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Forest bird diversity and edge effects on three glade types at Mount Meru Game Reserve, Tanzania

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This study examined the edge effects on forest bird diversity in five man-made, five upper natural and 15 lower natural glades in the Mount Meru Game Reserve, Tanzania from September 2005 to November 2005. Bird species composition differed significantly between the three glade types. Mountain Greenbul and Common Bulbul were indicators of forest edge habitat for upper natural and man-made glades, respectively. Bird total abundance, species richness and species diversity differed significantly with distance into the forest for all glade types, and decreased significantly with distance from the edge to the forest interior for man-made glades only. For upper natural glades, bird total abundance correlated positively with plant species richness and percentage basal cover for forbs. Most bird species strongly selected man-made glades over upper and lower natural glades, and strongly avoided upper natural glades. Habitat guilds in man-made glades were associated with foraging. Edge effects for all three glade types influenced bird total abundance and bird species composition, richness and diversity in the forest. In summary, forest glades and their edges have high conservation value for edge bird species. Therefore, clearing of the forest edges for man-made glades should continue in order to maintain these habitats for conservation purposes.

Key words: Edge effects, forest birds, forest edge, forest glades, indicator species.

INTRODUCTION

Habitats should not be viewed in isolation, as adjacent habitats, especially in forests, they harbour unique biological characteristics and associated species (Matlack and Litvaitis, 1999; Wunderle et al., 2005). In general, two habitats found flanking each other enhance species diversity at their shared edge (Sisk and Margules, 1993; Porensky, 2011). Edges specifically benefit bird species with different habitat requirements, including species that require specific habitat types, as well as generalists that occur on both sides of the edge (Harris, 1988; Sisk and Margules, 1993; Murcia, 1995; Turner, 1996; Matlack and Litvaitis, 1999).

Habitat edges influence different bird species in different ways. For some species, abundance may increase near the interface of two habitats (forest and surrounding; for other species, abundance may decrease, and for some, abundance may be relatively unaffected) (Sisk and Margules, 1993). In addition, while edge habitats are important for some bird species, it may also be incompatible with requirements of bird species at the forest interior, and thus, the proliferation of forest edges may threaten the diversity of interior bird species (Kruger and Lawes, 1997; Fink et al., 2006; Shlossberg and King, 2008).

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Abbreviations: MMGR, Mount Meru Game Reserve; **MRPP,** multiple response permutation procedure.

Glades are grass islands found in a forest, and present a clear edge between glade and forest vegetation. Glade edges may affect bird populations in both the glade and the surrounding forest by influencing the biotic and abiotic conditions (Murcia, 1995). Glade edge zones are hotter, drier and windier and absorb more solar radiation (Dunn, 2004). The distances that these edge effects penetrate into the forest vary based on the size of the glade and its edge habitats. In turn, this influences the diversity and abundance of birds found in this zone (Murcia, 1995). The edge microenvironment may have a significant impact on available resources; for example, an edge with large insect populations will attract a higher number of insectivorous bird species (Gutzwiller and Anderson, 1992; Murcia, 1995).

At edges, the change in plant species composition and structure influences bird distributions and densities (Harris, 1988; Terborgh, 1992; Murcia, 1995; Turner, 1996; Matlack and Litvaitis, 1999). Thus, edges become habitat for groups of birds that are dependent on dense, shrubby growth at forest edges (Matlack and Litvaitis, 1999). Not only natural processes, but also human activities are a driver for changes in plant composition and structure at forest edges (Rodewald and Andrew, 2005; Khanaposhtani et al., 2013; Khanaposhtani et al., 2013). In forests, the microclimate is controlled largely by the crown canopy, whereas in forests that have been cleared, the soil is the thermodynamically active surface controlling temperatures (Harris, 1988; Murcia, 1995; Turner, 1996; Zuidema et al., 1996; Baker et al., 2002). The intensity and extent of direct human disturbances on the vegetation, such as clear cutting, recreation and logging will all influence the plant composition at the edge (Mucina and Rutherford, 2006).

The removal of plants at the edge will also induce change in the microhabitat in the adjacent forest (Harper et al., 2005). Air heated after clearing moves into the forest, in turn, lowering humidity, drying leaf litter and glades are also areas where fires can start and the driving effects from the edge helps them to spread into the forest creating drought stress for plants species. The characteristics of forest edges also change through the succession process as forbs, shrubs and saplings emerge resulting in varied habitat types and resources at the edge. In turn, this increases bird abundance and diversity (Murcia, 1995; Matlack and Litvaitis, 1999; Fink et al., 2006).

Finally, the conservation role of small habitat patches, such as glades, depends on edge distance and patch size (Shaw, 1985; Gotmark and Thorell, 2003; Rodewald and Andrew 2005). Smaller glade patches have relatively more edge habitat with a relatively higher population of birds occurring near the edge, than large glade patches. Thus, the level of management required for each glade patch is determined by its size, as larger protected areas necessitate relatively less intensive management efforts (Bothma, 1989; Wunderle et al., 2005). In smaller glades, glade size may contribute to species extinction because mammals can easily access and prey on birds and their eggs (Zannethe and Jenkins, 2000).

At the Mount Meru Game Reserve (MMGR), there are three glade types (man-made, upper and lower natural types) found in different, but adjacent habitats. This provides an ideal area to study the distribution and diversity of birds found at forest edges. The objectives of the study were to: (1) understand the biodiversity value and the conservation role of glade edges by examining the patterns and processes that drive the interaction between birds, glades and the surrounding forest; (2) compare bird abundance, richness and diversity between man-made, and upper and lower natural glade types; and (3) provide management recommendations regarding whether man-made glades should be maintained or allowed to revert back to forests.

In this study, the forest edge is typically an abrupt transition between the forest and surrounding grassland habitat of the glade (Kruger and Lawes, 1997). The forest-glade edge investingated here is mainly caused by clearing the forest trees and shrubs in order to maintain grassland habitat for man-made glades and both types of glades are maintained by grazing ungulates.

MATERIALS AND METHODS

Study site

This study was conducted at MMGR, located at (03° 16' to 03° 20' S; 36° 45' to 36° 53' E) on the eastern slopes of Mount Meru, 350 km south of the Equator, 25 km from Mount Kilimanjaro and 35 km northeast of Arusha town. The reserve is 66 km^2 in size and is mountainous with elevations ranging from 1 473 to 4 566 m above sea level. The habitats of the reserve include evergreen forest, secondary forest, shrub land, wetlands and glades (Mangubuli and Lyamuya, 1988). MMGR has 33 glades: 6 man-made, 6 upper natural and 21 lower natural glades (Figure 1). The research design followed a three-way comparison of the avifauna of 25 glades: five man-made, 15 lower natural and five upper natural glades, located between 1,400 and 2,076 m.a.s.l. Upper natural glades occur on steep slopes above 2 000 m, on shallow soils with a rocky surface substratum that support grassland vegetation. Lower natural and man-made glades occur below 2,000 m.a.s.l. Lower natural glades were formed as a result of movement of mass of water, mud, rocks and lava that cascaded down the eastern side of the mountain meru that supported the growth of grass vegetation (Guest and Leedal, 1953). The man-made glades were created by clearing the forest trees and shrubs of the forest to form a grassland habitat. Both lower and upper natural are maintained by grazing animals and flooding of lower natural glades during the rainy season, while man-made glade are maintained by grazing action of animals and periodic slashing of encroaching shrubs and trees in the forest-glade edge and glade.

Bird surveys

Bird surveys were conducted from September 2005 to November 2005. In each of the 25 glades, three plots, measuring 10 m wide x 30 me long (300 m^2) were laid out into the forest from the forest-glade edge; plots were separated by 20 m buffer zones (Figure 2).

The avifauna of each plot was surveyed by two observers slowly

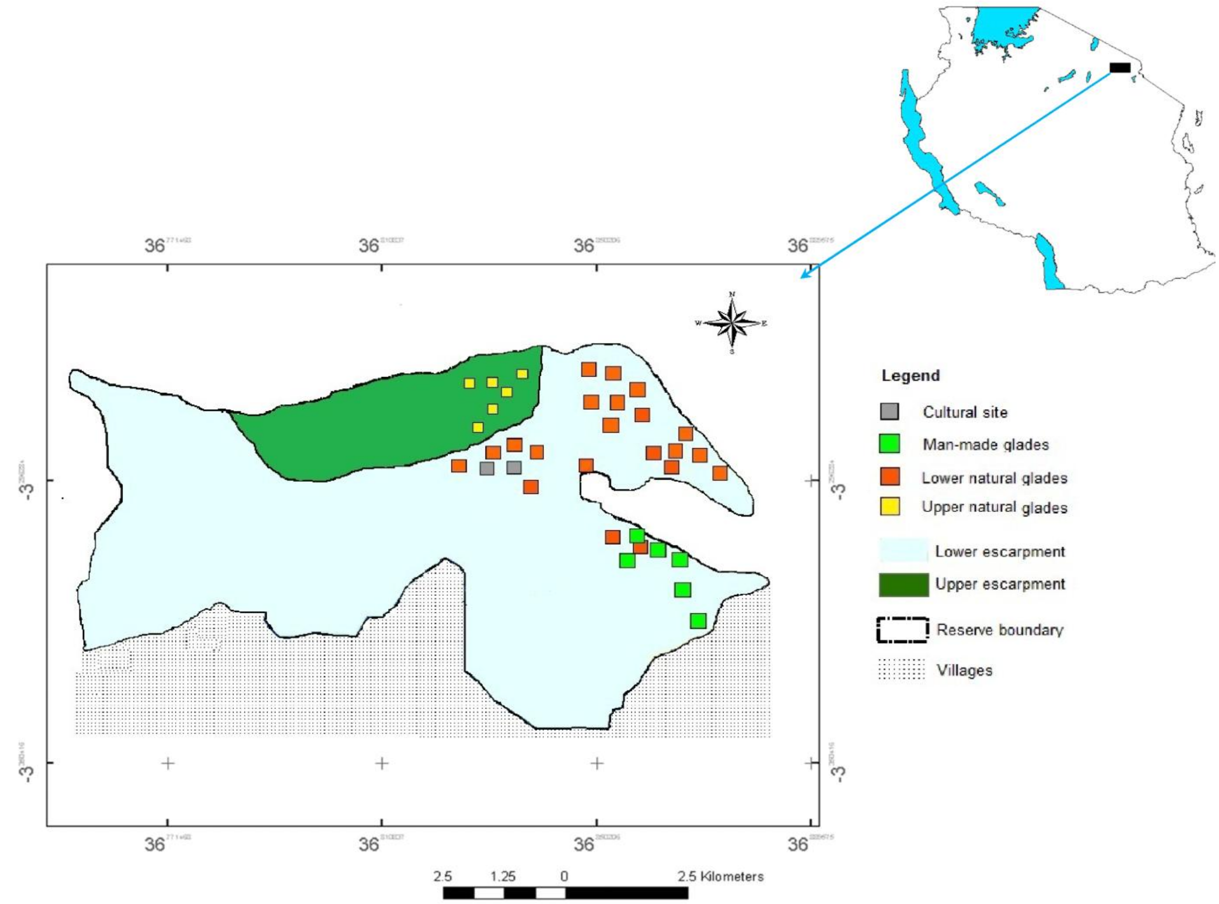

Figure 1. Map of Mount Meru Game Reserve in Tanzania, showing the location of the study area and the distribution of the 33 glades in the reserve.

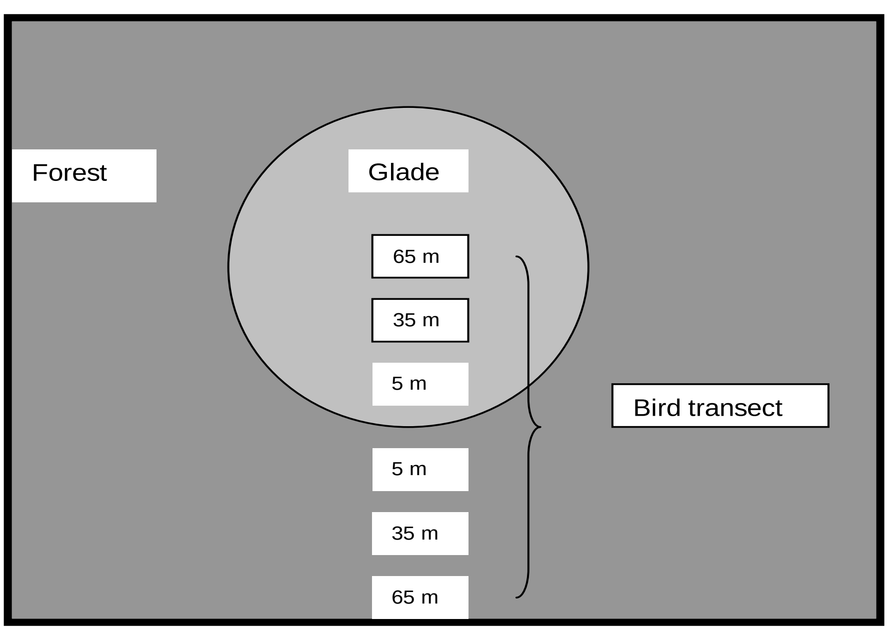

Figure 2. Schematic presentation of plots (10 m wide x 30 m long), 20 m apart at different distances (5 m, 35 m and 65 m) into a forest and glade.

walking along the plot and recording all individuals seen or heard from the forest floor to the canopy (Hutto et al., 1986). The bird surveys were conducted between 06:00 to 10:00 h, and again between from 16:00 to 18:00 h to overlap with the birds' activity periods. Plot surveys were conducted on five different days on each of the six plots for all 25 glades. During each visit to a glade, the sequence for surveying plots was altered randomly to avoid bias. From the five visits, the mean number of birds present for each species in a plot was calculated (Reynolds et al., 1980).

The multiple response permutation procedure (MRPP) was used to determine if bird species composition differed between the three glade types (McCunes and Mefford, 1999). MRPP is a non-parametric procedure that evaluates the uniqueness of a group relative to all other permutations (McCune and Grace, 2002). It generates a test statistic, *T*, with a more negative value indicating greater separation between groups. Also, a P-value is generated to describe the likelihood that the difference is due to chance and a measure of effect size, *A*, which describes within group homogeneity. The Sorensen similarity index analysis was used to compare similarity in species composition between the three glade types (Magurran, 2004; Direrud and Odegar, 2006).

For each glade type, the mean bird total abundance and species richness for the glade plots and the forest plots were calculated. In similar manner, the Shannon-Weiner Diversity Index (H') was used to calculate the species diversity (Zar, 1984). The IUCN Red List data status (endangered) of each species recorded was also noted (Stevenson and Fanshawe, 2002). Bird total abundance, species richness and species diversity were compared within and between the three glade types using ANOVAs.

Regression analysis was used to compare the relationship between the total abundance, percent basal cover and species richness of the four growth forms (forbs, grass, shrubs and dwarf-shrubs) and the three bird indices (total abundance, species richness and species diversity) for all three glade types.

To test for habitat selectivity by birds for the three glade types, Jacob's modification of Ivlev's index was used (Jacobs, 1974). For each species, the index produces a value ranging from -1 to +1, where negative values are indicative of avoidance and positive values are indicative of selection for a particular habitat.

An indicator species analysis was used to detect and describe the value of a bird species as a habitat indicator (McCunes and Mefford, 1999) for the three glades. The method combined information on relative abundance and frequency of each species in a particular habitat to produce an indicator value that ranges from zero to 100 (100 is a perfect indication).

Birds were classified into feeding guilds (e.g. frugivores), nesting guilds (e.g. hole nesters), and associated habitats (e.g. edge species) for the three glade types. Chi-square analysis was used to test for assosication of different user guilds with different glade types and into ecological traits (e.g. diet class inverterbrate), foraging substratum (e.g. aerial foraging), nesting habitat (e.g. artificial objects), natural habitat (e.g. forest) and regional status (e.g. resident) and conservation status (e.g. threatened) (Table 6)

RESULTS

Table 1 provides a list of bird species observed in the forest and glade interiors. Of the 68 bird species recorded, 11 were in all three glade types; 15 in man-made and lower natural glades; nine in lower and upper natural glades; four in man-made and upper natural; 13 in man-made glades only; four in upper natural glades only; and 16 in lower natural only. One threatened species, the Taveta Golden Weaver, occurred in the forest edge of man-made glades. Bird species composition in the three glade types differed significantly (MRPP; T = -7.71, A = 0.32, P < 0.001). The similarity index analysis for bird species showed that the three glade types were similar. Man-made, upper and lower natural glades were similar with a index of C_s = 0.891. Man-made and upper natural glades were more similar (C_s = 0.776) than upper natural and lower natural (C_s = 0.675) glades.

In the forest interior of lower natural, upper natural and man-made, bird total abundance per hecter was 430, 256 and 244, respectively. Bird species richness was highest in the forest of lower natural glades (49 species), followed by man-made (41) and upper natural glades (25). Species diversity (H') was higher in upper natural glades (0.14), than in man-made (0.06) and lower natural glades (0.06). The forest of man-made glades (0.84) harboured the most heterogeneous bird population, followed by lower natural (0.83) and upper natural (0.76) glades. The ANOVA comparison of bird indices is shown in Table 2.

Regression analysis showed a negative relationship between bird total abundance, species richness and species diversity for man-made glades, with R^2 equalling -0.53, -0.64 and -0.59, respectively Table 3. As shown in Figure 3, using an ANOVA comparison, bird total abundance (6.77), species richness (11.27) and diversity (11.38) differed significantly ($F_{(2,12)}$; $p < 0.01$) with distance from the forest edge into the forest interiors for man-made glades. For the glade interiors, only five bird species were recorded and no statistical comparison was performed for the three glade types.

Plant species richness was positively correlated with bird total abundance for upper natural glades only, and not for bird species richness and species diversity (R^2 = 0.31, 0.20, and -0.10 respecitively; $P < 0.05$). There was no relationship found between the total abundance, percent basal cover and canopy cover, species diversity of plants and the three bird diversity indices (total abundance, species richness, species diversity: $P > 0.5$). There was no correlation between plant total abundance, basal cover, canopy cover, species diversity and richness with the three bird indices in man-made ($P > 0.05$) and lower natural glades ($P > 0.05$)

The relationship between the total abundance, percent basal cover and species richness of the four growth forms (forbs, grass, shrubs and dwarf-shrubs) and the three bird indices (total abundance, species richness and species diversity) were examined for all three-glade types. In lower natural glades, only the bird total abundance was positively related to the total abundance of grasses (R^2 = 0.10, $P < 0.05$). In man-made glades, the total abundance of forbs was negatively related to the total bird abundance (R^2 = 0.27, $P < 0.01$) and species richness (R^2 = 0.28, $P < 0.05$). In upper natural glades, the percentage basal cover of forbs was positively related to the total bird abundance (R^2 = 0.28, $P < 0.05$).

As shown in Figure 4, man-made glades were highly selected (selective index >0.50); and upper natural

Table 1. A total of 68 bird species were recorded in the forest interior and five bird species in the glade interior. Scientific names of birds follow Stevenson and Fanshawe (2002). The glade type where each bird species was found is also provided.

Forest interior species	Scientific name	MM[a]	UN[b]	LN[c]
Abbysinica Crimsonwing	*Cryptospiza salvadorii*		v	
African Black-headed Oriole	*Oriolus larvatus*	v	v	v
African Dusky Flycatcher	*Muscicapa adusta*	v	v	v
African Emerald Cuckoo	*Chrysococcyx cupreus*			v
African Green-pigeon	*Treron calva*	v		v
African Grey Hornbill	*Tockus nasutus*	v		
African hill-Babbler	*Pseudoalcippe abyssinica*	v	v	v
African Paradise-flycatcher	*Terpsiphone viridis*	v	v	v
African Wood Owl	*Strix woodfordii*		v	
Amethyst Sunbird	*Chalcomitra amethystine*			v
Bar-tailed Trogon	*Apalodrma vittatum*		v	v
Bar-throated Apalis	*Apalis thoracica*		v	v
Black Cuckoo-shrike	*Campephaga flava*	v		
Black Saw-wing	*Psalidoprocne holomelas*	v		
Black-and-white Mannikin	*Lonchura bicolour*	v		v
Black-backed Puffback	*Dryoscopus cubla*	v	v	v
Black-capped Apalis	*Apalis nigriceps*		v	v
Black-fronted Bush-shrike	*Malaconotus nigrifrons*			v
Black-headed Apalis	*Apalis melanocephala*	v		v
Black-throated Wattle-eye	*Platysteira peltata*	v		v
Blue Mantled Crested Flycatcher	*Trochocercus cynomelas*			v
Brown Woodland Warbler	*Phylloscopus umbrovirens*		v	v
Brown-breasted Barbet	*Lybius melanopterus*	v		
Brown-crown Tchagra	*Tchagra australis*	v		
Cabani's Greenbul	*Phyllastrephus cabanisi*	v	v	v
Cape Robin-chat	*Cossypha caffra*	v		
Chin-spot Batis	*Batis molitor*	v		v
Collared Sunbird	*Hedydipna collaris*	v		v
Common Bulbul	*Pycnonotus barbatus*	v	v	v
Common Buzzard	*Buteo buteo*			v
Common Stonechat	*Saxicola torquata*	v		
Common Waxbill	*Estrilda astrild*	v		
Crowned Hornbill	*Tockus alboterminatus*			v
Evergreen Forest Warbler	*Bradypterus lopezi*		v	v
Forest Batis	*Batis mixta*	v		v
Green- backed Twinsspot	*Mandingoa nitidula*	v		v
Grey- headed Negrofinch	*Nigrita canicapilla*			v
Grey-backed Camaroptera	*Camaroptera brachyuran*	v		v
Hartlaub's Turaco	*Tauraco hartlaubi*	v	v	v
Kenrick's Starling	*Poeoptera kenricki*	v	v	
Lemon Dove	*Aplopelia larvata*		v	v
Lesser Honeyguide	*Indicator minor*			v
Little Greenbul	*Andropadus virens*	v		v
Montane Thrush	*Turdus abyssinicus*		v	
Montane White-eye	*Zosterops poliogaster*		v	v
Mountain Greenbul	*Andropadus nigriceps*		v	v
Mountain Yellow warbler	*Chloropeta similes*	v		
Moustached Green Tinkerbird	*Pogoniulus leucomystax*			v
Olive Sunbird	*Cyanomitra olivacea*			

Table 1. Contd.

Olive Woodpecker	*Dendropicos griseocephalus*		v	v
Red-chested Cuckoo	*Cuculus solitarius*			v
Red-headed Weaver	*Anaplectes rubriceps*			v
Ruppel's Robin-chat	*Cossypha semirufa*	v		v
Scaly Francolin	*Francolinus squamatus*			v
Scaly-throated Honeyguide	*Indicator variegates*			v
Silvery cheeked Hornbill	*Bycanistes brevis*	v		v
Speckled Mousebird	*Colius striatus*	v		
Striped-cheeked Greenbul	*Andropadus milanjensis*	v	v	v
Taveta Golden Weaver	*Ploceus castaneiceps*	v		
Thick-billed Seedeater	*Serinus burtoni*		v	
Trilling Cisticola	*Cisticola woosnami*	v		
Tropical Boubou	*Laniarius aethiopicus*	v		v
Variable Sunbird	*Cinnyris venusta*	v		
White-eared Barbet	*Stactolaema leucotis*	v		v
White-eyed Slaty Flycatcher	*Melaenornis fischeri*	v		v
White-starred Robin	*Pogonocichla stellata*	v	v	v
Yellowbill Coucal	*Ceuthmochares aereus*	v		
Yellow-breasted Apalis	*Apalis flavida*	v	v	
Glade interior species				
African Citril	*Serinus citrinelloides*	v	v	
Black Stork	*Ciconia nigra*			v
Black-and-white Mannikin	*Lonchura bicolour*	v	v	
Egyptian Goose	*Alopochen aegyptiacus*			v
Green Sandpiper	*Tringa ochropus*			v

[a] Man-made glades (MM); [b] upper natural glades (UN); [c] lower natural glades (LN).

Table 2. ANOVA comparison of forest edge and interior bird indices at 5 to 35 m and 65 m into the forest for each glade type.

Forest edge and interior bird indices	Glade type			ANOVA
	Lower natural	Upper natural	Man-made	
Total abundance				
5 m - 35 m	2.0 ± 1.9	3.6 ± 1.7	3.3 ± 2.4	5.40[a]
65 m	1.5 ± 1.5	3.5 ± 2.0	1.1 ± 1.7	3.41[b]
Species richness				
5 m - 35 m	4.4 ± 2.5	6.4 ± 2.5	6.1 ± 3.8	4.32[a]
65 m	3.9 ± 2.7	6.2 ± 1.9	2.2 ± 1.9	3.41[b]
Species diversity				
5 m - 35 m	0.1 ± 0.1	0.2 ± 0.1	0.1 ± 0.1	4.62[a]
65 m	0.2 ± 0.2	0.3 ± 0.1	0.1 ± 0.1	3.13

[a] $p < 0.01$; $F_{(2,76)}$; [b] $p < 0.05$; $F_{(2,22)}$.

glades had the highest habitat avoidance (selectivity index < -0.51), followed by lower natural and man-made.

Eight bird species were indicators species in the upper natural and man-made glades; no bird species was identified as an indicator in the lower natural glades (Table 4). In the upper natural and man-made glades, four bird species were indicators of the forest edge (5 - 35 m) and only one for the interior forest (65 m) (Table 5).

Habitat guilds

In man-made glades, aerial foragers (n=30) and ground and grass foragers (n=27) and mixed substratum

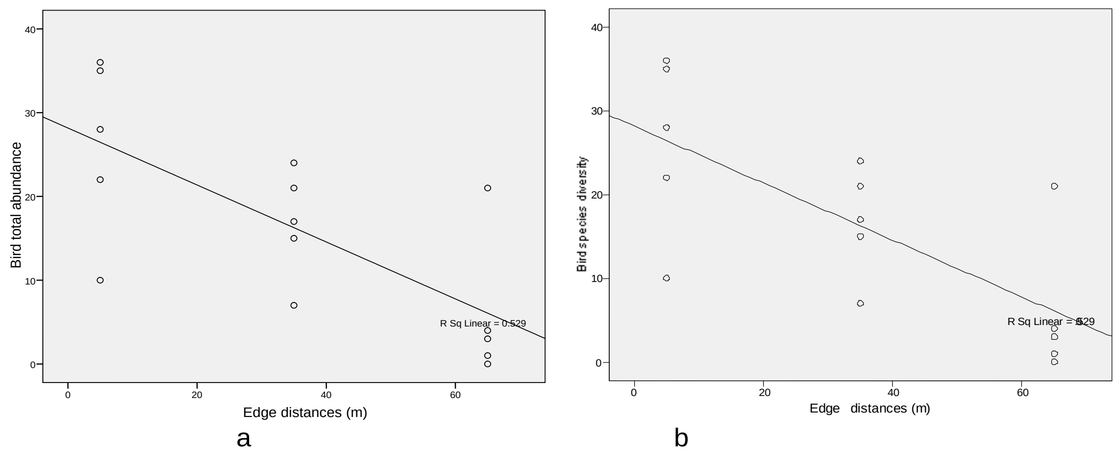

Figure 3a. Relationship between bird total abundance and edge distances for man-made glades and 3b. Relationship between bird species diversity and edge distances for man-made glades

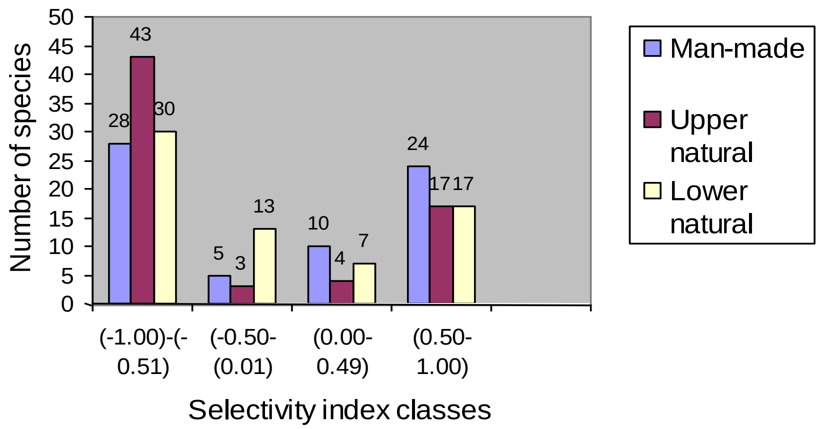

Figure 4. Number of bird species in each habitat-selectivity class, based on Ivlev's index, for man-made, upper and lower natural glades. Habitat selection classes: 0.50 to 1.00 = strong selection for glade type, -0.51 to -1.00 = strong avoidance for a particular glade type.

Table 3. Relationship between bird indices and distances into the forest for the three glade types.

Glade types	Bird indices	Regression (R^2)
	Total abundance	-0.02
Lower natural	Species richness	-0.03
	Species diversity	-0.06
	Total abundance	0.00
Upper natural	Species richness	0.00
	Species diversity	0.06
	Total abundance	-0.53[a]
Man-made	Species richness	-0.64[a]
	Species diversity	-0.59[a]

[a]p < 0.001.

foragers (n=4) were recorded. There was an association between foraging guilds and forest location (5 m, 35 m, and 65 m) from the forest edge, as aerial foragers were found predominantly near the edge and the other two guilds throughout the forest (χ^2_4 = 13.66, p < 0.001). In lower natural glades, most bird species were aerial foragers (n=57), followed by ground and grass (n=29), and mixed substratum foragers (n=5). The species from these foraging guilds could not be associated with their forest location, (χ^2_8 = 1.32, p = 0.86). In upper natural glades, only aerial foragers (n=35) and ground and grass foragers (n=20) were recorded, and the species from these foraging guilds could not be associated with their forest location (χ^2_6 =. 3.40, p = 0.76).

Forest interior bird species were dominant over forest edge species, and woodland and forest edge species for man-made (n = 34, 14 and 13), lower natural (n = 71, 16

Table 4. Indicator birds at 5, 35 and 65 m distance from the edge into the forest of the three glade types.

Glade type	Species name	Distance (m)	Indicator value
Upper natural	Montane White-eye	5	97.2[a]
	Mountain Greenbul	5	80.0[a]
	African Dusky Flycatcher	5	53.3[b]
	Montane White-eye	35	73.8[a]
	Brown Woodland Warbler	35	56.6[c]
	Montane white-eye	65	51.4[b]
Man-made	Collard sunbird	5	81.8[a]
	Black-backed puffback	5	60.0[b]
	Common Bulbul	5	57.1[b]
	Grey-backed Camaroptera	35	50.8[b]
Lower natural	None	None	None

[a]p < 0.001; [b] p<0.05; [c] p<0.01.

Table 5. Indicator birds at the forest edge (5-35m) and interior (65m) of the three glade types.

Glade type	Forest edge species	Indicator value	Forest interior species	Indicator value
Upper natural	Montane White-eye	92.1[a]	Montane White-eye	56.6[b]
	Mountain Greebul	75.8[b]		
	Brown Woodland Warbler	74.3[c]		
	Africa Dusky Flycatcher	53.3[b]		
Man-made	Common Bulbul	67.6[b]		
	Collard Sunbird	67.0[c]	Collard Sunbird	51.4[c]
	Black-throated Wattle-eye	57.9[b]		
	Chinspot Batis	57.6[c]		
Lower natural	None	None	None	None

[a] p<0.001; [b]p<0.01; [c] p<0.05.

and 4) and upper natural glades (n = 45, 6 and 4). There was no association between these habitat-type preferences and forest locations (5, 35 and 65 m) for man-made (χ^2_4 = 0.50, p = 0.90), lower natural (χ^2_4 = 1.60, p = 0.81), and upper natural (χ^2_4 = 4.16, p = 0.39) glades.

The bird species recorded for the three glade types were divided into six nesting habitat guilds: dwarf shrubs, shrubs multi-stemmed (< 5 m in height), shrub single stem, artificial objects, tree and shrubs. Tree nesters were dominant for lower natural glades (54 of 91 species), for upper natural glades (29 of 55 species) and for man-made glades (31 of 61 species). However, the species that used each nesting habitat could not be associated with the forest locations (5, 35 and 65 m) for lower natural glades (χ^2_8 = 2.48, p = 0.96), upper natural glades (χ^2_4 = 3.46, p = 0.90) and man-made glades (χ^2_6 = 3.65, p = 0.72).

Bird species recorded for the three glade types were divided into four diet user guilds. Insectivorous bird species were dominant over fruigivores, insectivorous and granivous for man-made glades (n = 29; 21, 7 and 4, respectively), lower natural glades (n = 52; 24, 7, and 8, respectively) and upper natural glades (n = 32; 15, 2 and 6, respectively). There was no association between these diet guilds and forest locations (5 m, 35 m and 65 m) for man-made (χ^2_4 = 2.83, p = 0.86), lower natural (χ^2_4 = 2.94, p = 0.94) and upper natural (χ^2_4 = 3.39, p = 0.76)

Table 6. Ecological traits of birds recorded in the three glades (man-made, lower and upper natural glades).

Species	Natural habitat	Diet class	Foraging substratum	Nest	Distribution	Status
Abbysinia Crimsonwing	F	S	GG	SSS	R	Nt
African Black- headed Oriole	F	I	AF	H	R	Nt
African Citril	W/F/E	S	AF	SSS	R	Nt
African Dusky Flycatcher	FE	I	AF	T	R	Nt
African Emerald Cuckoo	F	I	AF	AO	R	Nt
African Green-pigeon	F/W	F	AF	T	R	Nt
African Hill-babbler	F	I	GG	SMS	R	Nt
African Paradise-flycatcher	F/W	I	AF	SSS	R	Nt
African Wood Owl	F	I	AF	H	R	Nt
Amethyst Sunbird	F/E/W	N	AF	SSS	R	Nt
Bar-tailed Trogon	F/S/W	I	AF	H	R	Nt
Bar-throated Apalis	F/S/W	I	AF	SMS	R	Nt
Black backed Puffback	FE	I	AF	T	R	Nt
Black Cuckoo-shrike	F	I	AF	T	R	Nt
Black- fronted Bush Shrike	F	I	AF	T	R	Nt
Black Saw- wing	F/W	I	AF	RB	R	Nt
Black Stork	M	I/G	W	T	R	Nt
Black-and- white Mannikin	FE	S	GG	SMS	R	Nt
Black-capped Apalis	F	I	AF	SMS	R	Nt
Black-headed Apalis	F	I	AF	T	R	Nt
Black-throated Wattle-eye	F	I	AF	T	R	Nt
Blue Mantled Creasted Flycatcher	F	I	AF	SSS	R	Nt
Brown Woodland Warbler	F	I	GG	T	R	Nt
Brown-breasted Barbet	F/E	F	AF	H	R	Nt
Brown-crown Tchagra	F/E/W	I	GG	SMS	R	Nt
Cabani's Greenbul	F	I	GG	T	R	Nt
Cape Robin-chat	W	I	GG	SMS	R	Nt
Chin-spot Batis	FE	I	AF	T	R	Nt
Collard Sunbird	F	N	MF	SSS	R	Nt
Common Bulbul	FE/W	F	GG	T	R	Nt
Common Buzzard	F/W	SV	GG	T	R	Nt
Common Stonechat	W/F/E	F/I	GG	DS	R	Nt
Common Waxbill	W/F/E	S	GG	DS	R	Nt
Crowned Hornbill	F	I/SV	AF	H	R	Nt
Egyptian Goose	M	I/G	W	T	R	Nt
Evergreen Forest Warbler	F	I	GG	DS	R	Nt
Forest Batis	F	I	AF	T	R	Nt
Green Sandpiper	M	I	W	RB	R	Nt
Green-backed Twinsspot	FE	S	GG	SMS	R	Nt
Grey-backed Camaroptera	FE	I	GG	SSS	R	Nt

Table 6. Condt.

Grey-headed Negrofinch	F	S	MF	T	R	Nt
Hartlaub's Turaco	F	F	AF	T	R	Nt
Kenrick's Starling	F	F/I	AF	H	R	Nt
Lemon Dove	F	S	GG	T	R	Nt
Lesser Honeyguide	F/E	I	AF	H	R	Nt
Little Greenbul	F	F	GG	T	R	Nt
Montane Thrush	F	I	GG	SSS	R	Nt
Montane White-eye	F	F	AF	T	R	Nt
Mountain Greenbul	F	F	AF	T	R	Nt
Mountain Yellow Warbler	F	F	AF	DS	R	Nt
Moustached Green Tinkerbird	F	F	AF	T	R	Nt
Olive Sunbird	F	N	AF	SSS	R	Nt
Olive Woodpecker	F	I	AF	H	R	Nt
Red-chested Cuckoo	F/E	I	AF	AO	R	Nt
Red-headed Weaver	F	I	AF	SSS	R	Nt
Ruppel's Robin-chat	FE	I	GG	SMS	R	Nt
Scaly Francolin	F	I	GG	G	R	Nt
Scaly-throated Honeyguide	F	I	AF	H	R	Nt
Silvery cheeked Hornbill	F	F/SV	AF	H	R	Nt
Speckled Mousebird	S/FE	F/S	AF	SMS	R	Nt
Striped-cheeked Greenbul	F	F	AF	T	R	Nt
Taveta Golden Weaver	W	S	AF	SSS	R	T
Thick-billed Seedeater	F/E	S	AF	S	R	Nt
Trilling Cisticola	W/S	I	GG	DS	R	Nt
Tropical Boubou	FE	I	GG	SMS	R	Nt
Variable Sunbird	W	N	AF	SSS	R	Nt
White-eared Barbet	F/W	F	AF	H	R	Nt
White-eyed Slaty Flycatcher	F/E	F	AF	T	R	Nt
White-starred Robin	F	I	GG	G	R	Nt
Yellowbill Coucal	F/E	I	AF	SMS	R	Nt
Yellow-breasted Apalis	F/E/W	I	AF	SMS	R	Nt

Diet class: I= Invertebrates, SV = small vertebrates, S = seed, F = fruits, N = nectar. Foraging substratum: AF = Aerial foraging; tree or shrub (medium to high substratum, GG = Ground and grass (low substratum), MF = Mixed foraging substratum (Air, tree, ground), Artificial object (AO), near above water in marshes, reeds, riverbank (NAW). Nesting habitat: DS = dwarf shrubs, SMS = shrub multi-stemmed (< 5 m), SSS = shrub single stem, AO = artificial objects, T = tree, S = shrubs, RB = river back, natural habitat: F = forest, FE = forest edge, E = edge habitat, W = Woodland, M = marshes. Regional status: resident (R); migrant (M); conservation status: Non-threatened or threatened.

glades.

DISCUSSION

Birds in forests- Upper natural glades

For upper natural glades, bird species diversity was highest (including unique bird species), but the mean total abundance (birds per hectare) was lower and species richness was lowest as compared to lower natural glades. Seventeen species strongly selected upper natural glades (selective index > 0.05) vs. 43 species that strongly avoided upper natural glades (selective index-0.05). As compared to lower natural glades, for each bird that selected upper natural glades, two-and-a-half birds avoided the upper natural glades, that is, the ratio of avoidance was higher. The high avoidance of upper natural glades could be due to its location at a high altitude with relatively low temperatures that affected food availability (Haila, 1999; Hansen and Rotella, 1999). Hence, the upper natural glades were the least preferred.

The insectivorous (n = 32 species) were dominant over frugivorous (n = 15), granivorous (n = 6) and nectivorous (n = 2) in the forest edge of upper natural glades. The dominance of insectivorous over frugivorous was supported by their numbers, including four indicator birds feeding on insects, versus two feeding on fruits. Montane White-eye and Mountain Greenbull feeds on fruits and insects while, African Dusky Flycatcher and Brown Woodland Warbler feed on insects (Stevenson and Fanshawe, 2002; Sinclair and Ryan, 2003; Hockey at al., 2005; Del Hoyo et al., 2005; Del Hoyo et al., 2008). Edges in upper natural glades are exposed to more sunlight and rain, and therefore, more food is available for the birds to eat, nest, roost and perch.

In the forest edge of upper natural glades, the aerial foragers (n = 35) were dominant over ground and grass foragers (n = 20). The four aerial forager indicator birds observed were: Montane White-eye, African Dusky Flycatcher, Brown Woodland Warbler and Mountain Greenbull. These species, all habituate highland forests and are commonly found at forest edges (Stevenson and Fanshawe, 2002; Sinclair and Ryan, 2003; Chittenden 2007). This may be because the upper natural glades had the highest total plant stems per hectare, coupled with largest diameter of trees, which could be used as vantage points by aerial foragers when searching for food.

In the forest interior of upper natural glades, true forest species (n = 45) were also dominant over forest edge (n = 6), and woodland and forest edge species (n = 4). One reason for this could be that the forest interior species experienced less physical effects of microclimatic changes as compared to edge species. Another possibility is that there were direct biological effects on changes in species composition, abundance and distribution due to an edge effect (Gutzwiller and Anderson, 1998; Murcia, 1995). Also, the interior forest habitats harboured birds associated with forest interior habitats, such as the indicator bird, Montane White-eye that feeds on insects and fruit (Hockey et al., 2005; Del Hoyo et al., 2008). This species was the only indicator bird found in both forest edge and forest interior habitats, and thus, has a wide habitat tolerance.

In upper natural glades, bird total abundance, species richness and diversity was positively correlated with edge distance into the forest (R^2 = 0.00). This suggests that microclimatic changes were homogeneous along the forest edge and interior of upper natural glades leading to uniform species composition, abundance and distribution (Harper et al., 2005).

Birds in forest- Lower natural glades

For the lower natural glades, bird species richness and mean total abundance per hectare was almost double of that of upper natural glades. Although they had the highest number of unique bird species, the bird species diversity was lower than that of upper natural glades. The species composition of the bird population was more heterogeneous, indicating that different bird species used lower natural glades than upper natural glades. This was because of warmer temperature due to the location of lower natural glades at a lower altitude. This may have been influenced by climate and topography exerting a strong influence on bird habitat selection due to the availability of food (Haila, 1999; Hansen and Rotella, 1999).

Seventeen species strongly selected lower natural glades (selective index > 0.05) and 30 species strongly avoided lower natural glades (selective index - 0.05). Thus, for each species that selected lower natural glades, 1.8 species avoided lower natural glades, a lower ratio (less avoidance) as compared to upper natural glades. As noted above, the higher selection for lower natural glades was likely due to the location at a lower altitude. This finding is consistence with studies by Cooperider et al. (1986), Sinclair et al. (2006) and Kissling et al. (2007) who reported increased food production at lower altitude with warmer temperatures.

In lower natural glades, aerial foragers (n = 57), were dominant over ground and grass (n = 29) and mixed substratum (n = 5) foragers. Lower natural glades had higher number of aerial foragers than upper natural glades, with a ratio of 1:1.6, a higher ratio than upper natural glades, as there were more aerial foragers in lower natural glades than in upper natural glades. This showed that aerial foragers preferred lower natural glades as compared to upper natural glades, and this finding may be attributed to increased food production at lower elevation and warmer temperatures (Haila, 1999; Hansen and Rotella, 1999).

Furthermore, at the edge of lower natural glades, insectivorous (n = 52) species were dominant over frugivorous (n = 24) species, nectivorous (n = 7) species and granivorous (n = 8) species. Lower natural glades had higher number of insectivorous, almost double of upper natural glades with a ratio of 1:1.8 species, a higher ratio as compared to upper natural glades. Insectivores are predominantly aerial foragers and preferred forest edge habitats for easy detection of food (e.g. African Paradise-flycatcher) an aerial forager and insect eater (Hockey et al., 2005; Del Hoyo et al., 2006). Other studies have found that edges enable birds to have greater visibility as a predator avoidance strategy (Paton, 1993; Murcia, 1995; Baker et al., 2002). Insects are also easier to catch in the open edges as birds easily see them.

In lower natural glades, abundant birds were predominant forest species (n = 71) that were dominant over forest edge species (n = 16) and woodland and forest edge species (n = 4), and were predominant tree nesters. In lower natural glades, forest bird species were higher than upper natural glades with a ratio of 1:1.6 species, a higher ratio as compared to upper natural glades. Edges are typically hotter, drier, windier and sunnier than the forest interior (Harper et al., 2005). These conditions might have caused the birds to be less abundant at the edges as compared to the forest interiors that experience less microclimatic changes. The changes in microclimate along the forest edge and interior caused the observed variations in bird's number in the forest and forest edge habitats (Murcia, 1995).

In the lower natural glades, bird total abundance, species richness and diversity was negatively correlated with edge distance into the forest (R^2 = -0.00). High bird total abundance, species richness and diversity at the edge were the effects of microclimatic changes. The changes affected species composition, abundance and distribution along the forest edge and interior of lower natural glades due to altered habitat quality (Harper et al., 2005).

Birds in forest- man-made glades

In man-made glades, bird species richness and mean bird total abundance (per hectare) was lower than in neighbouring lower natural glades. The management practice of clearing two meters of trees and shrubs at the forest edge of man-made glades caused inherent unstable edge habitats. It is likely that this caused the lower number of bird total abundance and species richness in man-made glades as compared to lower natural glades.

Twenty-four species strongly selected man-made glades (selective index > 0.05) versus 28 species that strongly avoided lower natural glades (selective index- 0.05). Thus, for each bird that selected man-made glades, 1.2 birds avoided man-made glades and this ratio was the lowest as compared to lower natural glades. The high selection of man-made glades was due to warmer temperature at the lower altitude which supports high production of food (Cooperider et al., 1986; Sinclair et al., 2006; Kissling et al., 2007). Also, the management action of clearing trees and shrubs at the forest edge of man-made glades leads to dense vegetation of forbs and shrubs at the edge and these attracted birds to forage, roost and nest at the edge of man-made glades (Harper et al., 2005). This disturbance provides a good environment for bird species associated with disturbed habitats (Spies and Turner, 1999; Khanaposhtani et al., 2013).

In man-made glades, aerial foragers (n = 30) were dominant over ground and grass (n = 27), and mixed substratum foragers (n = 4). The dominance of aerial foragers over ground and grass foragers was because of their tendency to prefer edge habitats. This was supported by the presence of three edge indicator aerial foragers, the Collard Sunbird, Black-throated Wattle-eye and Chin-spot Batis, that forage by hawking, gleaning and hovering on insects to be caught in the air or inside the open canopy of evergreen forest edge (Hockey et al., 2005; Del Hoyo et al., 2005, 2008).

Furthermore, the insectivorous (n = 29) and frugivorous (n = 21) species were dominant over nectivorous (n = 7) and granivorous (n = 4). The dominance of insectivorous over frugivorous was because of their tendency to prefer edge habitats. This result was supported by presence of four edge indicator birds that feed on insects and two species that feed on fruits and nectar. The Common Bulbul and Collard Sunbird feed on fruits, insects, nectar, flowers and seeds, while the Black-throated Wattle-eye and Chin-spot Batis feeds on insects only (Hockey et al., 2005; Del Hoyo et al., 2005, 2008). Food types consumed by these species link them to the forest edge habitat, as edges in man-made glades are suitable for insectivorous and frugivorous birds.

In addition, forest species (n = 34) were dominant over forest edge species (n = 14) and woodland and forest edge species (n = 13) of man-made glades. There was an association found between foraging guilds and forest location, as aerial foragers were found predominantly near the edge. One indicator bird (Collard Sunbird) was found in the the forest interior. The Collard Sunbird is associated with forest interiors, versus four species (Common Bulbul, Collard Sunbird, Black-throated Wattle-eye and Chin-spot Batis) that are associated with forest edges (Hockey et al., 2005; Del Hoyo et al., 2005, 2008); these four species were predominately tree nesters. The Collard Sunbird was the only bird species found in both edge and interior forest habitat and hence, able to adapt to microclimate changes that occur between edge and interior forest habitat (Spies and Turner, 1999).

In the man-made glades, there was a sharp decrease in bird total abundance, species richness and diversity moving from the forest edge into the forest interior. The disturbance of clearing the forest edge for management purposes may have enhanced structural changes by increasing the density of different plant growth forms that occupy a site following the disturbance (Spies and Turner, 1999; Haila, 1999). Disturbance increases bird species and plant species diversity due to the creation of a more heterogeneous habitat environment (Von Amhild, 2005). This in turn, attracted more birds to the edge than to the forest interior such as, the Common Bulbul, Collard Sunbird and Black-throated Wattle-eye.

This study showed that the bird species composition (as analyzed by the MRPP) in the forest of man-made, upper and lower natural glades differed significantly between habitats, as well as the bird species composition at the forest edges. It further documented apparent positive edge effects as the forest of man-made glades had high bird total abundance, species richness and diversity at 5 and 35 m from the forest edge. These findings are similar to that of Chasko (1982) on forest edge bird diversity which is highest at the edge and McIntyre (1995), Lemait et al. (2012) and Khamoposhtani et al. (2013) that habitat structure and composition due to disturbance are important in shapping bird assembleges in Georgia, U.S.A Quèbec, Canada and Karaji Iran, respectively.

Most of the birds were on the forest edge, which are important habitats in continuous forest of MMGR. The edges have high conservation value for foraging, nesting and roosting by bird species associated with forest edges following the disturbance (Spies and Turner, 1999; Haila, 1999), for example in MMGR, by the Common Bulbul, Collard Sunbird and Black-throated Wattle-eye. The conservation value of the man-made glades in the continuous forest of MMGR is increased further by the presence of the threatened Taveta Golden Weaver, which was recorded only in the forest edge of man-made glades, and not in the forest edges of natural glades. The presence of Taveta Golden Weaver and other forest edge bird species may be due to the cultivation of a favoured habitat, a shrub dominated-one produced by the clearing of vegetation in the forest edge of man-made glades. Therefore, the addition of more man-made glades and the clearing of the forest edges of man-made glades should continue in order to maintain these habitats due to their high conservation values.

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