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Birds and bush fires in African savannahs

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Bush fires are widespread in African savannahs. Their impact on birds varies. Many insectivores temporarily profit from the insects escaping fire and smoke, whereas the burnt-through grass and herb layer facilitates feeding for some ground-foraging bird species. Nevertheless, bush fires have a direct, negative impact on many other ground-foraging birds. The average density of seed-eating birds in humid, African savannahs (annual rainfall >800 mm) was 15.9 birds/ha in unburned savannahs, compared to 3.3 birds/ha (–72%) in recently burned areas. No such difference was found for insectivorous bird species. Eleven of the 13 common ground-foraging migratory bird species were not affected by bush fires in Africa because they spend the northern winter in the arid and semi-arid zone, beyond the main bush-fire zone. In the long run, savannah-inhabitant birds profit from bush fires, simply because fires prevent open landscape from becoming overgrown with trees. However, the short-term implications of bush fires might be severe for seed-eating birds that rely on humid savannah, because of the more than 3 million km² in Africa burned annually, most comprises humid savannah.

Key words: bush fire, granivorous birds, insectivorous birds, savannah, Sahel

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Bush fires play a key role in determining the structure, functioning and dynamics of savannahs (Scholes & Archer 1977, Saab & Powell 2005, Hegazy & Lovett-Doust 2016). This has been the case in fire-prone regions from long before humans began to dominate the Earth (Pausas *et al.* 2009). At present, most bush fires – at least in the Sahel – are established by local people. Fires are ignited for a wide range of purposes, such as for land clearance or regeneration of plant food and for controlled burning in order to reduce the potential fuel load that would feed larger fires. Each year, Earth's surface experiences fires over an area totalling 4.9 million km², 70% of which comprises sub-Saharan Africa (Rano *et al.* 2021). Every year, 11% of African savannahs and other fire-prone landscapes is burnt. In climate zones with >800 mm rainfall per annum, bush fires are the instruments that create and maintain open savannah and prevent the landscape from being dominated by trees.

Bush fires promptly attract a variety of avian predators of various plumage to feast upon the small

mammals, reptiles and large insects (especially orthopterans) escaping from the flames and smoke, finding them easy prey. Egrets, herons, storks, kites, buzzards, hawks, falcons, pratincoles, terns, nightjars, kingfishers, bee-eaters, rollers, hornbills, swallows, fiscals, drongos, crows and starlings have long been known to congregate at bush fires in Africa and elsewhere (Büttikofer 1890, Thiollay 1971, Barnard 1987, Dean 1987, Schulz 1998, Bouwman & Hoffman 2007, Krook *et al.* 2007, Hovick *et al.* 2017). Even small fires are quickly detected and exploited. When food is hard to detect in the tall grasses of the humid savannahs (early dry season) or when food supplies are dwindling (later on in the dry season), bush fires not only expose large insects and vertebrates to ground-foraging birds, but also expose smaller insects to aerial insectivores (Thiollay 1971). We observed a typical example on 11 January 2017, when a recently ignited bush fire in Senegal (14.022°N, 15.151°W) attracted at least 110 Abyssinian Rollers *Coracias abyssinicus*. The Rollers began to arrive from all directions as soon as smoke

columns emerged from the fire scene. In West Africa, Abyssinian Rollers are territorial and widely spaced. Prior to the fire, we had recorded their territorial density in the immediate surroundings of the bush fire as 0.099/ha (25 counting sites, in a total area of 111 ha). Given this density, the bush fire may have attracted every individual within a radius of 1.94 km. Some 15 minutes after the fire had begun to attract birds, only an occasional straggler still headed towards the fire scene, but many Rollers had already made the return trip to their territories. We were unable to assess whether the returning birds had reached their digestive bottleneck (Karasov & McWilliams 2005), or whether the temporary food bounty had become depleted.

The after-effects of bush fires are manifold. Much of the ground vegetation is scorched and bare soil is covered by sooty debris (Photo 1). However, the intensity of a fire may vary greatly across its footprint. A fire sometimes bypasses patches of vegetation or travels so fast that part of the food supply of birds (seeds, insects) remains unaffected. Furthermore, many grasses have seeds with awns that facilitate their burial in the ground (Peart 1984). Seeds of *Hyparrhenia* grasses with long awns were found at a greater depth than those with shorter awns, enhancing their survival during intense bush fires (Garnier & Dajoz 2001). Seeds without awns can also end up below the surface, the smooth elliptical seeds of *Panicum* grass descending even to greater depths than awned seeds of *Aristida* (Carrière 1989). More than half of the grass seeds were found at >1 cm below the surface.

In this paper, we address three questions: (1) Which parts of the northern sub-Saharan Africa are most

prone to bush fires and which bird species occur in this fire zone, (2) What are the densities of ground-foraging birds in burned areas compared to unburned areas in the same zone, and (3) Is the response of insectivorous birds – in terms of densities in burned and unburned sites – similar to that of granivorous birds?

RESULTS

Extent and timing of grass fires

The fraction of burned sites in the savannah decreased with decreasing rainfall (Figure 1A), and fires were completely absent in sub-Saharan zones with an average annual rainfall of 500 mm or less. A similar trend was recorded for sites categorised as farmland or woodland, albeit at a lower level. The lack of bush fires in the arid zone equated with a lack of flammable vegetation, i.e. a vegetation cover in the dry season of less than 15% at annual rainfall < 600 mm (Figure 1B). The cover of the herbaceous layer increased up to 80% when rainfall exceeded 600 mm per annum, and on average was twice as low in burned sites than in unburned.

Our field data suggest that a large part of the savannah in the humid zone was burned (Figure 1A). Some sites were visited in December, but most were visited in January and February; the final burned area on these sites during the dry season must therefore have been larger than we measured, given the ongoing process of setting fire to savannah.

Remote sensing data confirm that a large part of the savannah is burned annually. The total surface of the

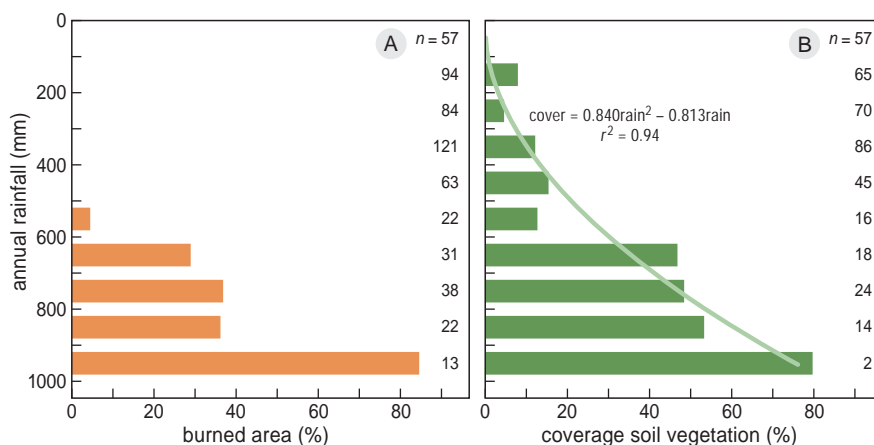
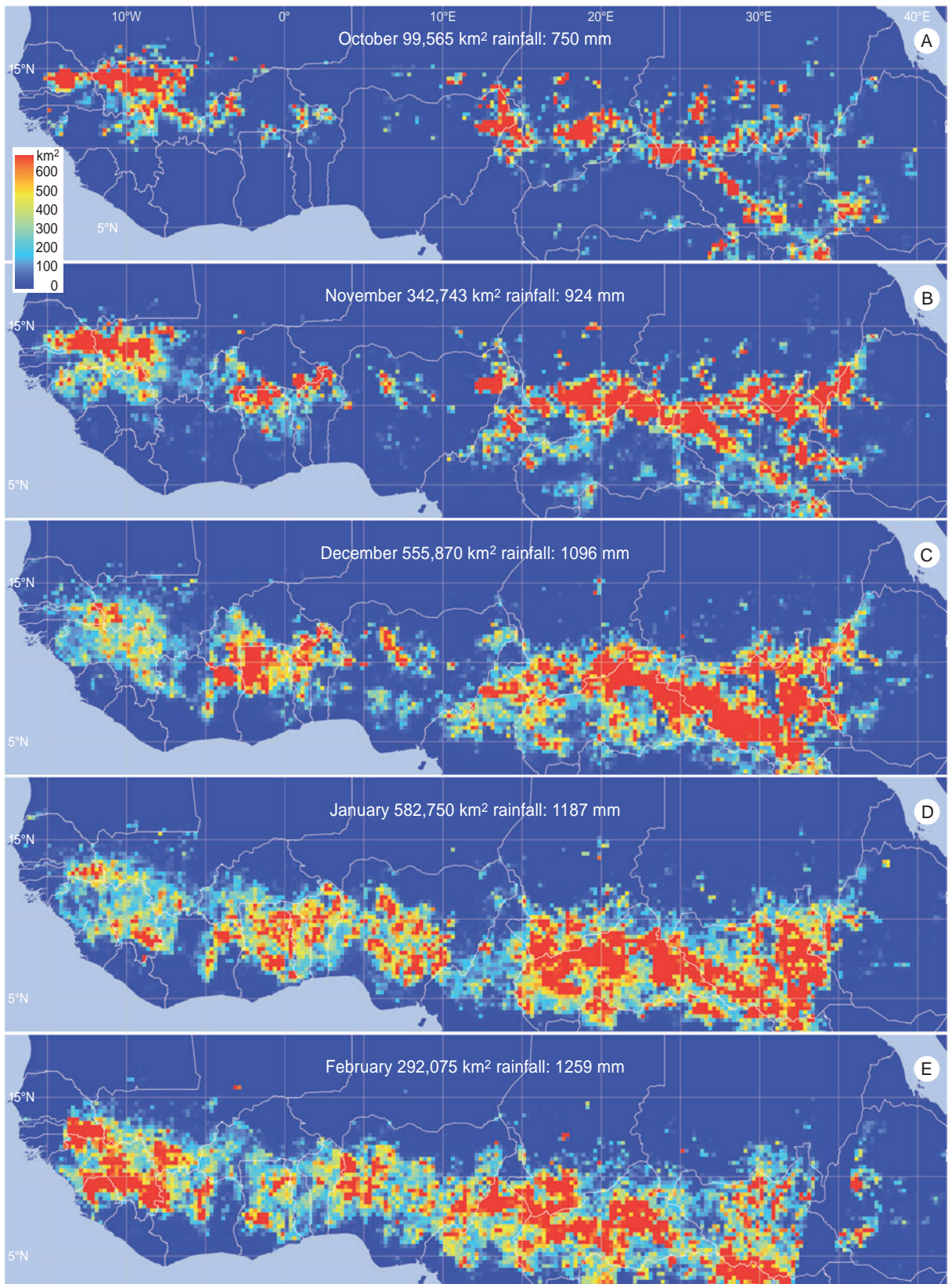


Figure 1. (A) Percentage of burned sites in savannah in the dry season (20 November – 10 March) between 7 and 22°N as a function of average annual rainfall. (B) Coverage of the herbaceous layer (%) on unburned savannah in January or February as a function of average annual rainfall. For location of the sites, see Zwartz *et al.* (2023a); not included are sites from Ethiopia, sites with a stony soil or sites classified as farmland or woodland. Number of sites (*n*) per rainfall zone is shown.



Photo 1. Grass fires in savannahs in the humid zone, (A and B) still burning or (C) shortly after the fire. The grass vegetation in the semi-arid (400–600 mm rain/year) and semi-humid zone (600–800 mm rain/year) is too sparse to fuel extensive grass fires, in contrast to the humid zone where tall grasses dominate. People establish fires mostly at the beginning of the dry season when the grass vegetation is not yet fully withered, to prevent fires from running rampant. Consequently, the grass vegetation is often only partially burned (photo C).



burned area within the region shown increased from 0.10 million km² in November to 0.58 million km² in January and then declined to 0.08 million km² in April (Figure 2). The sum of the monthly total burned area (2.13 million km²) overestimates the total surface of the burned area because some sites will have been classified as burned in more than one month. Using the maximum area burned per month per grid cell during seven months would give a total burned area of 1.03 million km² for the entire region. This is an underestimate, because within grid cells the areas burned during the different months in the dry season will not always overlap.

The fire zone shows a seasonal shift southward (Figure 2). Most bush fires in October and November

were recorded in the rainfall zone of 600–800 mm (5 and 13% of total surface, respectively), in the 700–1200 mm rainfall zone in December (13–16%) and in the 1000–1300 mm rainfall zone in January (15–17%). With a further increase of the annual rainfall and a larger part of the area covered by humid forests, the surface of burned areas declined (Figure 3).

In the semi-humid and humid zone (600–1200 mm) with a high coverage of farmland, such as in West Senegal, Nigeria and Ethiopia, far fewer bush fires were recorded than in the same zone with less farmland in Chad, Central African Republic and South Sudan (Figure 2H). On average, in grid cells without farmland, 46–61% of the area was burned, compared to just 7–9% in grid cells with >40% farmland (Figure 4).

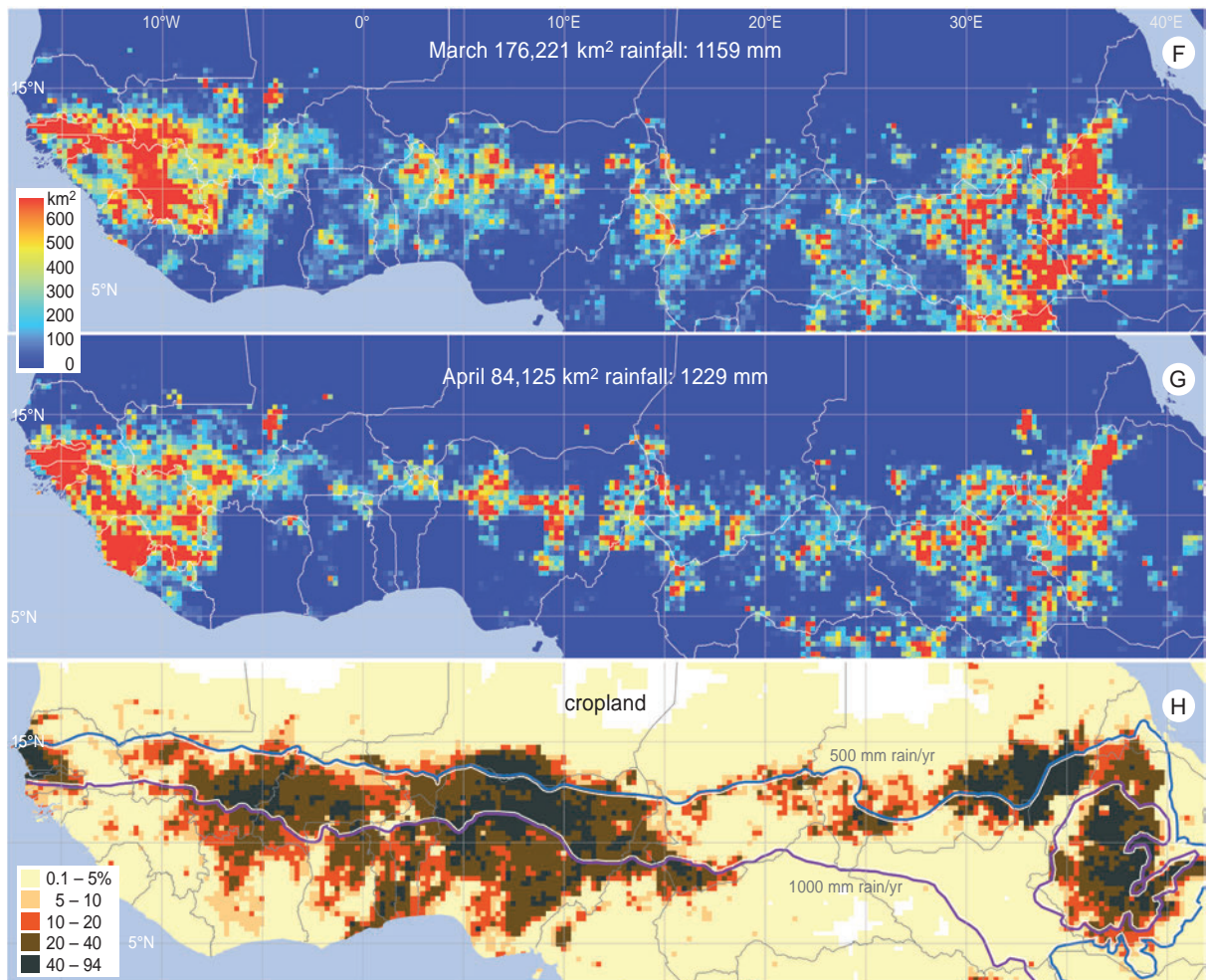


Figure 2. (A–G) Burned area (km²) in 1/4-degree grid cells between 3 and 20°N in six months in 2016 (Chuvienco *et al.* 2019). In red grid cells, at least half of the area is burned. Note that the surface area of grid cells varies per latitude and declines from 766 km² at 3°N to 711 km² at 20°N. Total burned area and average annual rainfall in the burned area were calculated for the region shown on the maps (source: Hijmans *et al.* 2005). (H) % cropland (source: Buchhorn *et al.* 2020) with 500- and 1000-mm isohyets.

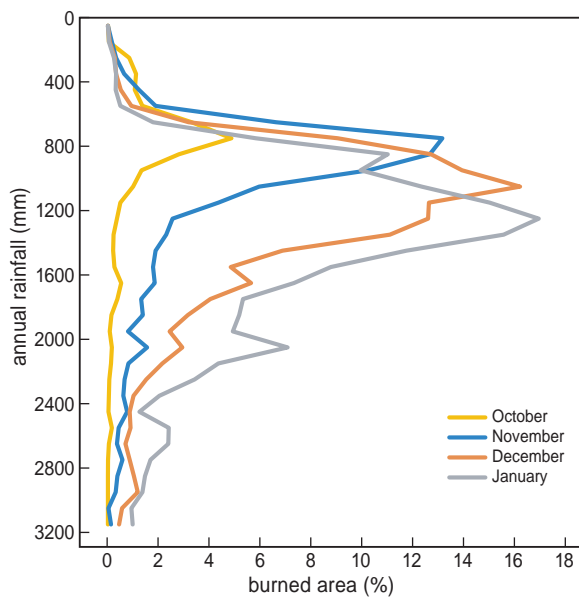


Figure 3. Area indicated as burned (%) during each of the first four months of the dry season in 2016 as a function of average annual rainfall; same data as Figures 2A–D. Source of data: Chuvieco *et al.* (2019).

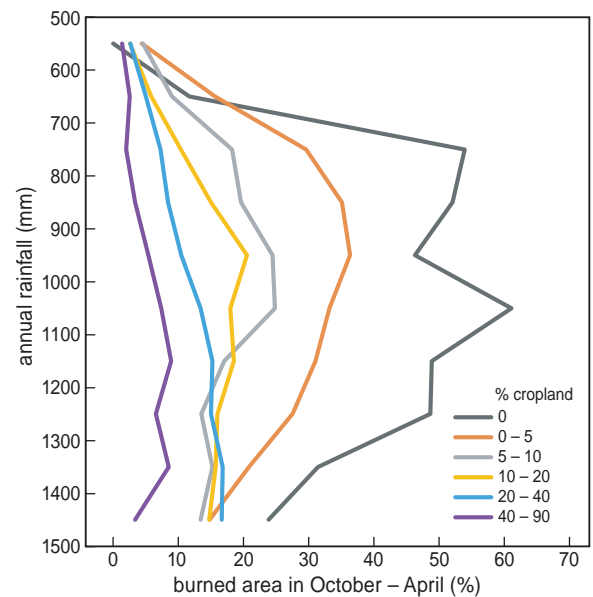


Figure 4. Area burned (%) in October–April in ten rainfall zones between 500 and 1500 mm/year (same data as Figure 2), given separately for $\frac{1}{4}$ -degree grid cells where the coverage of cropland varied between 0% and 40–90% (data from Figure 2H; for each grid cell the maximum burned area between October and April was used to calculate the average burned area per rainfall zone. Source of data: Chuvieco *et al.* (2019) for burned area and Buchhorn *et al.* (2020) for cropland.

Densities of ground-foraging birds in relation to burns

The average density (\pm SE) of ground-foraging granivores amounted to 15.9 ± 4.2 birds/ha in 18 unburned sites and 3.3 ± 0.8 birds/ha in 20 burned sites (Figure 5A). The overall density of Afro-tropical ground-foraging insectivores was much lower and differed only marginally between unburned (2.0 ± 0.5 birds/ha) and burned sites (1.4 ± 0.4 birds/ha). The difference was significant for granivores (ANOVA: $r^2 = 0.21$, $n = 38$, $P = 0.004$), but not for insectivores (ANOVA: $r^2 = 0.02$, $n = 38$, $P = 0.398$).

To assess the robustness of our results, we repeated the analysis for a smaller data set, excluding the only site from Ivory Coast, and for a larger data set by including the sites in Chad in a wider range of rainfall zones (62 sites with >700 mm rainfall, or 78 sites with >600 mm). The outcome was the same: significantly lower densities of seedeaters in burned areas, but no difference in densities of insectivores. The results were also unaffected when adding vegetation cover as a (non-significant) covariate.

Ground-foraging migrants were present in low densities in humid savannahs, but were significantly more common in unburned (0.25 ± 0.5 birds/ha) than in burned areas (0.07 ± 0.03 birds/ha, ANOVA: $P = 0.008$). Northern Wheatears *Oenanthe oenanthe* were

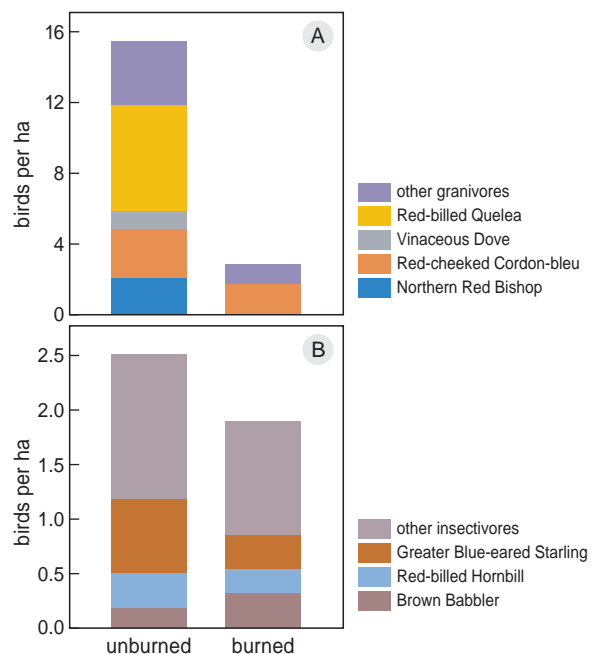


Figure 5. (A) Number of Afro-tropical ground-foraging birds per ha on recently burned ($n = 20$) or unburned ($n = 18$) savannah sites where annual rainfall was >800 mm, separately for (A) granivores and (B) insectivores.



Photo 2. Unburned savanna during the dry season in the semi-humid zone. (A) The vegetation consists mainly of annual grasses 10–40 cm high in the semi-humid zone. (B and C) In the humid zone, the savanna is mainly covered by tall perennial grasses such as *Andropogon* spp. and *Hypparrhenia* spp. of 60–120 cm height. Most grasses and herbs have already disappeared just after the rainy season in the arid and semi-humid zone due to heavy grazing of cattle, goats and sheep. The grazing pressure in the humid zone typically is lower, but is sufficiently high to create open spaces locally by grazing and trampling (Photo B).

rarely seen in burned areas, Western Yellow Wagtails *Motacilla flava* not at all. Tree Pipit *Anthus trivialis* and Whinchat *Saxicola rubetra* reached low densities in both burned and unburned sites. The low density of migrants in humid savannahs prevents any firm statement as to avoidance of burned areas or not.

DISCUSSION

Because many seeds on the surface are destroyed, grass fires are considered to have a negative impact on seed-eating birds, at least in the short term (Esque *et al.* 2010). In the longer term, undamaged seeds may become accessible after the fire-assisted removal of the vegetation, but this does not compensate for the initial losses. Furthermore, the seed bank will not be replenished until the next rainy season. Nevertheless, in the longer run, savannah-inhabiting birds will profit from bush fires, simply because fires prevent the open landscape from becoming overgrown with trees (Van Auken 2000, Staver *et al.* 2011, Smit & Prins 2015, Devine *et al.* 2017), facilitating feeding for ground-foraging granivorous birds. This is particularly evident in the more humid landscapes (>800 mm rainfall per annum) of sub-Saharan Africa, which experience lower grazing pressure than drier areas. In the semi-arid zone where fires are scarce anyway, the fortunes of eleven common ground-foraging migrants were unaffected by fires (compare Figure 3 in this paper with Figure 13A and 14A in Zwarts *et al.* 2023a). In the humid savannahs, the impact of grass fires on insectivorous ground-foraging birds is smaller than in the semi-humid savannahs for Afro-tropical species (Figure 5) and for two migrants, Tree Pipit and Whinchat. Essentially the same results were found in Kruger National Park (South Africa), where fire had a negative impact on the density of seed-eating birds and on birds that prefer cover of vegetation, but not on other bird species (Mills 2004). In Australia, the impact of fire was also found to be detrimental to most bird species, especially when the fires occurred in the late dry season (Woinarski & Recher 1997, Reside *et al.* 2012).

With a growing human population, a concomitant increase in frequency of bush fires would be expected. Surprisingly then, in northern sub-Saharan Africa the trend was downwards, at least between 1981 and 2018 (Otón *et al.* 2021). The decline in the frequency of fires occurred against a varied context:

(1) Due to the increase in livestock and higher grazing pressure, less grass is left in the dry season, and therefore less fuel is available for bush fires (Archibald

& Hempson 2016). Bush fires were, for instance, common in northern Senegal in the 1960s (visible on CORONA satellite photos), the 1970s (Morel & Morel 1978) and the 1980s (Le Houérou 1989), but in the same region we did not record any bush fires between 2011 and 2019. Since the 1960s, grazing pressure has increased to such an extent that grass is now completely removed by livestock early in the dry season (Zwarts *et al.* 2018, 2023b).

(2) At the same time, farmers converted savannah (fire-prone) into cropland (with much less fire; Wei *et al.* 2020).

(3) Rainfall in northern sub-Saharan Africa has (partly) recovered after the extremely dry period of 1969–1992. As long as the savannah vegetation remains wet, bush fires may be inhibited (Zubkova *et al.* 2019), although the opposite has been suggested for semi-arid savannahs where the fuel load of dead grass is higher in wet years (Le Houérou 1989, Smit & Prins 2015).

(4) Millions of ha of woody savanna and agroforestry parkland has been converted into cashew plantations in West Africa since 1980, resulting in a decline of bush fires because plantation owners protect the fire-sensitive cashew trees (Temudo & Abrantes 2014).

(5) Due to the increase of the human population and expansion of farmland and cashew plantations, at the expense of savannah, fires are probably smaller than in the past and consequently increasingly remain undetected by satellites using a sensor with coarse resolution (Rano *et al.* 2021).

Our study shows that the density of seed-eating birds in unburned savannah was 3.6 times higher than on recently burned savannah (Figure 5). This suggests a large impact of bush fires on the fortunes of an estimated four thousand million seedeaters between 7° and 22°N (Table 2 in Zwarts *et al.* 2023a). Our survey, however, has some caveats. First, the much lower densities in burned areas may be a methodological artefact if densities of birds had been higher in the sampled unburned sites compared with densities at the burned sites before the fires. We sought to mitigate this confounding factor by selecting counts from the same period (late February) and within a single region (36 of 38 sites in southern Chad). Thus, we selected sites where rainfall and woody cover in burned and unburned sites were similar, on average. Second, we do not know to what degree differences in the density of birds on burned and unburned sites was due to birds having moved from burned to unburned areas. The burned sites in southern Chad in February 2018 were largely situated around 18 and 19°E longitude in an area of at least 150 × 350 km. This region had been

almost completely burned, not just savannah but also farmland and woodland. When burned areas are this extensive, movements to unburned sites must have involved long flights. Third, in Chad, ground-foraging birds reached higher densities on humid savannahs than in West Africa (Figure 4 in Zwarts *et al.* 2023b), complicating estimates of how many birds are affected within the more than 1 million km² that is annually burned in Africa between 3 and 20°N (Figure 2). Clearly, here is scope for systematic fieldwork in fixed study plots before and after bushfire, as has been done in South Africa (Mills 2004, Krook *et al.* 2007, Bouwman & Hoffman 2007).

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SAMENVATTING

Natuurbranden zijn wijdverbreid in Afrikaanse savannes, vooral in regenrijke gebieden waar de bodem na de regentijd bedekt is met een dichte vegetatie van hoge grassen. Wanneer aan het begin van de droge tijd het verdroge savannegras massaal in brand wordt gestoken, heeft dat zowel positieve als negatieve effecten op de vogels. Veel insectenetters profiteren tijdelijk van de insecten die ontsnappen aan vuur en rook. Ook vogels die op de grond foerageren, hebben profijt van branden. Normaliter mijden zij savannes vanwege de hoge en dichte grasvegetatie. Een brand zorgt dan voor een toegankelijke, zij het zwartgeblakerde, vlakte. Savannebranden hebben echter ook een negatief effect doordat een deel van het potentiële vogelvoedsel (zaden, insecten) verbrandt. De gemiddelde dichtheid van zaadetende

vogels in vochtige, Afrikaanse savannes (jaarlijkse regenval > 800 mm) was tijdens het droge seizoen 15,9 vogels/ha in niet-verbrande savannes, vergeleken met 3,3 vogels/ha (–72%) in recent verbrande savannes. Een dergelijk verschil werd niet gevonden bij insectenetende vogelsoorten die op de grond foerageren. Boompieper *Anthus trivialis* en Paapje *Saxicola rubetra* overwinteren in Afrika in de natte savannegebieden en hebben daarom veelvuldig te maken met savannebranden. Elf andere soorten trekvogels, alle op de grond foeragerend, werden echter niet getroffen door savannebranden in Afrika, omdat ze de noordelijke winter doorbrengen in droge gebieden en daardoor buiten de belangrijkste brandzone blijven. Op de lange termijn is het waarschijnlijk dat savannevogels profiteren van bosbranden, simpelweg omdat branden voorkomen dat open landschap overgroeit raakt met bomen. Maar op de korte termijn is het effect negatief. Jaarlijks wordt in Afrika meer dan 3 miljoen km² savanne in brand gestoken. Door de schaal waarop het gebeurt, heeft het branden grote gevolgen voor zaadetende vogels van vochtige savannes.

RÉSUMÉ

Les feux de brousse sont très répandus dans les savanes africaines, en particulier dans les zones les plus humides où le sol est envahi par une végétation dense de hautes herbes après la saison des pluies. Les incendies qui surviennent en début de saison sèche ont des effets variés sur les oiseaux. De nombreux insectivores profitent de la manne temporaire des insectes qui fuient le feu et la fumée, tandis que certaines espèces granivores qui se nourrissent au sol profitent de la disparition de la végétation herbacée dense et haute qu'ils évitent habituellement pour accéder à de nouvelles ressources alimentaires. Cependant, ces feux ont également un impact négatif direct, car ils détruisent une partie de la nourriture disponible (graines, insectes). Ainsi, la densité moyenne d'oiseaux granivores dans les savanes africaines humides (précipitations annuelles > 800 mm) pendant la saison sèche est de 15,9 oiseaux/ha dans les savanes non brûlées, contre 3,3 oiseaux/ha (–72 %) dans les savanes récemment brûlées. Cette diminution d'abondance ne se retrouve pas chez les espèces insectivores se nourrissant au sol parmi lesquelles, sur les 13 espèces migratrices étudiées, seuls le Pipit des arbres *Anthus trivialis* et le Tarier des prés *Saxicola rubetra* qui hivernent dans les zones de savane humide subissent les effets néfastes des feux de brousse. Les 11 autres espèces passent l'hiver septentrional dans des zones sèches et restent donc en dehors de la principale zone d'incendies. À long terme, les oiseaux de la savane bénéficient vraisemblablement des feux de brousse qui empêchent la fermeture des habitats. Mais à court terme, les espèces qui dépendent des graines de graminées des savanes humides pourraient être sévèrement touchées : la majeure partie des plus de 3 millions de km² de savane brûlés chaque année en Afrique concernent ces habitats.

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