are comparatively well studied. Both theory (Connell, 1978) and empirical evidence (Hobbs and Huenekke, 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 Andrén, 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 presenceabsence 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 gonolok 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 bicolour) 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

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