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Shrub-dwelling birds in the Sahel forage less often on the ground in grazed areas

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Shrub-dwelling birds may resort to ground-foraging in the Sahel when opportunities are favourable. Several arboreal and semi-arboreal passerines, both African and European, were frequently recorded foraging on the ground, but not in heavily grazed areas. Grazed, dry savannah probably has fewer insects on the ground, which is often devoid of vegetation in the dry season. Shrub-dwelling birds foraged more frequently on the ground in the eastern Sahel, where grazing pressure is lower. In the Sahel grazing pressure increased fourfold since the 1960s, presumably reducing opportunities for arboreal bird species to facultatively forage on the ground. Due to increased grazing pressure, Common Whitethroats *Curruca communis* and other shrub-dwelling passerines may have lost a specific niche within their foraging habitat. This has compounded the greater losses associated with declines of woody vegetation during the drought years since the late 1960s.

Key words: shrub-dwelling birds, Sahel, grazing pressure

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Numbers of cattle, sheep and goats in Africa grazing in the dry belt of the northern tropics have quadrupled between the 1960s and the 2010s (www.fao.org/faostat/en/#data/TP). At first glance, the impact of grazing on the vegetation might seem small. After all, each rainy season, whether of short or long duration, transforms a desert-like landscape into a green plain with lush vegetation of mainly annual grasses grazed by livestock, the standard feature of the Sahelian savannah. However, a closer look reveals that the mounting grazing pressure has negatively impacted a multitude of bird species that inhabit this region during the dry season. This is particularly evident in granivorous birds, for which grass seeds are a staple food, but insects and rodents are equally affected. The soil seed bank is a key factor in the entire savannah ecosystem, across several trophic levels (Le Houérou 1989). Take, for example, raptors and owls, which suffer from the after-effects of drought, namely that rodent numbers plummet due to the paucity of grass seeds in a parched landscape (Morel & Morel 1978). Seed production in

the herbaceous layer is extremely variable, depending on vegetation type, soil type, annual rainfall and grazing pressure of livestock (e.g. Bille 1977, Grouzis 1988, Le Houérou 1989, Sternberg *et al.* 2003). The huge decline in seed-eating birds, as ascertained for NW Senegal between the 1970s and the 2010s, is the inevitable outcome of these processes, heavy grazing being the most consistent driver (Zwarts *et al.* 2018, 2022c).

Arboreal birds feeding on insects, fruit and nectar in tree canopies are, by the very nature of their foraging niche, exempt from the negative impact of declining seed stock and ground-dwelling insects. However, they are not exempt from the negative impact of grazing *per se*. Although most arboreal bird species strictly forage in tree canopies, several species will leave the trees and shrubs to additionally forage for insects on the ground beneath. We expected adverse effects of grazing on insect abundance on the ground, resulting in fewer opportunities for arboreal bird species to forage on the ground, especially in heavily grazed areas. Additionally,

we expected a seasonal decline in the frequency of ground-foraging among arboreal birds due to the gradual removal of ground vegetation by grazing livestock over the course of the dry season (Figure 1 in Zwarts *et al.* 2022b).

METHODS

The basic methods used to record birds are described in Zwarts & Bijlsma (2015). Upon detection, all birds were assigned to either tree/shrub or ground/herbaceous layer. The categories do not necessarily equate to foraging habitats. Some species, such as European Pied Flycatcher *Ficedula hypoleuca* and Common Redstart *Phoenicurus phoenicurus*, may search for insects in the lower canopy, performing sallies from a branch to capture flying prey or to pounce on ground-dwelling insects. These sit-and-wait predators are excluded from the present analysis. Cricket Warblers *Spiloptila clamans*, mainly foraging in *Leptadenia pyrotechnica*, a desert shrub which was often <1 m high, were also excluded because of inconclusive foraging niches (ground or low vegetation).

For five relevant bird species and one species-pair, sufficient data were collected to test our expectations, i.e. three common Afro-tropical species (Tawny-flanked Prinia *Prinia subflava*, Black Scrub Robin *Cercotrichas podobe*, Green-backed Camaroptera *Camaroptera brachyura*), one Afro-Palaearctic species (Rufous-tailed Scrub Robin *Cercotrichas galactotes*) and three Palaearctic migrants (Common Whitethroat *Curruca communis* and the species-pair Iberian Chiffchaff *Phylloscopus ibericus*/Common Chiffchaff *P. collybita*). Among the

Palaearctic migrants, Common Whitethroat is the only arboreal species in the Sahelian drylands that routinely forages in low woody vegetation and sometimes on the ground (Cramp 1992), just as it does during the breeding season in Europe (Mason 1976, Halupka *et al.* 2002). Iberian Chiffchaffs were recorded in West Africa, all North of 13°N and West of 4°W, partly overlapping with Common Chiffchaff (all North of 10°N and West of 2°W), but these species were sometimes not specifically identified and therefore lumped under ‘Chiffchaff’. As in the breeding area, Chiffchaffs in Africa are supposed to be essentially woodland birds (Cramp 1992), but in West Africa we recorded most Chiffchaffs in flooded forests or near water, sometimes even foraging on floating vegetation. Incidentally, all Chiffchaffs recorded in Ethiopia were Common Chiffchaff.

The data set used in this paper is described in Zwarts *et al.* (2022a). To investigate the impact of grazing on birds, we also specifically targeted three areas in western Senegal where domestic livestock had been excluded:

Widou Thiengoly enclosure, total surface 23.6 ha, where grazing was excluded for 33 years (Miehe *et al.* 2010); situated at 15.94°N and 15.29°W; average annual rainfall 338 mm; visited in January and December 2014 (see Photo 1B in Zwarts *et al.* 2022b; Figure 4 in Zwarts *et al.* 2018); rainfall data, averaged over the period 1969–1990, are taken from Hijmans *et al.* (2005).

Guembeul Natural Reserve (720 ha), a lagoon surrounded by drylands with a dense woody vegetation of mainly *Acacia tortilis* and locally *Prosopis juliflora* and *Salvadora persica* (<https://rsis.ramsar.org/ris/338>). Grazing pressure is extremely low with no livestock and

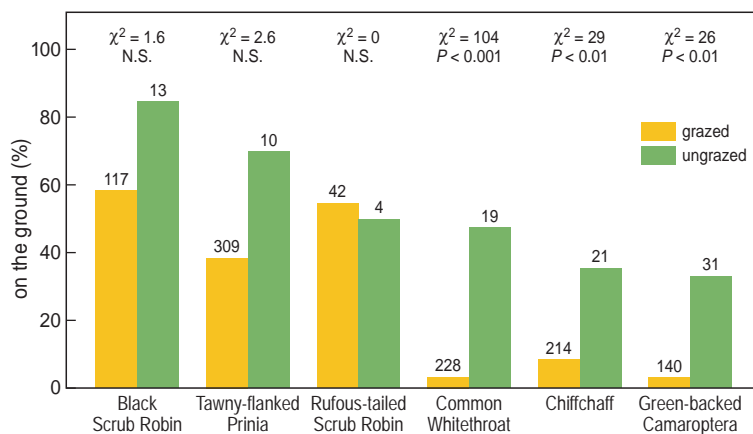


Figure 1. Percentage of shrub-dwelling birds foraging on the ground in Senegal in three areas where livestock were excluded ('ungrazed') and elsewhere in West Africa ('grazed'; 17–9°W). Number of birds observed is shown at the top of the bars. The results of six χ^2 -tests ($df = 1$) are given above the bars.

only few Scimitar Oryx *Oryx dammah* and Dama Gazelles *Gazella dama*. The area is situated at 15.92°N and 16.46°W; average annual rainfall 302 mm; visited in January 2014.

Bandia Wildlife Reserve (3400 ha) comprises a fenced area with reintroduced populations of Warthog *Phacochoerus africanus*, Buffalo *Syncerus caffer*, Roan Antelope *Hippotragus equinus*, Giraffe *Giraffa camelopardalis*, etc. (Vincke et al. 2005, Hejmanová et al. 2010). Within the reserve, the grazing pressure is low, contrasting strongly with that of livestock in the area outside the fence. The reserve was established in 1986 and expanded in 1998, 2004 and 2007. It gradually turned from open heavily grazed savannah into woody savanna comparable to the savanna existing in 1968 (Zwarts et al. 2015b); situated at 14.54°N and 16.98°W; average annual rainfall 542 mm; visited in November 2013 and 2015 and January 2014 (see Photo 1D in Zwarts et al. 2022b).

The two ungrazed sites in the arid zone of northern Senegal (Widou Thiengoly and Guembeul) had a low vegetation of grasses and forbs during the dry season in contrast to the grazed surroundings where the ground was completely bare at the time of our visits. This contrast was less pronounced in Bandia. In all sites the remaining above-ground vegetation was completely withered during our visits in November–February.

To test longitudinal variation in the fraction of birds foraging on the ground, all data were split in six bands

covering the entire width of the Sahel (limits at 9°W, 0°, 10°E, 25°E, 34°E and 42°E (see map in Figure 2).

RESULTS

In the Widou Thiengoly enclosure, all three Common Whitethroats present foraged on the ground, as did 6 out of 16 birds in the two other areas without grazing. In grazed areas in West Africa (west of 9°W) only 3.5% (8 out of 228 birds) of Common Whitethroats were recorded as foraging on the ground. A similar difference, albeit less pronounced, was found for Chiffchaff, Green-backed Camaroptera and (statistically not significant) Tawny-flanked Prinia and Black Scrub-Robin. In contrast, half of the very few Rufous-tailed Scrub Robins in ungrazed sites were recorded on the ground, very similar to those in grazed areas (Figure 1).

If grazing has a negative impact on ground-foraging of shrub-dwelling passerines, we would expect a lower incidence of ground-foraging in the western Sahel than in the eastern Sahel due to substantial differences in grazing pressure (Figure 2 and 3 in Zwarts et al. 2022b). Excluding the birds from non-grazing enclosures in the westernmost section of the Sahel, all investigated shrub-dwelling species, except Common Whitethroat, showed the expected trend (Figure 2). Birds foraged less frequently on the ground in the three western longitudinal zones than in the three eastern zones.

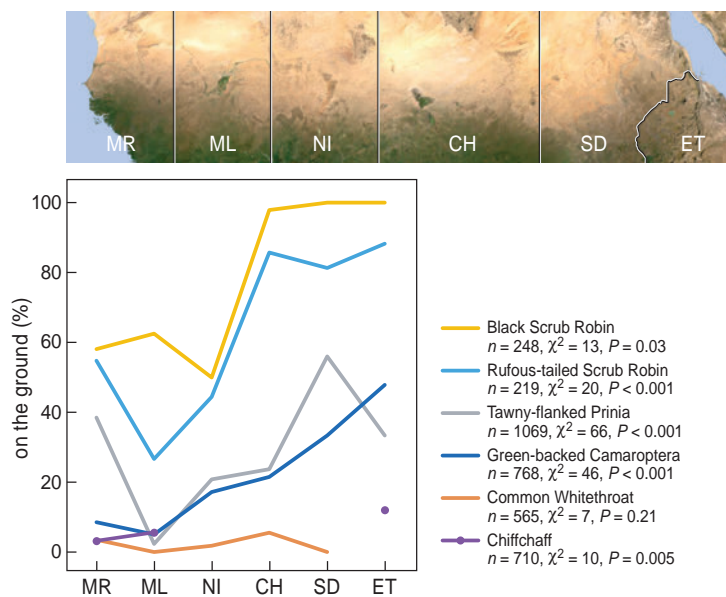


Figure 2. Percent of six tree-dwelling bird species foraging on the ground in six longitudinal bands between 7 and 22°N. The results of the six χ^2 -tests ($df = 5$) are given. Satellite image: Earthstar Geographics.

Using the same data set as in Figure 2, we calculated the seasonal variation in ground-foraging across September through March. The expected decline in the average percent of ground-foraging in grazed plots was found only for Tawny-flanked Prinia ($P < 0.001$; linear regression declining from 44% in September to 0% in March), but not in the other five species.

DISCUSSION

The impact of grazing on the frequency of ground-foraging was, as expected, high for essentially arboreal species that normally forage low in trees and in shrubs with the occasional foray into herbs and on the ground below woody vegetation (Figure 1). For these species, like Chiffchaff, Common Whitethroat and Green-backed Camaroptera, grazing *de facto* reduced the foraging repertoire to near-exclusive foraging in woody vegetation. A large difference was also found in species for which ground-foraging is essentially the main strategy of obtaining food, as in the scrub robins (Figure 1 and 2). The Tawny-flanked Prinia (for which we had insufficient data for the ungrazed sites; Figure 1) is a shrub-dwelling species that also forages on the ground. Detailed observations by McLean (2017) showed that even when on the ground food items were taken from the vegetation. Ground vegetation in the Sahel vanishes during the dry season soon after the last rain in October (Figure 1 in Zwarts *et al.* 2022b), which may explain why the fraction of ground-foraging Tawny-flanked Prinias declined from 44% in October to 0% in March. No such seasonal decline was obvious in the other five species, probably because these species are not bound to vegetation when they forage on the ground and search for insects on bare patches where they probe the soil, hop among leaf litter, peer under dead leaves, peck among stones and make sallies to catch insects from plants or from the air.

In Europe, many species largely or partly depend on insect food or seed gathered from the ground. For example, when captive Common Redstart were offered the choice to either forage on bare ground with few insects or in dense vegetation with many insects, they selected bare ground, probably because the few prey on bare ground are easier to detect than insect prey in dense vegetation (Martinez *et al.* 2010). This probably also applies to other sit-and-wait predators as Woodchat Shrike *Lanius senator* and Great Grey Shrike *Lanius excubitor* which need a good view from a perch. Other ground-foraging long-distance migrants, like Eurasian Hoopoe *Upupa epops*, Eurasian Wryneck *Jynx torquilla*,

European Turtle Dove *Streptopelia turtur* and Ortolan Bunting *Emberiza hortulana*, prefer as foraging habitat a mixture of bare and sparsely vegetated ground. Their decline in Europe is associated with the loss of half-open habitats. The former mosaic of varied ground vegetation has transformed into a dense and more homogeneous, herbaceous layer where their main food (e.g. seeds, ants and their pupae) is more difficult to access (Schaub *et al.* 2010, Menz & Arlettaz 2011, Weisshaupt *et al.* 2011, Dunn 2021). During the dry season in Africa, ground-foraging birds in savannahs face the very opposite, though equally negative in its outcome: due to mounting grazing pressure, the Sahel has become more barren. Ungrazed areas with some vegetation remaining are getting scarcer. In the western Sahel, exclosures were eye-catching pinpricks amidst savannah resembling a desert (Figure 4 in Zwarts *et al.* 2018; Photos 1 and 3 in Zwarts *et al.* 2022b). Foraging conditions for ground-foraging arboreal birds deteriorate when the herbaceous layer has been removed by heavy grazing. Several studies found a decline of insects at high grazing pressure and loss of herbaceous layer (e.g. Seymour & Dean 1999, DeBano 2006, Moran 2014, Kaiser *et al.* 2015, Zhu *et al.* 2015, Ma *et al.* 2017). Intensively grazed land is littered with cowpats and droppings of goats and sheep, but our observations showed that dung when dehydrated did not attract insects in noteworthy numbers (R.G. Bijlsma unpubl. data).

Our preliminary conclusion is that due to increased grazing pressure, Common Whitethroats and other shrub-dwelling passerines have lost part of their foraging habitat, especially in the western Sahel where the grazing pressure is higher. This loss compounds greater losses associated with declines in woody vegetation during the drought years since the late 1960s (Gonzalez 2001, Zwarts *et al.* 2018), probably more so for Common Whitethroat, Chiffchaff and possibly Common Redstart (given their frequent forays to the ground), than for strictly arboreal migrants, such as Western Bonelli's Warbler *Phylloscopus bonelli*.

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SAMENVATTING

De meeste vogels die in bomen foerageren, komen zelden aan de grond. Dat ligt anders voor soorten die zich veel in struiken ophouden en geregeld een uitstapje naar de grond maken om een insect op te pikken. In de Sahel is dat niet anders. Hier zijn het vooral Grasmussen *Curruca communis*, Tjiftjaffen *Phylloscopus collybita* en Iberische Tjiftjaffen *P. ibericus* die tijdens het droge seizoen onder struiken op de grond naar insecten zoeken. Hetzelfde gedrag zien we bij Afrikaanse struikbewoners als Roestflankprinia *Prinia subflava* en Mekkercamaroptera *Camaroptera brachyura*. De Sahel wordt intensief begraasd door runderen, schapen en geiten, vooral in het westelijke deel. Er zijn maar heel weinig gebieden waar vee wordt buitengesloten. Juist in die exclusies vonden we opvallend vaak dat de genoemde soorten op de grond foerageerden. In begraasde gebieden kwam dat veel minder voor. Dat begrazing van bodemvegetatie door vee een grote rol speelt bij wel of niet of de grond foerageren, bleek bij een vergelijking van de mate van grondfoerageren door struikbewoners in de westelijke en oostelijke Sahel. In de westelijke Sahel (intensief begraasd) werden voornoemde soorten minder vaak foeragerend aan de grond gezien dan in de oostelijke Sahel (minder intensief begraasd). De vermoedelijke verklaring is dat begrazing de bodemvegetatie elimineert, en daarmee het leefgebied voor insecten. Voor vogels die zowel in bomen en struiken als op de grond foerageren is het dan niet langer de moeite waard om in intensief begraasde gebieden op de grond naar insecten te zoeken. De graasdruk is in de Sahel verviervoudigd tussen 1960 en 2010. We weten niet of de struikvogels vroeger vaker op de grond foerageerden dan nu, maar dat ligt wel voor de hand. Voor bijna alle Europese vogelsoorten die in de Sahel overwinteren, zijn de omstandigheden in de afgelopen ruime halve eeuw verslechterd. We vermoeden dat in het bijzonder de Grasmus in de Sahel meer terrein heeft verloren (bomen, struiken én bodemvegetatie) dan andere trekvogels die uitsluitend in boomkronen foerageren.

RÉSUMÉ

La plupart des oiseaux qui se nourrissent dans les arbres descendent rarement au sol. À l'inverse, les espèces qui fréquentent préférentiellement les arbustes s'y posent régulièrement pour y capturer des insectes. Au Sahel, ce sont principalement la Fauvette grisette *Curruca communis*, le Pouillot véloce *Phylloscopus collybita* et le Pouillot ibérique *P. ibericus* qui cherchent des insectes au sol sous les buissons pendant la saison sèche. Le même comportement peut être observé chez les passereaux sédentaires de la brousse africaine comme la Prinia modeste *Prinia subflava* et le Camaroptère à tête grise *Camaroptera brachyura*. Le Sahel est intensivement pâturé par des bovins, des ovins et des caprins, surtout dans sa partie occidentale, et rares sont les zones dont le bétail est exclu. C'est précisément dans celles-ci que nous avons rencontré les espèces susmentionnées à une fréquence remarquablement élevée, alors que nous les avons trouvées moins fréquemment dans les zones pâturées. La comparaison des fréquences d'alimentation au sol entre l'Ouest (intensivement pâturé) et l'Est du Sahel (moins intensivement pâturé) révèle le rôle majeur du pâturage dans le comportement alimentaire des espèces des milieux arbustifs. Ces espèces sont moins fréquemment observées au sol dans le Sahel occidental, probablement car le pâturage élimine la végétation au sol, donc l'habitat des insectes. La pression de pâturage au Sahel a quadruplé entre 1960 et 2010 et a donc vraisemblablement fortement réduit les opportunités alimentaires au sol pour les insectivores des arbustes. Pour la quasi-totalité des espèces d'oiseaux européens hivernant au Sahel, les conditions se sont détériorées au cours du demi-siècle dernier. Nous soupçonnons que la Fauvette grisette, en particulier, a souffert d'une perte d'habitat plus importante que les espèces migratrices qui se nourrissent exclusivement dans le houppier des arbres.

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