Effects of fire on bird diversity and abundance in an East African savanna

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Abstract

Fire is an important determinant of many aspects of savanna ecosystem structure and function. However, relatively little is known about the effects of fire on faunal biodiversity in savannas. We conducted a short-term study to examine the effects of a replicated experimental burn on bird diversity and abundance in savanna habitat of central Kenya. Twenty-two months after the burn, Shannon diversity of birds was 32% higher on plots that had been burned compared with paired control plots. We observed no significant effects of burning on total bird abundance or species richness. Several families of birds were found only on plots that had been burned; one species, the rattling cisticola (*Cisticola chiniana*), was found only on unburned plots. Shrub canopy area was negatively correlated with bird diversity on each plot, and highly correlated with grass height and the abundance of orthopterans. Our results suggest that the highest landscape-level bird diversity might be obtained through a mosaic of burned and unburned patches. This is also most likely to approximate the historical state of bird diversity in this habitat, because patchy fires have been an important natural disturbance in tropical ecosystems for millennia.

Key words: Africa, bird, diversity, fire, savanna

Résumé

Le feu s'avère un déterminant important de plusieurs aspects de la structure et fonctionnement de l'écosystème de savane. Cependant, relativement peu est connu sur les effets du feu sur la biodiversité des faunes dans les savanes. Nous avons mené une ètude à court terme afin d'examiner les effets d'un incendie répliqué expérimental sur la diversité et l'abondance d'oiseaux dans un habitat de savane au Kenya. Vingt-deux mois après l'incendie la diversité selon l'index de Shannon fut 32% plus grande dans les zones brûlées que dans les zones de contrôle appariées. Nous n'avons constaté aucun effet significatif de l'incendie sur l'abondance des oiseaux ni sur la profusion d'espèces. Plusieurs espèces d'oiseaux furent trouvées seulement dans les zones brûlées ; alors qu'une espèce – la cisticole chiniana (*Cisticola chiniana*), fut trouvée seulement dans les zones non-brûlées. L'étendue du feuillage corrèlait de façon négative avec la diversité d'oiseaux dans chaque zone, et corrélait fortement avec l'hauteur de l'herbe et l'abondance d'orthopterans. Nos résultats impliquent que la plus grande diversité d'oiseaux au niveau du paysage est obtenue à travers une mosaïque de zones brûlées et non-brûlées. Il est probable que ceci soit une approximation de l'état historique de la diversité d'oiseaux dans cet habitat, parce que les incendies irréguliers ont été une perturbation naturelle importante dans les écosystèmes tropicaux depuis des millénaires.

Introduction

Fire plays a critical role in structuring tropical savanna ecosystems (Bourlière, 1982). For example, fire can inhibit tree recruitment by killing young trees (Norton-Griths, 1979) and is therefore one important determinant of the tree : grass ratio in savannas (van Langevelde *et al.*, 2003). Recent studies suggest that increases in grazing result in decreased fuel load for fires, which can lead to decreased fire frequency and consequent shrub encroachment (Roques, O'Connor & Watkinson, 2001; van Langevelde *et al.*, 2003).

Despite the importance of fire in savanna ecosystems, most fire studies have focused on the effects of fire on vegetation; less attention has been paid to the effects of fire on faunal diversity (e.g. Parr & Chown, 2003). Some

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savanna animals are sensitive to disturbance by fire and may be ecological indicators of fire history (Orgeas & Andersen, 2001; Parr, Bond & Robertson, 2002). In southern Africa, most studies of the effects of fire on faunal diversity have focused on responses by single species of mammals or birds (Parr & Chown, 2003), and only a single study reported by Parr & Chown (2003) in their survey of southern African fire research reported the effects of fire on bird diversity. Further, most studies of fire effects on savannas have been carried out opportunistically in response to natural fires; few studies have used experimental burns, which can be carefully controlled and replicated (Parr & Chown, 2003). To our knowledge, no studies have considered the impacts of fire on the diversity and abundance of birds in east African savannas.

We conducted a short-term, preliminary investigation of the effects of fire on bird abundance and diversity in a tropical savanna of central Kenya, taking advantage of a replicated experimental burn which took place 2 years prior to our study. We also considered the impacts of the burn on vegetation and insect abundance and diversity, which we considered potential drivers of changes in avian diversity.

Methods

This study was conducted during January 2003 at the Mpala Research Centre, Laikipia District, Kenya. Mpala is located approximately 50 km north of the equator, northwest of Mt Kenya at an altitude of 1800 m. Average monthly high temperatures range from 25 to 33°C with lows from 12 to 17°C (Okello & Young, 2000). Rainfall is strongly seasonal and averages 500–600 mm per year. Typically, January begins the dry season, a period of little or no rain which lasts until March, and the heaviest rainfall in March–June. A second wet season occurs in October–November. Our observation period was preceded by relatively heavy rainfall, with 177 mm of rain falling in November and December 2002, compared with a long-term average of 122 mm in those months.

The field site was situated in black cotton soils characterized as *Acacia* wooded grassland (Young *et al.*, 1998). *Acacia drepanolobium* Harms ex Sjostedt is the dominant tree in this ecosystem, although other tree species (*A. mellifera* Benth., *A. brevispica* Harms, *Balanites aegyptica* Wall.) and woody vegetation (*Cadaba farinosa* Forssk., *Rhus natalensis* Bernh. ex Krauss, *Lycium europaeum* L.) are present as well (Young *et al.*, 1998). Five grasses (*Themeda triandra* Forssk., *Pennisetum mezianum* Leeke, *P. stramineum* Peter, *Brachiaria lachnantha* Stapf, *Lintonia nutans* Stapf) and four forbs (*Aerva lanata* Juss. ex Schult., *Rhinacanthus ndorensis* Schweinf. & Mildbr., *Dyschoriste radicans* Kuntze, and *Commelina* spp. Plum. ex L.) dominate the understorey (Young *et al.*, 1998).

Large herbivores present at the study site include elephants (*Loxodonta africana* Blumenbach), giraffes (*Giraffa camelopardalis* L.), elands (*Taurotragus oryx* Pallas), Burchell's zebras (*Equus burchelli* Gray), Grevy's zebra (*E. grevyi* Oustalet), Grant's gazelles (*Gazella granti* Brooke), Jackson's hartebeests (*Alcelaphus buselaphus* Pallas), steinbucks (*Raphicerus campestris* Thunberg), cape buffalos (*Syncerus caffer* Sparrman), domestic cattle and sheep. Carnivores include lions (*Panthera leo* L.), leopards (*P. pardus* L.), cheetahs (*Acinonyx jubatus* Schreber), spotted hyenas (*Crocuta crocuta*), striped hyenas (*Hyaena hyaena* L.), black-backed jackals (*Canis mesomelas* Schreber), white-tailed mongooses (*Herpestes ichneumon* L.) and servals (*Felis serval* Schreber).

The avian fauna in the study area comprises approximately 75 species, of which nine are seasonal migrants. The most conspicuous species include rattling cisticolas (*Cisticola chiniana* Smith), superb starlings (*Lamprotornis superbus* Ruppell), ring-necked doves (*Streptopelia capicola somalica* Sundevall), taita fiscals (*Lanius dorsalis* Cabanis), Speke's weavers (*Ploceus spekei* Heuglin), yellow-bellied eremomelas (*Eremomela icteropygialis abdominalis* Lafresnaye) and pied wheatears (*Oenanthe pleschanka* Lepuchin), which are seasonal migrants. The two most abundant raptor species are black-shouldered kites (*Elanus c. caeruleus* Desfontaines) and common kestrels (*Falco tinnunculus* L.), which are seasonal migrants.

This study was conducted on four approximately 1-ha (see below) plots burned in March 2001 and four unburned control plots. Each of the burn plots was burned completely, removing all grasses and understorey, although most (>94%) *A. drepanolobium* trees survived the burn (T.M. Palmer, pers. comm.). Habitat surrounding the burn plots was not burned; the size of the experimental burns was comparable with that of small-scale naturally occurring fires in this area. Approximately 2 years after the burns, when we conducted our observations, grasses and shrubs were beginning to return but the trees remained mostly devoid of foliage. Burn plots were paired with adjacent control plots with similar overstorey vegetation composition. Two pairs of burn and control plots were 100 × 100 m, one pair was 88 × 100 m, and the fourth pair was 112 × 100 m. The minimum distance between plots was 100 m. In each plot, we demarcated a 10-m wide edge zone inside the outermost edge.

Bird observations

All observations were made from the centre of each plot. In a 3-week period, we observed each plot a total of five times for 30 min during each observation, for a total of 150 min of observation on each plot. Half of the observations within each plot took place in early morning (07.45–09.30 hours) and half in late afternoon (15.45–17.30 hours), when temperatures were relatively cool and bird activity was highest. We observed plots in random order. However, to prevent overlap in bird sightings, we did not observe neighbouring plots in consecutive observation periods. For each sighting, we recorded the species, the perching location within the plot (e.g. tree species or ground), and the activity of the bird observed. Birds were recorded only if they perched, or were actively foraging in the plot. Birds that landed in the edge zone were noted. Birds flying overhead but not landing in the plot were not recorded. Aerial feeders (swallows and swifts) were not recorded due to the difficulty in distinguishing foraging flights from local movements. Birds were subsequently categorized for diet type and foraging guild using information from a combination of field observations and publications (Mackworth-Praed & Grant, 1952, 1955; Feare, 1984; Zimmerman, Turner & Pearson, 1996).

Insect survey

At the midpoint of our bird observations, we used a sweep net (38-cm diameter) to survey insects, sweeping approximately 100 times along a 100-m transect through the centre of each plot. Insects were collected from the net and frozen. We then sorted the insects into the orders, Orthoptera (grasshoppers, crickets), Coleoptera (beetles), and Diptera (flies), which account for the majority of the insects present. Insects from other orders were pooled and included in the total insect biomass. After drying outside for approximately 24 h, the insects were weighed and counted. We determined the biomass and number of insects in each order, then combined all the insects to find the total biomass for each plot sample.

Vegetation survey

We determined the average grass height on each plot by dropping a square of cardboard (0.5 × 0.5 m) every 5 m along a 100-m transect through the centre of the plot. At each point along the transect, we measured the height of the cardboard at each corner and then averaged these values to get an average grass height for that point. We then averaged the heights for each point to obtain an average for each plot.

We measured the canopy area of all trees and woody vegetation other than *A. drepanolobium*, including *A. mellifera*, *A. brevispica*, *B. aegyptiaca*, *C. farinosa*, *R. natalensis*, *L. europaeum* and *Boscia angustifolia*. *Acacia drepanolobium* were not sampled because birds were only rarely seen in or near canopies of this species. We recorded the height, width and length of the canopy to the nearest 0.01 m, and then calculated the canopy area of each individual using the formula for the area of a circle.

Analyses

We excluded from analyses any birds that were observed only in the edge zones surrounding the plots. We tested the effects of burn treatment on bird abundance, species richness, and Shannon diversity (base 10) using paired t-tests. These dependent variables were normally distributed (Systat 10.0; SPSS Inc., 2000) and so did not require transformation. To determine the impacts of burning on the abundance and diversity of different types of birds, we performed multivariate analyses of variance (Statistica; StatSoft, Inc., 2001) with birds grouped by (i) foraging guilds (hawkers, gleaners, ground-foragers, and bark-foragers), and (ii) dietary preferences (insectivores, granivores).

To determine the effects of burning on habitat variables (shrub canopy area, tree canopy area, grass height, and the abundances of Coleoptera, Diptera and Orthoptera), we conducted paired *t*-tests. We examined correlations among habitat variables using a Pearson correlation matrix. To assess whether any habitat variables were significant predictors of either bird diversity or abundance, we conducted forward stepwise multiple regressions with $\alpha = 0.15$ for inclusion in the models.

Results

In this short-term study, we observed a total of 245 birds of 21 species. Plots that had been burned had 32% greater Shannon diversity than did control plots (burned average ± SE: $H' = 0.92 \pm 0.02$; control: $H' = 0.70 \pm 0.08$; $P < 0.05$). There was also greater diversity in burn than control plots when we excluded the most abundant species, the rattling cisticola (*C. chiniana*), from our analyses ($P < 0.05$). There were no significant differences in either total bird abundance (burned: 31.5 ± 6.4; control: 23.4 ± 5.9; $P = 0.23$) or total species richness (burn: 9.75 ± 0.5; control: 6.8 ± 1.5; $P = 0.17$) between burn and control plots.

Burning had a significant effect on the abundances of birds in different foraging guilds (Wilks' lambda = 0.01, $F_{4,3} = 54.9$, $P < 0.01$). Hawkers were significantly more abundant on burn plots than on control plots (burn: 3.5 ± 0.29; control: 0.25 ± 0.25), though there were no significant differences in the abundances of gleaners, ground foragers, or bark foragers between burn and control plots (Fig. 1). The abundances of birds in different dietary guilds (insectivores, granivores) were not significantly affected by burning (Wilks' lambda = 0.82, $F_{2,5} = 0.53$, $P = 0.62$). Some orders of birds were present only on burn plots. For example, members of the Motacillidae and Laniidae were relatively abundant on burn plots but were never seen on control plots (Fig. 2). Conversely, members of the Sylviidae, especially the rattling cisticola (*C. chiniana*), were abundant on control plots, but were rare on burn plots (Fig. 2).

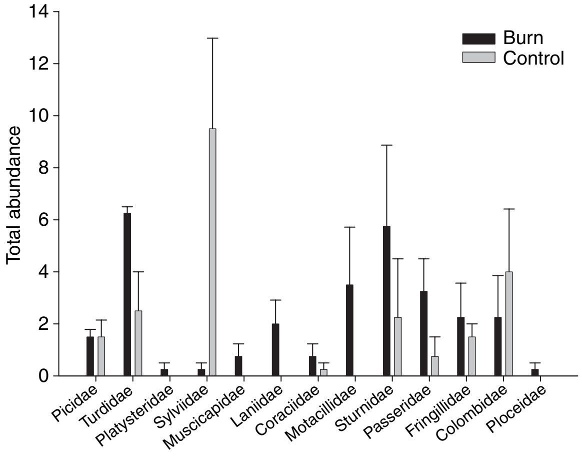

Fig 2 Effects of experimental burns on abundances of birds in different families. Birds in five families (e.g. Laniidae) were only observed on burned plots. Birds in the Sylviidae were more abundant on unburned plots.

Grass was approximately five times taller on control plots (burn: 5.3 ± 0.5 cm; control: 25.7 ± 2.0 cm; $P << 0.01$). The average canopy area of woody species other than *A. drepanolobium* was 0.32 m^2 on burned plots and 3.27 m^2 on control plots. Insects in the orders Orthoptera and Diptera were more than twice as abundant on control plots compared with burn plots (Orthoptera: $P = 0.02$; Diptera: $P = 0.02$). Abundances of Coleoptera were not significantly influenced by burning ($P = 0.11$).

Forward stepwise regression of insect and vegetation factors on Shannon diversity of all birds revealed that shrub canopy area was negatively correlated with Shannon diversity ($r^2 = 0.68$, $P = 0.12$; Fig. 3). Based on a Pearson correlation matrix, shrub canopy area was positively correlated with both grass height ($r = 0.79$, $P = 0.019$) and the abundance of orthopterans ($r = 0.73$, $P = 0.05$). Grass height was also highly correlated with the abundance of both orthopterans ($r = 0.95$, $P < 0.01$)

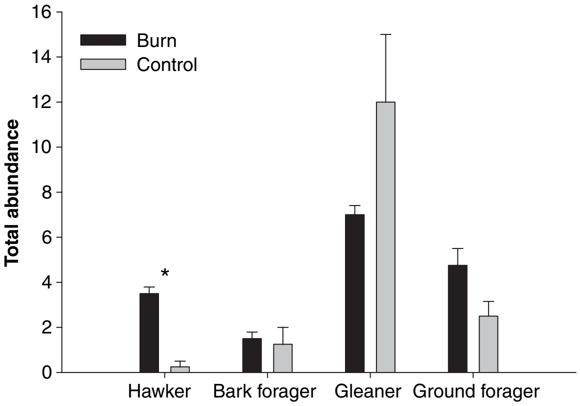

Fig 1 Effects of experimental burns on abundances of birds in different foraging guilds. Hawkers were more abundant on burn plots ($P < 0.01$).

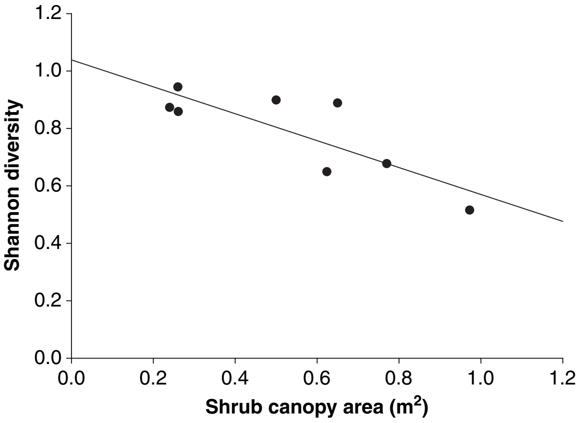

Fig 3 Effect of total shrub canopy area on Shannon diversity of birds. Plots with higher total shrub canopy area had lower bird diversity ($r^2 = 0.68$, $P = 0.01$).

and dipterans ($r = 0.84$, $P < 0.01$). No insect or vegetation parameters were significant predictors of bird abundance in our analysis.

Discussion

Plots that had been burned 2 years before our study had 32% higher Shannon diversity of birds than did unburned control plots. These effects on bird diversity appear to have been indirect, mediated by the effects of the burn on vegetation. Burned plots had significantly smaller shrub canopy area, shorter grass, and fewer orthopterans and dipterans than did unburned plots. Shrub canopy area was a significant predictor of bird diversity on each plot, and was also highly correlated with grass height and the abundance of orthoperans.

Most species were more abundant on burned than unburned plots, though one species, the rattling cisticola (*C. chiniana*, Sylviidae), was only found on unburned plots (Fig. 2; Table 1). This primarily insectivorous species is disproportionately abundant in black cotton habitat, representing 35% of birds observed on unburned plots. The increase in diversity in burned plots thus appears to result in part from a decrease in the abundance of the most common species. A study of the diet of eight cisticola species in South Africa revealed that up to 35% of their diet consisted of grass or other types of seeds (Kopij, 2001), though they are primarily considered insectivores (Mackworth-Praed & Grant, 1952, 1955). The absence of rattling cisticolas in burned plots, which had little grass cover, may have resulted from reduced abundance of grass seed. Burned plots also had lower shrub canopy area, and rattling cisticolas perch in trees and shrubs to make their distinctive rattling call (Mackworth-Praed & Grant, 1955). Thus, burned plots might have offered both less food and fewer perches for this species.

The absence of rattling cisticolas on burned plots coincided with the appearance of several species found only on burned plots, including the pale flycatcher (*Bradornis pallidus*) and the plain-backed pipit (*Anthus leucophrys*), both of which are insectivores. Thus, the increase in bird diversity on the burned plots might have resulted from competitive release of insectivorous birds following declines in the abundances of rattling cisticolas.

Our data were collected during a short period of observation (one month) during a single season 2 years after the burn. The results reported here, therefore, might reflect transient dynamics rather than some equilibrial state. However, because effects of fire are, by their nature, dynamic both in time and across space, assessment of these

Table 1 Species observed during the study and their average abundances (±SE) on burned and control plots

Family	Species	Common name	Foraging guild	Diet	Avg. control (±SE)	Avg. burned (±SE)
Colombidae	*Streptopelia capicola*	Ring-necked dove	Ground forager	Granivore	3.75 (2.46)	2.25 (1.60)
Coraciidae	*Coracias caudata*	Lilac-breasted roller	Hawker	Insectivore	0.25 (0.25)	0.75 (0.48)
Fringillidae	*Serinus reichenowi*	Yellow-rumped seedeater	Ground forager	Granivore	1.00 (0.58)	2.25 (1.32)
Laniidae	*Lanius doralis*	Taita fiscal	Hawker	Insectivore	0 (0)	2.00 (0.91)
Motacillidae	*Anthus leucophrys*	Plain-backed pipit	Ground forager	Insectivore	0 (0)	4.00 (2.16)
Muscicapidae	*Bradornis pallidus*	Pale flycatcher	Hawker	Insectivore	0 (0)	0.75 (0.48)
Passeridae	*Passer rufocintus*	Rufous sparrow	Ground forager	Granivore	0.75 (0.75)	3.25 (1.25)
Picidae	*Campethera nubica*	Nubian woodpecker	Bark forager	Insectivore	0.75 (0.48)	1.25 (0.48)
Picidae	*Dendropicos fuscenscens*	Cardinal woodpecker	Bark forager	Insectivore	0.50 (0.30)	0.25 (0.25)
Platysteridae	*Batis molitor*	Chin-spot batis	Gleaner	Insectivore	0 (0)	0.25 (0.25)
Ploceidae	*Ploceus spekei*	Speke's weaver	Ground forager	Granivore	0.50 (0.50)	0.25 (0.25)
Sturnidae	*Lamprotornis chalybaeus*	Blue-eared starling	Ground forager	Insectivore	0.50 (0.50)	0.50 (0.50)
Sturnidae	*Lamprotornis superbus*	Superb starling	Ground forager	Insectivore	2.50 (1.66)	5.25 (3.09)
Sylviidae	*Cisticola chiniana*	Rattling cisticola	Gleaner	Insectivore	8.50 (3.57)	0 (0)
Sylviidae	*Eremomela icteropygialis*	Yellow-bellied eremomela	Gleaner	Insectivore	0.75 (0.75)	0.25 (0.25)
Sylviidae	*Sylvietta whytii*	Red-faced crombec	Gleaner	Insectivore	0.25 (0.25)	0 (0)
Turdidae	*Monticola saxatilis*	Common rock thrush	Ground forager	Insectivore	0.25 (0.25)	0.50 (0.29)
Turdidae	*Oenanthe oenanthe*	Northern wheatear	Gleaner	Insectivore	0.75 (0.48)	2.25 (1.11)
Turdidae	*Oenanthe pleschanka*	Pied wheatear	Gleaner	Insectivore	1.25 (0.95)	2.75 (0.25)
Turdidae	*Oenanthe isabelline*	Isabelline wheatear	Gleaner	Insectivore	0 (0)	0.50 (0.5)

dynamics seems necessary to understand long-term, large-scale effects of fire. Only intensive, long-term studies can determine the trajectory of the response of bird communities to fires in east African savannas. For qualitative comparison, we made observations using the same methods at a single nearby site that had been burned experimentally 5 years earlier (Okello & Young, 2000). The species composition of birds at this site was similar to the composition at our unburned sites, including the presence of many rattling cisticolas (*C. chiniana*), suggesting that the effects of fire on bird diversity in this habitat last longer than 2 years, but perhaps <5 years. However, these observations were made at a single burned site; only further replicated studies could determine the duration of fire effects on bird communities in this region. Future comparative and empirical research should also address both (i) the degree to which experimental burns in this habitat mimic the characteristics of naturally occurring fires in frequency, intensity, and extent, and (ii) the appropriate scale of controlled burns for managing for bird diversity.

The differences in species composition between burned and unburned plots suggest that the highest landscape-level bird diversity might be obtained through a mosaic of burned and unburned patches. This is also most likely to approximate the historical state of bird diversity in this habitat, because patchy fires have been an important natural disturbance in tropical ecosystems for millenia (Bourlière, 1982).

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