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Nest sites selection by sympatric cavity-nesting birds in miombo woodlands

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Deforestation and habitat fragmentation have long been known as drivers of wildlife depletion but information on their specific impacts on cavity-nesting birds in the miombo woodlands has been lacking. A comparative study of disturbed and undisturbed sites was conducted in miombo woodlands of Zambia to assess impacts of environmental stressors on birds. Foot patrols were employed to locate, identify and count host trees and cavities for cavity-nesting birds on twenty 200 m × 200 m sample plots. Undisturbed forests had three times more cavities (the nesting sites for birds), while there were 24.6% fewer abandoned cavities in undisturbed forests than in disturbed forests. The rate of cavity abandonment was about twice as high in human-dominated forests compared to undisturbed forests (61.3% c.f. 31.9%). Cavity-nesting birds preferred larger (> 36.0 cm diameter at breast height) and taller (> 5.0 m) trees for nest placement, especially in human-dominated forests. A number of cavity-nesting birds preferred *Brachystegia spiciformis* (zebrawood), *Julbernadia paniculata* (munsa), *Parinari curatellifolia* (mobola-plum) and *Uapaca kirkiana* (mahobohobo) as host trees to 14 other miombo tree species. Arnot's Chat (*Myrmecocichla arnoti*) had a wider selection of host trees for cavity-nesting than the other 40 cavity-nesting birds in the study areas. Anthropogenic activities such as uncontrolled firewood collection, wild fires, logging, and land clearing for agriculture negatively influenced wood abundance and diversity, with potential implications for persistence of cavity-nesting birds. The negative impacts of anthropogenic activities could be counteracted by conservation strategies such as implementation of sound forest policies, integrative land use practices, sustainable livelihood security and stakeholders' awareness of the need to safeguard forest-dependent avifauna.

Conservation implications: This comparative study unravels specific anthropogenic impacts on the cavity-nesting birds in the miombo woodlands, which would be relevant for designing and implementing targeted biodiversity conservation interventions against negative local environmental values and attitudes that support rural development on the expense of conservation of biodiversity such as birds.

Introduction

Cavity-nesting birds use hollow spaces as nesting sites. Nest site selection by cavity-nesting birds is influenced by multiple factors such as habitat conditions, life-history traits and tree preferences of cavity-nesting birds (Politi & Hunter 2009). Most cavity-nesting birds prefer sizeable trees of > 30 cm in diameter at breast height (DBH) (Lehmkuhl *et al*. 2003), though younger trees may have suitable cavities depending on the species of the tree and on factors such as the frequency and intensity of fires and disease (Gibbons *et al*. 2002). Cavity abundance is influenced by the species of tree, DBH, position on the trunk, and whether the tree is alive or dead (Carlson, Sandström & Olsson 1998). Wood that is susceptible to insects and fungi due to low resin levels in the wood is more conducive to cavity formation (Shigo & Marx 1977). Other tree-dependent characteristics for cavity formation include the porosity, texture of the wood, and exposure to light (Saab, Dudley & Thompson 2004). Cavity-nesting birds select nests based on the depth of the cavity (Belthoff & Ritchison 1990), the body size of bird species (Carlson *et al*. 1998) and the orientation of the entrance (Radford & Du Plessis 2003).

The structural condition of both dead and living trees determines the extent and nature of cavity development. The presence of dead wood or broken treetops promote development of cavities by cavity-nesting birds, though with reduced permanence compared to living trees especially in trees with high compartmentalisation (a process of isolating fungal affected sapwood tissue) which facilitates sapwood growth (Lehmkuhl *et al*. 2003). Fire-scarred woods are prone to higher cavity holding rates than wood that is not exposed to fires, because fire induces weakness that makes it easy for excavators (Hunter & Mazurek 2003). Sometimes fires are followed by termite and fungal attacks in cracked and scarred portions of trees (Jackson & Jackson 2004). Therefore, cavity formation is greatly affected by the frequency and intensity of fires. In addition to fire-scarring of forested areas, the cavity-nest densities and nest survival for cavity-nesting birds are influenced by the periods since fires occurred and wood logging (Saab, Russell & Dudley 2007). Further, foraging excavators may also serve as vectors by depositing fungal spores or *hyphae* at the tree cracks, which eventually develop into fungal conks (Farris, Huss & Zack 2004).

Predation is another form of disturbance that influences nest site selection by cavity-nesting birds (Wesolowski 2002). Nest predation commonly involves depredation of eggs or chicks by reptilian and mammalian tree-climbers, and birds of prey (Wilson *et al.* 1998). The suitability of potential nest sites is also based on the prospects offered of avoiding predation and maximisation of reproductive success for cavity-nesting birds. The choice of nest sites by cavity-nesting birds is often influenced by factors such as the height above the ground, vegetal concealment of entrances of cavities, and neighbouring vegetation type due to edge effects (Fisher & Wiebe 2005). Site-choice may be further influenced by competition. Inter-specific competition for cavities involves multiple species of cavity-nesting birds and other taxa such as various mammal species (Kappes & Davis 2008). Mammals, birds, amphibians, reptiles, and insects can compete for cavities to fulfil various behavioural needs such as resting, roosting, breeding, feeding, and hiding (Gibbons *et al*. 2002). In cases of intense inter-specific competition, resource partitioning is a common strategic response by the species involved (Harrington *et al*. 2009). An example of such resource partitioning is in the use of different sized cavities by species of different sizes. Relatively small sized cavities form realised niches for small cavity-nesting birds by excluding larger nest users. In addition, cavity-nesting birds employ exclusionary strategy of territorialism (Wesolowski 1989). For instance, Starlings (*Sturnus vulgaris*) are known to constrain Tree Swallows (*Tachycineta bicolour*) to smaller nest sizes and remote nest sites from woodlands (Dobkin *et al*. 1995). In another example, woodhoopoes defend their core territorial areas where suitable cavities for roosting and breeding are found from competitor species (Du Plessis 1992; Du Plessis, Simmons & Radford 2007). Some cavity-nesting birds shift their nesting behaviour seasonally due to aggressive competition from other species (Koenig 2003). Further, anthropogenic disturbances are among key drivers of nest choice and abandonment rates of cavities by birds, especially during breeding season (Richardson & Miller 1997). Removal of wood by humans negatively reduces the availability and diversity of cavities for birds (Du Plessis 1995). Cavity-nesters also frequently experience intra-specific competition, either due to low supply of cavities for nest sites or due to competition for vantage points (Czeszczewik & Walankiewicz 2003).

Miombo woodlands are rich in cavities, albeit there is a lack of information on the conservation status of cavity-nesting birds or on availability of nest sites in the miombo woodlands. The miombo woodlands are dry tropical deciduous forests growing in central and southern parts of Africa (Schwartz, Caro & Banda-Sakala 2002), covering ~10% of the continent (Millington *et al*. 1994). Miombo woodlands comprise mostly the family *Fabaceae* and the genera *Brachystegia*, *Julbernardia* and *Isoberlini*a (Dewees *et al*. 2011; Ryan, Williams & Grace 2010). Various tree species are found in a miombo biome including *Brachystegia spiciformis* (zebrawood), *Julbernardia paniculata* (munsa), *Julbernardia globiflora* (mnondo), *Parinari curatellifolia* (mobola-plum), *Syzygium guineense* (waterberry), *Uapaca species* (mahobohobo) and *Isoberlinia angolensis* (kapane). A characteristic of miombo woodlands is that the constituent trees grow to great heights and girths (Frost 1996), providing significant resources for humans and wildlife. For humans, miombo woodlands provide highly valued timber, non-timber forest products such as fruits, edible caterpillars and mushrooms, while for wildlife of various taxa, miombo woodlands provide food and habitats (Kalaba, Quinn & Dougill 2013).

Miombo woodlands are inhabited by a wide range of species of cavity-nesting birds such as woodpeckers, barbets, owls, hornbills, woodhoopoes, rollers, kingfishers and starlings (Dowsett, Aspinwall & Dowsett-Lemaire 2008; Hockey, Dean & Ryan 2005; Leonard 2005). The cavity-nesting birds seek wood crevices to use as nesting places, landmarks for their territories, provision of insects as source of food to those that are also insectivores, and protection from the direct sunlight and precipitation (Ober & Minogue 2007). However, miombo woodlands are under acute threat from expanding human activities such as deforestation that results from timber harvesting, charcoal production, uncontrolled human-induced wild fires, and clearance of vegetation for agriculture, settlement and industry (Turner II, Lambin & Reenberg 2007). Unlike natural factors such as droughts, and wild fires from lightening which are stochastic in nature, anthropogenic factors causing deforestation are usually deterministic and often result in environmental degradation. Zambia for example, suffers some of the fastest rates of deforestation in the world, losing an estimated total area of forests of between 2500 km^2 per year and 3000 km^2 per year (Ministry of Tourism, Environment and Natural Resources; United Nation's Food and Agricultural Organisation 2008).

Despite extensive studies globally on the ecology of cavity-nesting birds (e.g. Cockle, Martin & Wesolowski 2011; Kemp 2000; Rhodes, O'Donnell & Jamieson 2009), empirical evidence of impacts of anthropogenic activities on cavity-nesting birds in the miombo woodlands has been lacking. Miombo woodland transformation results in multi-scale landscape dynamics in what are social–ecological systems, leading to various structural and process responses (Zurlini *et al*. 2013). Structural responses relate to changes in species composition and diversity while process responses relate to evolutionary and ecological functional elements of woodlands. Shifts such as land use transformations would likely require landscape-based interventions for biodiversity conservation (Benayas & Bullock 2012; Jones *et al*. 2010). Natural ecosystems can assimilate some disturbance, while at the same time maintaining ecological processes through resilience (Carpenter & Brock 2008; Walker & Salt 2006). Birds act as bio-indicators of ecosystem performance in increasingly human-modified systems (Holt & Miller 2011; Mayer, Donovan & Pawlowski 2014).

We assessed the impacts of human activities such as uncontrolled firewood collection, logging, fires, and land clearing for commercial purposes on cavity-nesting birds. Key research questions included the assessment of: (1) to what extent do human-induced disturbances affect wood abundance and diversity? (2) How do wood abundance and diversity influence nest site selection by sympatric cavity-nesting birds in the miombo woodlands?

Methods

Study sites

We used two study sites: the human-dominated Mwekera National Forests No. 6 in Kitwe, and the undisturbed forests of Chimfushi Wildlife Orphanage in Chingola, both in the Copperbelt province of Zambia (Figure 1) (hereafter referred to as Mwekera and Chimfushi). Miombo woodlands cover ~45% of Zambia's landmass (Stringer *et al*. 2012) and in both study areas, the vegetation is predominantly miombo, characterised by vegetation types in Table 3. In the case of Mwekera, there are also exotic *Eucalyptus globulus* (blue gum), *Eucalyptus tereticornis* (forest red gum), *Pinus kesiya* (khasi), *Pinus oorcarpa* (ocote chino) and *Pinus merkusii* (merkus) plantations.

Mwekera

The average human population density in the Copperbelt province is 63.0 persons per km^2, with an average annual rate of population growth of 2.2% (Central Statistical Office 2012). Mwekera (~111 km^2) lies at an elevation of 1245 m a.s.l – 1310 m a.s.l., with an annual average ambient temperature of 19.7 °C, and mean annual rainfall of 1300 mm. The area forests were established as a National Forest to protect the Mwekera stream catchment, which is part of the Kafue River system. However, the Mwekera forests have been undergoing rapid degradation mainly due to unauthorised settlements (Zimba 2007). Historical research suggests that the Mwekera forests supported a higher diversity of birds, mammals and reptiles in the past than what persist today (Dowsett *et al*. 2008; Leonard 2005). For instance, mammals such as elephants (*Loxodonta africana*), lions (*Panthera leo*), leopards (*Panthera pardus*), eland (*Taurotragus oryx*), sable (*Hippotragus niger*) and impala (*Aepyceros melampus*), in addition to several bird species, have been extirpated in the last three decades due to human-induced disturbances (P.M. Fushike, pers. comm., 05 December 2014). However, various species of small-bodied species of wildlife such as rodents, lizards and squirrels persist.

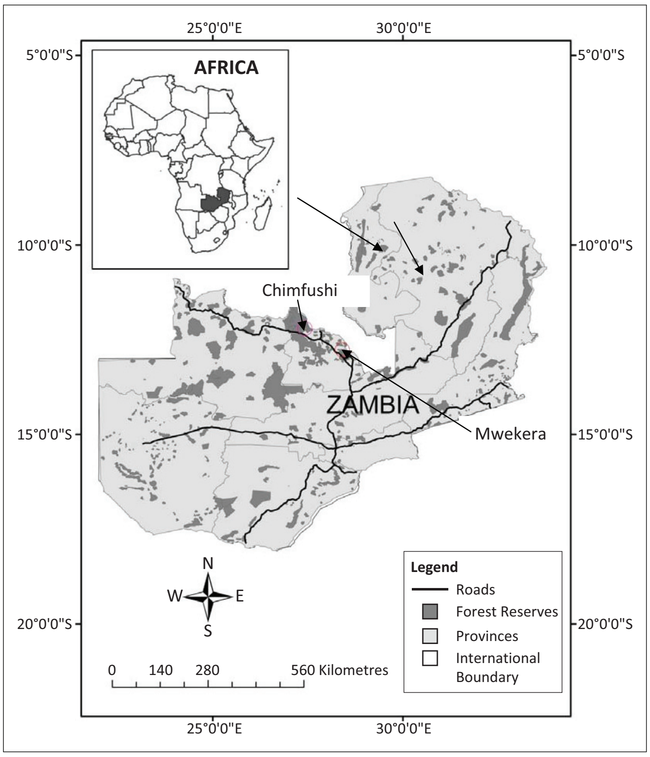

FIGURE 1: Locations of Mwekera National Forests No. 6 and Chimfushi Wildlife Orphanage forests in Zambia.

Chimfushi

Chimfushi is a private farm (~93 km^2) on the banks of the Kafue River, in Chingola District, Copperbelt Province of Zambia (Figure 1). Management of the property excludes human intrusions into the area. Chimfunshi occurs at an altitude of 1280 m above sea level and has mean annual temperature and precipitation of 20.7 °C and 1200 mm respectively. The area is used primarily as a sanctuary for orphaned chimpanzees (*Pan troglodytes*) but is also populated with blue monkeys (*Cercopithecus mitis*), sitatungas (*Tragelaphus spekii*), hippos (*Hippopotamus amphibius*) and Nile crocodiles (*Crocodylus niloticus*) in addition to a variety of other mammals, birds, reptiles and amphibians.

Data collection protocols

We conducted bird surveys at the two sites during August and September 2014 for owls and in November–February 2014/2015 for the rest of the cavity-nesting birds. These periods coincided with the time when most of the tree cavity-nesting birds such as southern ground hornbills, barbets, hornbills, and woodpeckers have their breeding seasons (Hockey *et al*. 2005). Observations were conducted during 09:00–11:00 hrs when birds were typically active. Data was collected from ten randomly selected sampling plots of quadrats that measured 200 m x 200 m in size, and were located at least 500 m away from vegetation ecotones. The plots were visited and inspected once every fortnight during the survey period. Although the number of bird species was not enumerated in this study, data on species presence and absence were recorded. Two observers searched each plot for tree cavities and dead wood. The use of cavities by birds was ascertained by remote observations of bird nesting, feeding, and social behaviour around the nesting sites (Dowsett *et al*. 2008; Leonard 2005; Newman & Read 2008). By using this indirect method, we did not need to reach and inspect physical features such as remnants of eggshells, feathers and droppings in the nests, thereby minimising disturbances to the cavity-nesting birds. Therefore, consistent bird activity in the form of nesting, feeding and roosting at the nest sites during the breadth of study period (or lack thereof) was taken as being indicative of whether the respective nests were still active or abandoned. Placement of nests was indirectly measured from tree DBH approximately 1.3 m above the ground to determine the tree size preferences by cavity-nesting birds and angular measurements for estimation of tree heights were made by use of Suunto hypsometer clinometers, following standard methods described by Avery and Burkhart (1994) and Leverett (2010). Hundred-metre measuring steel tape and rope were also used for estimation of distances. Enumerated trees were marked and tagged with metal plates for ease of subsequent identification. Differences in tree diameters over study period were not obtained on assumption that in-season variations resulting from contraction and expansion of trees were insignificant during the relatively short peak season for the breeding cavity-nesting birds as suggested by Krauss *et al.* (2007) and O'Brien *et al.* (2008). Dried and rotting wood was considered dead; wood in a posture perpendicular to flat ground (with about zero slope) was taken as standing wood, while wood prostrating on the ground was considered 'lying' wood. Tasco binoculars, with magnification of 20×, were used to aid in identifying cavity-nesting birds. Guide books were used for taxonomic classification of plants and birds (Leonard 2005; Newman & Read 2008).

Analyses

Minitab (2004), (Minitab Inc., Pennsylvania, USA), version 14 statistical software was used in the statistical analyses. Two-sample *T*-test was used to establish whether the quantum of trees and active cavities significantly varied or not between the two study sites, using the procedure stipulated by Fowler, Cohen and Jarvis (2006). Relative plant species abundance was analysed for comparative commonness or rarity in the two study sites (McGill *et al*. 2007). Since diversity is non-linear, beta diversity which compares elements of diversity such as different vegetation communities was adopted. Thus, we derived comparable estimates of the effective number of tree cavities for bird nesting from exponentials of Shannon-Weaver indices (Jost 2006; Magurran 2004). From conservation perspective, Shannon-Weaver index is used to measure and compare components of conservation status between different sites with similar environments (Fowler *et al*. 2006). It is represented by $H' = -\Sigma P_i (lnP_i)$, where H' is diversity index, P_i is the proportion of each component in the sample and lnP_i = natural logarithm of this proportion. The higher the H' value, the greater the diversity. Use of indices is important and common in biodiversity monitoring due to the difficult in elucidating absolute enumeration of biodiversity (Barry *et al*. 2013; Tuomisto 2012). In the case of bird abundance, presence or absence data were analysed for each cavity-nesting bird.

Results

Species presence and absence

There were 41 cavity-nesting bird species at the two study sites (Table 1). Cavity-nesting birds with the highest number of species were owls (seven species), woodpeckers (six species) and kingfishers (six species) and the birds with the lowest number of species were chats and parrots (Table 1). Out of the 41 bird species in the study sites, only 12.2% (n = 5) occurred in human-dominated forests (Table 1).

Wood, cavities and cavity-nesting birds interrelationships

The undisturbed and disturbed forests had mean tree densities of 3.2 ± 0.02 trees per ha (range: 2–5 trees per ha) and 1.8 ± 0.05 trees per ha (range: 1–2 trees per ha) respectively. Mean tree densities in undisturbed forests were significantly higher than in disturbed forests (T-test=5.52; df = 9; P < 0.001). The mean abundance of active cavities was higher in the undisturbed site relative to disturbed sites at 17.4 ± 2.4 (range: 11–26) and 4.0 ± 1.1 (range: 1–7) (T-test = 12.79; df = 9; P < 0.001, Table 2). The number of tree cavities in undisturbed forests was 139.6% greater than in disturbed forests out of the 360 tree cavities that were recorded in the study area. Similarly, the number of tree cavities with active bird presence was 321.9% greater in the undisturbed forests than disturbed forests. The remainder of the 146 cavities in the study area were abandoned by the cavity-nesting birds. There were 24.6% fewer abandoned cavities in undisturbed than in disturbed forests (Table 2). The rate of cavity abandonment was about twice as high in human-dominated forests compared to undisturbed forests (61.3% c.f. 31.9%) (Tables 2 and 3).

Undisturbed forests had 71.9% more dead wood than human-dominated forests, as recorded from a total of 14 tree species and 201 dead wood (Table 2). More than two thirds of dead wood with cavities was found in undisturbed forests. There were 44.8% more wood without cavities in human-dominated forests relative to undisturbed forests.

TABLE 1: Presence and absence of key cavity-nesting birds in Mwekera National Forests No. 6 and the Chimfushi Wildlife Orphanage forests, Copperbelt Province, Zambia, 2014.

Bird species	Scientific names	Mwekera (human-dominated forests)		Chimfushi (undisturbed forests)	
		Presence	Absence	Presence	Absence
Wood Owl	*Strix woodfordii*	x	-	-	x
Barn Owl	*Tyto alba*	-	x	x	-
African Scops Owl	*Otus senegalensis*	x	-	x	-
White-faced Scops Owl	*Otus leucotis*	-	x	x	-
Spotted Eagle Owl	*Bubo africanus*	-	x	x	-
Giant Eagle Owl	*Bubo lacteus*	-	x	x	-
Barred Owlet	*Glaucidium capensis*	-	x	x	-
Bearded Woodpecker	*Thripias namaquus*	-	x	x	-
Olive Woodpecker	*Mesopicos griseocephalus*	-	x	x	-
Cardinal Woodpecker	*Dendropicos fuscescens*	x	-	x	-
Golden-tailed Woodpecker	*Campethera abingoni*	x	-	x	-
Bennett's Woodpecker	*Campethera bennetti*	-	x	x	-
Little-spotted Woodpecker	*Campethera cailliautii*	-	x	x	-
Southern Ground Hornbill	*Bucorvus cafer*	-	x	x	-
Crowned Hornbill	*Tockus alboterminatus*	-	x	x	-
Pale-billed Hornbill	*Tockus pallidirostris*	-	x	x	-
Trumpeter Hornbill	*Bycanistes bucinator*	-	x	x	-
Arnot's Chat	*Myrmecocichla anorti*	x	-	x	-
Mosque Swallow	*Hirundo senegalensis*	-	x	x	-
Red-breasted Swallow	*Hirundo semirufa*	-	x	x	-
Lesser-striped Swallow	*Hirundo abyssinica*	-	x	x	-
Greater-striped Swallow	*Hirundo cucullata*	-	x	x	-
European Swallow	*Hirundo rustica*	-	x	x	-
Meyer's Parrot	*Poicephalus meyeri*	-	x	x	-
Half-collared Kingfisher	*Alcedo semitorquata*	-	x	x	-
Malachite Kingfisher	*Alcedo cristata*	-	x	x	-
Brown-headed Kingfisher	*Halcyon albiventris*	-	x	x	-
Striped Kingfisher	*Halcyon chelicuti*	-	x	x	-
Giant Kingfisher	*Megaceryle maxima*	-	x	x	-
Pied Kingfisher	*Ceryle rudis*	-	x	x	-
European Roller	*Coracias garrulus*	-	x	x	-
Lilac-breasted Roller	*Coracias caudatus*	-	x	x	-
Broad-billed Roller	*Eurystomus glaucurus*	-	x	x	-
Red-billed Wood hoopoe	*Phoeniculus purpureus*	-	x	x	-
Hoopoe	*Upupa epops*	-	x	x	-
Whyte's Barbet	*Stactolaema whytii*	-	x	x	-
Miombo pied Barbet	*Tricholaema frontata*	-	x	x	-
Black-collared Barbet	*Lybius torquatus*	-	x	x	-
Black-backed Barbet	*Lybius minor*	-	x	x	-
Sharp-tailed Starling	*Lamprotornis acuticaudus*	-	x	x	-
Violet-backed Starling	*Cinnyricinclus leucogaster*	-	x	x	-

Cavity-nesting birds' adaptation strategies

Birds placed their cavity-nests at greater heights in human-dominated forests than in undisturbed forests (Table 2). Out of the 201 recordings of dead wood, 81 were prostrate while 123 were standing: a greater proportion of standing wood was found in undisturbed forests (Table 2). Prostrate wood in human-dominated forests included those that were cut by humans and left to dry. Diameter at breast height for the trees used by cavity-nesting birds ranged from 31.2 cm to 39.2 cm while cavity-nest height ranged from 3.2 m to 5.7 m above the ground (Table 2). Although undisturbed forests had suitable trees (> 36.0 cm tree DBH and > 5.0 m high) for cavity-nesting birds, a substantial proportion of nests (48.3%) were also placed in small trees (< 36.0 cm DBH and < 5.0 m high). In contrast, a small proportion of only 20% of the total cavity-nests were placed < 5.0 m in trees of < 36.0 cm DBH in human-dominated forests. In the entire study area, the cavity-nesting birds preferred large tall trees for nesting as depicted in Figures 2 and 3. The effective number of active cavities was almost three times greater in undisturbed forests than in the human-dominated forests, indicating enhanced nesting sites in the former (Table 2).

The tree species richness was higher in undisturbed forests (inverse of Simpson's richness index = 12.6) than in human-dominated forests (inverse of Simpson's richness index = 10.0). Further, cavity-nesting birds showed varied preferences for host trees (Tables 3 and 4). *B. spiciformis, J. paniculata, P. curatellifolia* and *Uapaca kirkiana* hosted a greater variety of cavity-nesting birds than other host trees. Arnot's Chats had a wider selection of host trees for cavity-nesting than other cavity-nesting birds.

TABLE 2: Parameters explaining occurrence of tree cavities in Mwekera National Forests No. 6 and the Chimfushi Wildlife Orphanage forests, Copperbelt Province, Zambia, 2014.

Parameter	Mwekera (human-dominated forests)			Chimfushi (undisturbed forests)		
	Range per site	Mean ± SE per site	Total in Mwekera	Range per site	Mean ± SE per site	Total in Chimfushi
Number of active cavities	1–7	4.0±1.1	41	11–26	17.4±2.4	173
Number of abandoned cavities	1–12	6.6±2.1	65	2–13	8.0±1.9	81
Number of dead wood with cavities	2–5	3.2±0.5	32	6–14	9.8±1.6	98
Number of dead wood without cavities	2–7	4.2±1.0	42	1–5	3.0±0.7	29
Number of standing wood	1–5	3.2±0.8	33	6–11	9.0±0.9	90
Number of lying wood	2–6	4.2±0.7	43	1–8	3.8±1.2	38
Mean DBH (cm)	31.2–35.9	33.6±1.0	-	33.2–39.2	36.4±0.9	-
Nest height (m)	4.0–5.7	5.2±0.3	-	3.2–5.1	4.6±0.4	-
Effective number of active cavities†	-	-	2.7	-	-	7.4

†, Effective number of active cavities for bird nesting indicated the comparable number of cavities where there was active presence of birds.

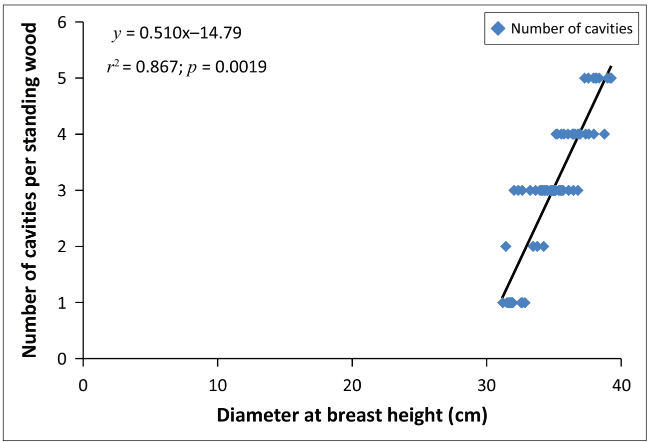

FIGURE 2: Correlates between number of cavities per standing wood and diameter at breast height in the study areas of Chimfushi and Mwekera forests, Zambia, in 2014.

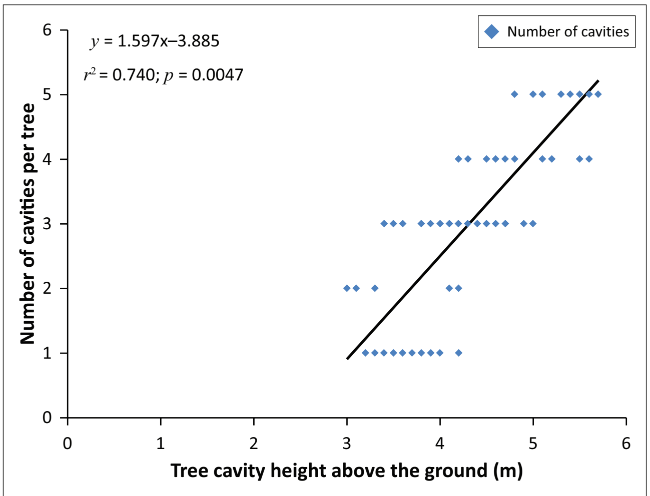

FIGURE 3: Correlates between number of cavities per standing wood and minimum tree height in the study areas of Chimfushi and Mwekera forests, Zambia, in 2014.

Discussion

Persistence of sympatric cavity-nesting birds

In this study, undisturbed forests found in the Chimfushi area supported a more diverse array of cavity-nesting birds than human-dominated forests in Mwekera. In both forest types, environmental conditions were similar except for the direct anthropogenic factors such as uncontrolled firewood collection, logging, wild fires, and land clearing for agriculture purposes that occurred in the Mwekera forests. The aforementioned anthropogenic factors could have been responsible for the occurrence of much less abundance and diversity of cavity-nesting birds in the Mwekera forests than the Chimfushi forests. According to Trzcinski, Fahrig and Merriam (1999) and Roberts (2007), environmental factors such as deforestation and habitat fragmentation might trigger the presence or absence of certain cavity-nesting birds in a particular area. Based on studies conducted elsewhere, it would also appear that undisturbed forests contain more cavity-nesting birds than disturbed forests, due in part to increased availability of nesting sites (dos Anjos 2006; Reid *et al*. 2014). Some bird species in the study areas might have been affected by direct persecution by humans and other predators. For instance, owls are persecuted by local communities based on superstitions surrounding them (Lee & Irwin 2005), despite owls being natural biological control agents of pests such as rodents and insects in agrarian and semi-urban landscapes (Meyer 2008).

In both study areas, the most prevalent cavity-nesting birds were the African Scops Owl and the Wood Owl and these birds had successfully adapted thus far to the human-dominated landscapes. There is the likelihood that both the African Scops Owl and Wood Owl species persist on the abundant rodents and insects found in human-dominated landscapes (Carrete *et al*. 2010; Dowsett *et al*. 2008). However, the quantity and diversity of bird species any forest can support depend on the capacity of the vegetation to absorb disturbance (Carpenter & Brock 2008; Folke *et al*. 2010). Cavity-nesting bird populations are largely resident and non-migratory in nature (Reid *et al*. 2014; Wilson & Hockey 2013). On the other hand, secondary cavity-nesting birds such as southern ground hornbills, Arnot's Chats, and White-faced Scops Owls are likely to be more negatively impacted by the absence of the host vegetation than primary cavity-nesting birds that create their own tree cavities, without having to adopt or re-use the existing cavities. The dependence on existing cavities by secondary cavity-nesting birds speculates why secondary cavity-nesting birds have difficulties to survive forest disturbance trajectories such as forest succession and transformations (Martin & Eadie 1999).

TABLE 3: Tree species and their associated nesting cavities in the 20 sample plots in Mwekera National Forests No. 6 and the Chimfushi Wildlife Orphanage forests, Copperbelt Province, Zambia, 2014.

Tree species	Mwekera (human-dominated forests)				Chimfushi (undisturbed forests)			
	Quantity (number)	Proportion (%)	Active cavities (number)	Abandoned cavities (number)	Quantity (number)	Proportion (%)	Active cavities (number)	Abandoned cavities (number)
Parinari curatellifolia	11	15.7	10	1	14	10.6	37	3
Brachystegia boehmii	10	14.3	5	36	11	9.1	4	5
Lannea discolour	4	5.7	0	2	19	13.6	9	12
Brachystegia spiciformis	10	14.3	2	9	10	7.6	6	2
Julbernardia paniculata	8	11.4	4	0	10	7.6	3	7
Vitex doniana	4	5.7	0	0	13	9.1	68	2
Albizia anthunesia	7	10.0	0	0	8	6.1	4	3
Pterocarpus angolensis	4	5.7	7	0	11	7.6	8	13
Uapaca kirkiana	3	4.3	0	10	10	7.6	7	22
Anisophyllea boehmii	4	5.7	13	0	7	6.1	19	7
Isoberlinia angolensis	4	5.7	0	7	9	6.1	0	4
Diplorhynchus condylocarpon	1	1.4	0	0	5	4.6	7	1
Bridelia micrantha	0	0	0	0	3	3.0	0	0
Hymonecardia acidia	0	0	0	0	2	1.5	1	0
Total	**70**	**100**	**41**	**65**	**132**	**100**	**173**	**81**

In addition, cavity dwelling bird species such as Bearded Woodpecker (*Thripias namaquus*), Olive Woodpecker (*Mesopicos griseocephalus*), Cardinal Woodpecker (*Dendropicos fuscescens*) and Golden-tailed Woodpecker (*Campethera abingoni*) implement various survival strategies against predation risks, including predator avoidance and narrowing sizes of entrance holes (Kemp 2001; Reed 2001). According to Sinclair, Fryxell and Caughley (2006), the ability for birds to adapt to environmental changes through use of rare resources by generalist foraging and nesting behaviour in a range of habitat conditions may contribute to the persistence of particular avifauna.

Wood abundance and its influence on nesting cavities

The quantity of suitable wood for nesting cavities is typically a limiting factor for populations of cavity-nesting birds (Laudenslayer 2002; Newton 1998). Adverse anthropogenic activities such as land clearing for agriculture, logging, uncontrolled fires and firewood collection can reduce the number of cavities below a critical threshold for the persistence of cavity-nesting birds. Human-induced and uncontrolled bush fires in the miombo woodlands are common, especially in Zambia where implementation of forestry policies and laws are relaxed (Eriksen 2007). However, factors such as the abundance of live or dead, rotten or solid, broken or intact wood, and also the presence or absence of certain wood types are particularly important in determining the persistence of cavity-nesting birds.

Adaptation of cavity-nesting birds to human disturbances

In this study, 81.3% of active nests were found placed high on large-diameter trees (Figures 2 and 3). The selection of large-diameter trees in human-dominated forests indicated that there was a preference by birds to use of large-diameter nest trees over small ones. The reason cavity-nesting birds preferred large-diameter trees could have been that birds enjoyed protection from predation, competition and some human disturbances, maximised nest space and thermal insulation (Laudenslayer 2002). For instance, nests placed in high cavities suffer lower predation rates and enjoy higher success for persistence (Joy 2010). In this regard, birds counteract environmental adversity by adapting their behaviour.

Our analysis buttresses the theory of 'realised ecological niche' – a nesting site where birds would actually thrive amidst adversaries (Sinclair *et al*. 2006). However, while there are still some species that have adapted to numerous disturbances in the Mwekera forests, dead wood which provides preferred resources for cavity-nesting birds are more prone to fires and collection for human use than fresh standing trees, especially in unmanaged forests (Stephens 2004). In addition, due to anthropogenic disturbance, juvenile and coppicing trees are often not allowed to grow older to provide decaying portions for creation of cavities. The sourcing of firewood is also selective because local communities target certain tree species, in particular those with hard wood which often provide ideal habitats for cavity-nesting birds.

Conservation implications

Avian species conservation in changing environments demands that there should be monitoring, integrated land management and concerted effort (Nelson 2008). Thus, physical and cognitive aspects of conservation need to be addressed to ensure persistence of cavity-nesting birds. Physical aspects of such interventions include implementation of policies, forest management plans and best practices. Cognitive aspects of the appropriate interventions include integrating supportive perceptions and attitudes in resource users. For instance, stakeholders' awareness of ecological processes and the structure of miombo woodlands associated with bird conservation are critical in the light of many forest

TABLE 4: Cavity-nesting birds and their preferred host tree species in Mwekera National Forests No. 6 and the Chimfushi Wildlife Orphanage forests, Copperbelt Province, Zambia, 2014.

Cavity-nesting birds	Tree species													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Wood Owl	-	-	-	M	-	-	-	-	-	-	-	-	-	-
Barn Owl	-	-	-	C	-	-	-	-	-	-	-	-	-	-
African Scops Owl	-	-	-	-	M	-	-	-	-	-	-	-	-	-
Giant Eagle Owl	-	C	-	-	-	-	-	C	-	-	C	-	-	-
White-faced Scops Owl	C	-	-	C	-	-	-	-	-	-	-	-	-	-
Spotted Eagle Owl	C	-	-	-	-	-	-	-	-	-	-	-	-	-
Barred Owlet	-	-	-	-	C	-	-	-	-	-	-	-	-	-
Bearded Woodpecker	-	-	-	-	-	-	C	-	-	-	-	C	-	-
Olive Woodpecker	-	-	-	-	-	C		-	-	C	-	-	-	-
Cardinal Woodpecker	-	-	-	-	M	-	-	M	-	-	-	-	-	C
Golden-tailed Woodpecker	M	-	-	-	-	-	-	-	-	-	-	-	-	-
Bennett's Woodpecker	-	-	-	-	-	C	-	-	-	-	-	-	-	-
Little-spotted Woodpecker	-	-	-	-	C	-	-	-	-	-	-	-	-	-
Southern Ground Hornbill	C	-	-	-	-	-	-	-	-	-	-	-	-	-
Pale-billed Hornbill	-	-	-	-	-	-	-	C	-	-	-	-	-	-
Crowned Hornbill	C	-	-	C	-	-	-	-	-	-	-	-	-	-
Trumpeter Hornbill	-	-	-	-	C	-	-	-	-	-	-	-	-	-
Arnot's Chat	C	M	C	-	-	-	C	-	C	M	-	-	-	-
Greater-striped Swallow	-	-	-	-	-	C	-	-	-	-	-	-	-	-
Mosque Swallow	-	-	-	-	-	-	-	-	-	-	-	-	C	-
Red-breasted Swallow	-	-	C	-	-	C	-	-	-	-	-	-	-	-
Lesser-striped Swallow	-	-	C	-	-	-	-	-	-	-	-	-	-	-
European Swallow	-	-	-	-	-	-	C	-	-	-	-	-	-	-
Meyer's Parrot	-	-	-	C	-	-	-	-	-	-	C	-	-	-
Half-collared Kingfisher	-	-	-	-	-	-	-	-	C	-	-	-	-	-
Malachite Kingfisher	-	-	-	C	-	-	-	-	-	-	C	-	-	-
Brown-headed Kingfisher	-	-	-	C	-	-	-	-	-	-	-	-	-	-
Striped Kingfisher	-	-	-	-	-	-	-	-	-	-	C	-	-	-
Giant Kingfisher	-	-	-	C	-	-	-	-	C	-	-	-	-	-
Pied Kingfisher	-	-	-	-	C	-	-	-	C	-	-	-	-	-
European Roller	-	-	C	-	-	-	-	-	-	-	-	-	-	-
Lilac-breasted Roller	-	-	-	-	-	C	-	-	-	-	-	-	-	-
Broad-billed Roller	-	-	-	-	-	-	-	-	-	-	-	C	-	-
Red-billed Wood hoopoe	-	-	-	-	-	-	-	-	-	-	-	C	-	-
Hoopoe	-	-	-	-	-	-	-	-	-	-	-	C	-	-
Black-backed Barbet	-	-	-	-	-	-	-	-	C	-	-	-	-	-
Black-collared Barbet	-	-	-	-	-	-	-	-	-	C	-	-	-	-
Miombo pied Barbet	-	C	-	-	C	-	-	C	-	-	-	-	-	-
Whyte's Barbet	-	C	-	-	-	-	-	-	-	-	-	-	-	-
Violet-backed Starling	-	-	-	-	-	-	-	-	-	-	-	-	C	C
Sharp-tailed Starling	-	-	-	-	-	-	-	-	C	-	C	-	-	C

1, Parinari curatellifolia; 2, Brachystegia boehmii; 3, Lannea discolour; 4, Brachystegia spiciformis; 5, Julbernadia paniculata; 6, Vitex doniana; 7, Albizia anthunesia; 8, Pterocarpus angolensis; 9, Uapaca kirkiana; 10, Anisophyllea boehmii; 11, Isoberlinia angolensis; 12, Diplorhynchus condylocarpon; 13, Bridelia micrantha and 14, Hymonecardia acidia.

M, Mwekera; C, Chimfushi.

provisioning functions and services. However, attempts to implement the Forest Policy of 1998 in Zambia face challenges as the legal aspects of forest resource management are still under the *Forest Act* of 1973, despite having the *Forest Act* of 1999 formulated. The old *Forest Policy and Forest Act* in use do not suit the changing environment, making understanding and appreciation by multiple stakeholders of the role of natural resources difficult.

Anthropogenic activities such as the lighting of fires, collection of dead wood, and land clearing affect the existence of forested lands, thereby threatening the persistence of cavity-nesting birds (Lee & Irwin 2005; Newton 1998). For instance, small patches of woodlands isolated by human activities are avoided by the cavity-nesting birds even if they contain suitable nest sites (Loman 2006). Therefore, steps are needed from multiple stakeholders, including wildlife managers, policy makers and local communities to ensure the preservation of bird diversity and retention of ecological processes such as nesting, breeding, feeding and roosting. Such steps will help local communities derive benefits from ecosystem services such as ecotourism, which depends on birds and other wildlife species (Snyman 2012). Further, for cavity-nesting bird restoration programmes, there is need to explore and investigate effectiveness of use of artificial nest sites (Wilson & Hockey 2013) and rehabilitation of disturbed woodlands (Benayas & Bullock 2012; Gomez 2014).

Conclusion

The survival prospects of cavity-nesting birds are greatly influenced by the extent of human disturbance of woodlands. The negative effects of disturbance of woodlands may result in the local extinction of certain bird species and significant impacts on the structure and behaviour of bird communities. Additional research is required to investigate further the impacts of human activities on bird species, particularly of other species groupings, and also the impacts of climate change on the distribution and abundance of birds.

The abundance and diversity of wood in miombo systems influence the availability of tree cavities to primary and secondary cavity-nesting birds. Human impacts that reduce abundance and diversity of wood have a negative bearing on cavity-nesting birds. However, these species can be effectively protected by increasing forest protection through sound policies and sustainable land use practices, awareness creation and provision of sustainable livelihoods to rural populations.

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Competing interests

The authors declare that they have no financial relationships which may have inappropriately influenced them in writing this article.

Authors' contributions

V.R.N was team leader, made experimental and project design and wrote the manuscript, F.C.C, E.C-K. and P.A.L. participated in project design and execution.

References

Avery, T.E. & Burkhart, H.E., 1994, *Forest measurements*, 4th edn., McGraw-Hill Inc., New York.

Barry, J., Birchenough, S., Norris, B. & Ware, S., 2013, 'On the use of sample indices to reflect changes in benthic fauna biodiversity', *Ecological Indicators* 26, 154–162. http://dx.doi.org/10.1016/j.ecolind.2012.11.004

Belthoff, J.R. & Ritchison, G., 1990, 'Nest-site selection by Eastern screech owls in Central Kentucky', *Condor* 92, 982–990. http://dx.doi.org/10.2307/1368734

Benayas, J.M.R. & Bullock, J.M., 2012, 'Restoration of biodiversity and ecosystem services on agricultural land', *Ecosystems* 15, 883–899. http://dx.doi.org/10.1007/s10021-012-9552-0

Carlson, A., Sandström, U. & Olsson, O., 1998, 'Availability and use of natural tree holes by cavity nesting birds in a Swedish deciduous forest', *Ardea* 86, 109–119.

Carpenter, S.R. & Brock, W.A., 2008, 'Adaptive capacity and traps', *Ecology and Society* 13, 40, viewed 03 January 2015, from: http://www.ecologyandsociety.org/vol13/iss2/art40/

Carrete, M., Lambertucci, S.A., Speziale, K., Ceballos, O., Travaini, A., Delibes, M. *et al*., 2010, 'Winners and losers in human-made habitats: Interspecific competition outcomes in two Neotropical vultures', *Animal Conservation* 13, 390–398. http://dx.doi.org/10.1111/j.1469-1795.2010.00352.x

Central Statistical Office (CSO), 2012, *Zambia 2010 census of population and housing,* Central Statistical Office, Lusaka.

Cockle, K.L., Martin, K. & Wesolowski, T., 2011, 'Woodpecker, decay, and the future of cavity-nesting vertebrate communities worldwide', *Frontiers in Ecology and the Environment* 9(7), 377–382. http://dx.doi.org/10.1890/110013

Czeszczewik, D. & Walankiewicz, W., 2003, 'Natural nest sites of the Pied Flycatcher *Ficedula hypoleuca* in a primeval forest', *Ardea* 91, 221–230.

Dewees, P., Campbell, B., Katerere, Y., Sitoe, A., Cunningham, A.B., Angelsen, A. *et al*., 2011, *Managing the miombo woodlands of Southern Africa: Policies, incentives, and options for the rural poor,* Program on Forests, Washington, DC.

Dobkin, D.S., Rich, A.C., Pretare, J.A. & Pyle, W.H., 1995, 'Nest–site relationships among cavity-nesting birds of riparian and snowpocket aspen woodlands in the northwestern Great Basin', *Condor* 97, 694–707. http://dx.doi.org/10.2307/1369178

dos Anjos, L., 2006, 'Bird species sensitivity in a fragmented landscape of the Atlantic forest in Southern Brazil', *Biotropica* 38, 229–234. http://dx.doi.org/10.1111/j.1744-7429.2006.00122.x

Dowsett, R.J., Aspinwall, D.R. & Dowsett-Lemaire, F., 2008, *The birds of Zambia*, Tauraco Press, Liège.

Du Plessis, M.A., 1992, 'Obligate cavity-roosting as a constraint on dispersal of green (red-billed) woodhoopoes: Consequences for philopatry and the likelihood of inbreeding', *Oecologia* 90, 205–211. http://dx.doi.org/10.1007/BF00317177

Du Plessis, M.A., 1995, 'The effects of fuel wood removal on the diversity of some cavity-using birds and mammals in South Africa', *Biological Conservation* 74(2), 77–82. http://dx.doi.org/10.1016/0006-3207(95)00016-W

Du Plessis, M.A., Simmons, R.E. & Radford, A.N., 2007, 'Behavioural ecology of the Namibian Violet Woodhoopoe *Phoeniculus damarensis*', *Ostrich* 78(1), 1–5. http://dx.doi.org/10.2989/OSTRICH.2007.78.1.1.45

Eriksen, C., 2007, 'Why do they burn the 'bush'? Fire, rural livelihoods, and conservation in Zambia', *Geographical Journal* 173(3), 242–256. http://dx.doi.org/10.1111/j.1475-4959.2007.00239.x

Farris, K.L., Huss, M.J. & Zack, S., 2004, 'The role of foraging woodpeckers in the decomposition of ponderosa pine snags', *Condor* 106, 50–59. http://dx.doi.org/10.1650/7484

Fisher, R.J. & Wiebe, K.L., 2005, 'Nest site attributes and temporal patterns of Northern flicker nest loss: Effects of predation and competition', *Oecologia* 147, 744–753. http://dx.doi.org/10.1007/s00442-005-0310-2

Folke, C., Carpenter, S.R., Walker, B., Scheffer, M., Chapin, T. & Rockstrom, J., 2010. 'Resilience thinking: Integrating resilience, adaptability and transformability', *Ecology and Society* 15, 20, viewed 21 December 2014, from http://www.ccologyandsocicty.org/voll5!iss4/art20/

Fowler, J., Cohen, L. & Jarvis, P., 2006, *Practical statistics for field biology*, 2nd edn., John Willey and sons, West Sussex, England.

Frost, P., 1996, 'The ecology of miombo woodlands', in B. Campbell (ed.), *The miombo in transition: Woodlands and welfare in Africa,* pp. 11–57, Centre for International Forestry Research, Bogor.

Gibbons, P., Lindenmayer, D.B., Barry, S.C. & Tanton, M.T., 2002, 'Hollow selection by vertebrate fauna in forests of southeastern Australia and implications for forest management', *Biological Conservation* 103, 1–12. http://dx.doi.org/10.1016/S0006-3207(01)00109-4

Gomez, E.D., 2014, 'Effects of tree retention on cavity-nesting birds in northern Sweden', M.Sc. thesis, Sweden University of Agricultural Sciences, Umea.

Harrington, L.A., Harrington, A.L., Yamaguchi, N., Thom, M.D., Ferreras, P., Windham, T.R. *et al*., 2009, 'The impact of native competitors on an alien invasive: Temporal niche shifts to avoid interspecific aggression', *Ecology* 90, 1207–1216. http://dx.doi.org/10.1890/08-0302.1

Hockey, P.A.R., Dean, W.R.J. & Ryan, P.G. (eds.), 2005, *Robert's birds of Southern Africa*, 7th edn., John Voelcker Bird Book Fund, Cape Town.

Holt, E.A. & Miller, S.W., 2011, 'Bio-indicators: Using organisms to measure environmental impacts', *Nature Education Knowledge* 2, 1–10.

Hunter, J.E. & Mazurek, M.J., 2003, 'Characteristics of trees used by nesting and roosting Vaux's Swifts in northwestern California', *Western Birds* 34, 225–229.

Jackson, J.A. & Jackson, B.J.S., 2004, 'Ecological relationships between fungi and woodpecker cavity sites', *Condor* 106(1), 37–49. http://dx.doi.org/10.1650/7483

Jones, L., Jaspars, S., Pavanello, S., Ludi, E., Slater, R., Arnall, A. *et al*., 2010, 'Responding to a changing climate: Exploring how disaster risk reduction, social protection and livelihoods approaches promote features of adaptive capacity', Working Paper 319, Overseas Development Institute, London, viewed 09 November 2014, from http://www.odi.uk/resources/download/4790.pdf

Jost, L., 2006, 'Entropy and diversity', *Oikos* 113, 363–375. http://dx.doi.org/10.1111/j.2006.0030-1299.14714.x

Joy, J.B., 2010, 'Characteristics of nest cavities and nest trees of red-breasted sapsuckers in coastal montane forests', *Journal of Field Ornithology* 71, 525–530. http://dx.doi.org/10.1648/0273-8570-71.3.525

Kalaba, F.K., Quinn, C.H. & Dougill, J.A., 2013, 'The role of forest provisioning ecosystem services in coping with household stresses and shocks in miombo woodlands, Zambia', *Ecosystem Services* 5, 143–148. http://dx.doi.org/10.1016/j.ecoser.2013.07.008

Kappes, J.J. & Davis, J.M., 2008, 'Evidence of positive indirect effects within a community of cavity-nesting vertebrates', *Condor* 110, 441–449. http://dx.doi.org/10.1525/cond.2008.8472

Kemp, A.C., 2000, 'Southern ground hornbill', in K.N. Barnes (ed.), *The Eskom red data book of birds of South Africa, Lesotho and Swaziland*, pp. 117–119, Birdlife South Africa, Johannesburg.

Kemp, A.C., 2001, 'Family Bucerotidae (hornbills)', in J. Del Hoyo, A. Elliott, & J. Sargatal (eds.), *Handbook of birds of the World, Volume 6: Mousebirds to hornbills,* pp. 436–526, Lynx Editions, Barcelona.

Koenig, W.D., 2003, 'European Starlings and their effect on native cavity-nesting birds', *Conservation Biology* 17, 1134–1140. http://dx.doi.org/10.1046/j.1523-1739.2003.02262.x

Krauss, K.W., Keeland, B.D., Allen, J.A., Ewel, K.C. & Johnson, D.J., 2007, 'Effects of season, rainfall and hydrogeomorphic setting on mangrove tree growth in Micronesia', *Biotropica* 39, 161–170. http://dx.doi.org/10.1111/j.1744-7429.2006.00259.x

Laudenslayer, Jr. W.F., 2002, 'Cavity-nesting bird use of snags in eastside pine forests of northeastern California', in W.F. Laudenslayer Jr., P.J. Shea, B.V. Valentine, C.P. Weatherspoon, and T.E. Lisle (eds.), *Proceedings of the Symposium on the Ecology and Management of Dead Wood in Western Forests,* pp. 223–236, Pacific Southwest Forest and Range Experimentation Station, Berkeley, CA.

Lee, D.C. & Irwin, L.L., 2005, 'Assessing risks to spotted owls from forest thinning in fire-adapted forests of the western United States', *Forest Ecology and Management* 211, 191–209. http://dx.doi.org/10.1016/j.foreco.2005.02.001

Lehmkuhl, J.F., Everett, R.L., Schellhaas, R., Ohlson, P., Keenum, D., Riesterer, H. *et al*., 2003, 'Cavities in snags along a wildfire chronosequence in eastern Washington', *Journal of Wildlife Management* 67, 219–228. http://dx.doi.org/10.2307/3803077

Leonard, P., 2005, *Important bird areas in Zambia,* Zambia Ornithological Society, Lusaka.

Leverett, R.T., 2010, 'Measuring tree height by tape and clinometers scenarios', *Bulletin of Eastern Native Tree Society* 5(3&4), 3–12.

Loman, J., 2006, 'Does nest site availability limit the density of hole nesting birds in small woodland patches?', *Web Ecology* 6, 37–43. http://dx.doi.org/10.5194/we-6-37-2006

Magurran, A.E., 2004, *Measuring biological diversity,* Blackwell Scientific Press, Oxford.

Martin, K. & Eadie, M.J., 1999, 'Nest webs: A community-wide approach to the management and conservation of cavity-nesting forest birds', *Forest Ecology and Management* 115, 243–257. http://dx.doi.org/10.1016/S0378-1127(98)00403-4

Mayer, A.L., Donovan, R.P. & Pawlowski, C.W., 2014, 'Information and entropy theory for the sustainability of coupled human and natural systems', *Ecology and Society*, 19, 11, viewed 23 February 2015, from http://dx.doi.org/10.5751/ES-06626-190311

Mcgill, B.J., Etienne, R.S., Gray, J.S., Alonso, D., Anderson, M.J., Benecha, H.K., et al., 2007, 'Species abundance distributions: Moving beyond single prediction theories to integration within an ecological framework', *Ecology Letters* 10, 995–1015. http://dx.doi.org/10.1111/j.1461-0248.2007.01094.x

Meyer, S., 2008, *The barn owl as a control agent for rat populations in semi-urban,* University of Witwatersrand, Johannesburg.

Millington, A.C., Chritchley, R.W., Douglas, T.D. & Ryan, P., 1994, 'Prioritization of indigenous fruit tree species based on farmers evaluation criteria: Some preliminary results from central region, Malawi', in *Proceedings of the Regional Conference on Indigenous Fruit Trees of the Miombo Ecozone of Southern Africa, Mangochi, Malawi*, January 23–27, 1994, ICRAF, Nairobi, pp. 97–105.

Ministry Of Tourism, Environment and Natural Resources (MTENR) and United Nation's Food and Agricultural Organisation (FAO), 2008, *Integrated land use assessment, 2005–2008*. Forestry Department, MTENR, Lusaka and United Nation's FAO, Rome.

Minitab, 2004, *Minitab*, ver. 14, Minitab Inc., Pennsylvania.

Nelson, F., 2008, *Integrative thinking for a changing planet,* Maliasili Initiatives, Arusha.

Newman, K. & Read, C., 2008, 'Birds', in V. Carruthers (ed.), *The wildlife of Southern Africa: The larger illustrated guide to the animals and plants of the region,* pp. 114–163, Random House Struik, Cape Town.

Newton, I., 1998, *Population limitation in birds,* Academic press, Cambridge, MA.

Ober, H.K. & Minogue, P.J., 2007, *Dead wood: Key to enhancing wildlife diversity in forests,* Wildlife Ecology and Conservation, Gainesville, FL.

O'Brien, J.J., Oberbauer, S.F., Clark, D.B. & Clark, D.A., 2008, 'Phenology and stem diameter increment seasonality in a Costa Rican wet tropical forest', *Biotropica* 40, 151–159. http://dx.doi.org/10.1111/j.1744-7429.2007.00354.x

Politi, N. & Hunter, M. Jr., 2009, 'Nest selection by cavity-nesting birds in subtropical montane forests of Andes: Implications for sustainable forest management', *Biotropica* 41(3), 354–360. http://dx.doi.org/10.1111/j.1744-7429.2008.00481.x

Radford, A.N. & Du Plessis, M.A., 2003, 'The importance of rainfall to a cavity-nesting species', *Ibis* 145, 692–694. http://dx.doi.org/10.1046/j.1474-919X.2003.00198.x

Reed, J.M., 2001, 'Woodpeckers and allies', in C. Elphick, J.B. Dunning, Jr. & D. Sibley (eds.), *The Sibley guide to bird life and behaviour,* pp. 380–1437, Christopher Helm, London.

Reid, J.L., Mendenhall, C.D., Rosales, J.A. Zahawi, R.A. & Holl, K.D., 2014, 'Landscape context mediates avian habitat choice in tropical forest restoration', *PLoS One* 9(3), e90573, viewed 3 January 2015, from http://dx.doi.org/10.1371/journal.pone.0090573

Rhodes, B.K., O'Donnell, C.F.J. & Jamieson, I.G., 2009, 'The role of predation, microclimate and cavity abundance in the evolution of New Zealand's tree-cavity nesting avifauna', *Notornis* 56, 190–200.

Richardson, C.T. & Miller, C.K., 1997, 'Recommendations for protecting raptors from human disturbance: A review', *Wildlife Society Bulletin* 25, 634–638.

Roberts, D.L., 2007, 'Effects of tropical forest fragmentation on ecology and conservation of migrant and resident birds in lowland Costa Rica', PhD Thesis, University of Idaho, Moscow.

Ryan, C., Williams, M. & Grace, J., 2010, 'Above and belowground carbon stocks in a miombo woodland landscape of Mozambique', *Biotropica* 43, 423–432. http://dx.doi.org/10.1111/j.1744-7429.2010.00713.x

Saab, V.A., Dudley, J. & Thompson, W.L., 2004, 'Factors influencing occupancy of nest cavities in recently burned forests', *Condor* 106, 20–36. http://dx.doi.org/10.1650/7485

Saab, V.A., Russell, R.E. & Dudley, J.G., 2007, 'Nest densities of cavity-nesting birds in relation to postfire salvage logging and time since wildfire', *Condor* 109, 97–108. http://dx.doi.org/10.1650/0010-5422(2007)109[97:NDOCBI]2.0.CO;2

Schwartz, M.W., Caro, T.M. & Banda-Sakala, T., 2002, 'Assessing the sustainability of harvest of *P. angolensis* in Rukwa region, Tanzania', *Forest Ecology and Management* 170, 259–269. http://dx.doi.org/10.1016/S0378-1127(01)00774-5

Shigo, A.L. & Marx, H.G., 1977, *Compartmentalization of decay in trees*, USDA Forest Service Agriculture Information Bulletin 405, Washington, DC.

Sinclair, A.R.E., Fryxell, J.M. & Caughley, G., 2006, *Wildlife ecology, conservation and management,* 2nd edn., Blackwell Publishing, Malden, MA.

Snyman, S., 2012, 'The role of ecotourism employment in poverty reduction and community perceptions of conservation and tourism in Southern Africa', *Journal of Sustainable Tourism* 20, 395–416. http://dx.doi.org/10.1080/09669582.2012.657202

Stephens, S.L., 2004, 'Fuel loads, snag abundance, and snag recruitment in an unmanaged Jeffrey pine-mixed conifer forest in Northwestern Mexico', *Forest Ecology and Management* 199, 103–113. http://dx.doi.org/10.1016/j.foreco.2004.04.017

Stringer, L., Mngoli, M., Dougill, A., Mkwambisi, D., Dyer, J. & Kalaba, F., 2012, 'Challenges and opportunities for carbon management in Malawi and Zambia', *Carbon Management* 3, 159–173. http://dx.doi.org/10.4155/cmt.12.14

Trzcinski, M.K., Fahrig, L. & Merriam, G., 1999, 'Independent effects of forest cover and fragmentation on the distribution of forest breeding birds', *Ecological Applications* 9, 586–593. http://dx.doi.org/10.1890/1051-0761(1999)009[0586:IEOFCA]2.0.CO;2

Tuomisto, H., 2012, 'An updated consumer's guide to evenness and related indices', *Oikos* 121, 1203–1218. http://dx.doi.org/10.1111/j.1600-0706.2011.19897.x

Turner II, B.L., Lambin, E.F & Reenberg, A., 2007, 'The emergence of land change science for global environmental change and sustainability', *Proceedings of the National Academy of Sciences* 104, 20666–20671. http://dx.doi.org/10.1073/pnas.0704119104

Walker, B. & Salt, D., 2006, *Resilience thinking: Sustaining ecosystems and people in a changing world,* Island Press, Washington, DC.

Wesolowski, T., 1989, 'Nest-sites of hole-nesters in a primaeval temperate forest (Bialowieza National Park, Poland)', *Acta Ornithologica* 25, 321–351.

Wesolowski, T., 2002, 'Anti-predator adaptations in nesting Marsh Tits *Parus palustris*: The role of nest-site security', *Ibis* 144, 593–601. http://dx.doi.org/10.1046/j.1474-919X.2002.00087.x

Wilson, G. & Hockey, P.A.R., 2013, 'Causes of variable reproductive performance by southern ground hornbill *Bucorvus leadbeateri* and implications for management', *Ibis* 155, 476–484. http://dx.doi.org/10.1111/ibi.12042

Wilson, P.R., Karl, B.J., Toft, R.J., Beggs, J.R. & Taylor, R.H., 1998, 'The role of introduced predators and competitors in the decline of Kaka (*Nestor meridionalis*) populations in New Zealand', *Biological Conservation* 83, 175–185. http://dx.doi.org/10.1016/S0006-3207(97)00055-4

Zimba, S.C., 2007, *The fate of forest reserves in Zambia, a case study of Mwekera national forest No. 6,* Mission Press, Ndola.

Zurlini, G., Petrosillo, I., Bruce-Jones, K. & Zaccarelli, N., 2013, 'Highlighting order and disorder in social–ecological landscapes to foster adaptive capacity and sustainability', *Landscape Ecology* 28, 1161–1173. http://dx.doi.org/10.1007/s10980-012-9763-y