# Downstream Ecological Consequences of Livestock Grazing in the Sahel: A Space-For-Time Analysis of the Relations between Livestock and Birds

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# Downstream ecological consequences of livestock grazing in the Sahel: a space-for-time analysis of the relations between livestock and birds

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Bird counts in the Ferlo, NW Senegal had shown that the density of ground-foraging birds was much lower in grazed than in ungrazed savannah: 84% fewer granivorous birds and 64% fewer insectivorous birds. Between 1960 and 2010, in three areas within the same region, granivores declined by 39–97% and insectivores by 61–91%, losses attributable to the steadily increasing livestock grazing pressure. If these trends hold for all Sahelian rangelands, the extrapolation at the time indicated that 1.5 billion birds would have been lost in just half a century. The aim of this space-for-time substitution study was to investigate whether that extrapolation can be substantiated with data from the eastern Sahel. To permit analysis of the spatial and seasonal variation in grazing pressure and its impact on ground-foraging granivorous and insectivorous birds, we counted birds in 1901 sites across the entire region (Mauritania to Ethiopia) and took landscape photos of these sites to evaluate livestock presence. We also estimated livestock density from our counts of cowpats and of droppings of sheep and goats, and the cover of the soil vegetation. Within the same rainfall zone (200–400 mm/year), the grazing pressure was higher in the Ferlo than elsewhere in the Sahel. Grazing pressure declined in the Ferlo in the course of the dry season, indicating that cattle food supply became depleted. No such seasonal decline was recorded elsewhere in the Sahel. The same pattern was found for ground-foraging birds: a decline during the dry season in the Ferlo, but nowhere else in the same Sahel rainfall zone. Indeed, in the 1960s and 1970s, when the grazing pressure was much lower than today, there were no records of a seasonal decline of ground-foraging birds in the Ferlo. The much lower densities of seed-eating birds in the Ferlo were not exhibited elsewhere in the Sahel, which is consistent with the phenomenon of local overgrazing. The previous extrapolated loss of 1.5 billion birds is therefore too high, because conditions in the Ferlo were found to differ from those experienced elsewhere in Sahel's arid zone. The actual overall loss cannot be specified due to lack of bird counts from the past in the eastern Sahel. The comparison of grazing pressure and bird densities across all rainfall zones of the western and eastern Sahel shows that increasing livestock densities negatively impact bird numbers. Livestock grazing pressure in the west was higher than in the east and most ground-foraging bird species were less common in the west than in the east. Furthermore, the majority of ground-foraging species in West Sahelian savannahs were exclusively confined to the arid and semi-arid zone, but in the east, these species were more widely distributed and also occupied the more humid zone to the south.

Key words: Sahel, livestock, ground-foraging birds

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With a land surface of 30 million $km^2$, Africa is a large continent that is home to millions of long-distance migratory birds from Europe and Asia in winter (Moreau 1972). The question to what extent the decline of many European breeding populations of migratory birds is due to changes in their African wintering grounds has proven difficult to answer (Salewski & Jones 2006, Sanderson 2006, Zwarts *et al.* 2009, Morrison *et al.* 2013, Adams *et al.* 2014, Atkinson *et al.* 2014). Deforestation, conversion of savannah into cropland, and short- and long-term changes in annual rainfall act on vast geographic scales and are no doubt major factors in the fortunes of long-distance migrants. This paper investigates another factor that might have a large negative impact on migratory bird numbers: the overall increase of livestock. In particular, the region between 7 and 22°N, an area of 10 million $km^2$, has experienced significant increases in the numbers of grazing herds of cows, goats and sheep since at least 1960. For instance, FAO data (www.fao.org/faostat/en/#data/TP) showed that cattle numbers in 21 countries, fully or partly situated between these latitudes, on average have increased exponentially by 2.30% per year, from a total of 60 million in 1961 to 231 million in 2019. Sheep increased by 2.78% per year from 50 million in 1961 to 256 million to 2019, goats by 3.45% per year from 45 to 311 million. The accuracy of the FAO data is uncertain, but there can be no doubt that grazing pressure is mounting, driven by the 2.61% annual increase of the human population in the same 21 countries, from 106 million in 1950 to 607 million in 2020 (https://esa.un.org/unpd/wpp). In fact, Bonnet-Dupeyron's (1945) estimate for the same region (excluding Sudan and Ethiopia) in the early 1940s amounted to only 7 million cattle, an indication that cattle numbers have been increasing for a long time indeed.

Grazing alters the age structure and density of the vegetation and the species composition of the plant community (Chapin *et al.* 2002). Such changes have substantial impact on breeding and foraging birds in multiple ways (e.g. Barzan *et al.* 2021). The impact of grazing is evident in semi-arid and humid tropical areas where in the absence of livestock, savannah turns into acacia woodland within a brief period of time (Photo 1D). In contrast, when arid areas lack domestic grazing, a savannah landscape with scattered trees will hardly change (Photo 1B). This does not imply, however, that grazing on savannahs in the arid zone does not affect foraging birds. In the Sahel, as in other drylands, grasses and forbs grow during the short rainy season after which they die back; during this stage seeds ripen and are shed. For example, in Argentinian drylands, seed density on the ground during the dry season was 74% lower in grazed sites than in ungrazed, and the density of seed-eating finches was 48% lower (Gonnet 2001). In heavily grazed sites, seed density was reduced by 95% and bird density by 70%. The finches preferred grass seeds, taking 52–92% of the annual production during the dry season (Pol *et al.* 2014). When the density of preferred seeds became too low, some birds switched to other food resources, but most dispersed to other places (Marone *et al.* 2017). In Britain, nine ground-foraging bird species in winter foraged in lower densities when seed density had become depressed, sites being abandoned when seed density dropped too low (Stephens *et al.* 2003).

During the long dry season (October–June), the seeds produced by annual grasses and forbs in the Sahelian savannah are the only food resource for many ground-foraging bird species (Keith *et al.* 1992, Fry & Keith 2004). In Fété Olé, a site in the arid north of Senegal, on average, 80 grasses and forbs per $m^2$ produce 50,000 seeds at the end of the rainy season. Nine months later at the start of the next rainy season, 500 seeds per $m^2$ remain to germinate. Only 80 seeds/$m^2$ survive to begin the next annual cycle (Bille 1992). Rodent predation is a prime cause of the 90% decline of seeds during the dry season (Poulet 1974), followed by birds (Morel & Morel 1970, 1972a) and insects (Gillon & Gillon 1974; Gillon *et al.* 1983). The annual variation in seed predation is large and is dependent mostly on the variation of annual rainfall (Bille 1974). In dry years with low seed production, many seed-eating birds die, and the survivors are in poor condition and often unable to breed (Morel & Morel 1974). When grazing pressure structurally reduces seed availability, bird populations of granivorous birds will decline (Zwarts *et al.* 2023c).

Previous research had shown that in the Ferlo granivorous birds had declined by 39–97% and insectivorous birds by 61–91% over the last 20–50 years (Zwarts *et al.* 2018). Bird counts from 20–50 years ago, such as performed in the Ferlo (Supplementary Material), have not been carried out elsewhere in the Sahel, at least to our knowledge. We therefore do not know whether birds in the Sahel have declined as much as in the Ferlo, but if they have done so, the implications would be large, given the size of the Sahel, which extends by 6000 km from the Atlantic Ocean to the Red Sea. If the birds in the Sahel have declined as much as in the western Ferlo, an extrapolated 1.5–2 billion birds, among which 300–400 million Afro-Palearctic migrants, would have been lost in just half a century (Zwarts *et al.* 2018).

However, the Ferlo may not be representative of the arid Sahelian savannah at large. First, the western Sahel is more densely populated than the eastern Sahel (see Figure 8 in Zwarts *et al.* 2023a). Second, the grazing pressure in NW Senegal may be especially high because of the proximity of the Senegal River and seasonal waterbodies (see Photo 1 in Zwarts *et al.* 2023c). Third, the density of large, mechanised boreholes in the western Ferlo is unprecedented, facilitating the conversion of remote drylands into grazing grounds (Photo 2).

In this paper we use a space-for-time approach (i.e. analysing spatially separated sites where environmental gradients serve as proxies to understand temporal processes) to re-examine the hypothesis that livestock grazing reduces ground-foraging bird populations in the Sahel. We compare recent bird densities and grazing pressure of the Ferlo with those elsewhere in the Sahel, and also of the western and eastern Sahel, under the assumption that grazing is the main cause of declines of ground-foraging birds.


**Photo 1.** Grazed and ungrazed savannah during the dry season; average annual rainfall (based on Hijmans *et al.* 2005) is given on each image. (A) The history of this Mauritanian exclosure is unknown. (B) In the NW Senegal site, livestock had been excluded from the fenced area since 1992 (Miehe 2007), 22 years before the picture was taken. The density of seed-eating birds in the exclosure was six times higher than in the grazed area beyond the fence. (C) When the picture was taken, this exclosure in Mali was less than two years old (visible on Google Earth on 10 January 2008, but not on 15 April 2007). Note the high density of cowpats on the bare ground in the grazed areas of A, B and C. (D) A fence with a track on both sides separates open savannah (with tall baobabs) grazed daily by livestock from a nearby village (left of the fence) and woody savannah (with low Red Acacia *Acacia seyal*) in the West Senegal Bandia Reserve (right of the fence), subject to low grazing pressure of wild herbivores. Satellite photos from 1968 and high-resolution satellite images available since 2003 show that a densely wooded savannah in 1968 has turned into an almost bare savannah in 2003, but since the construction of the fence in 2004, the Bandia Reserve transformed back into a densely wooded savannah within a few years (Hejcmanová *et al.* 2009, Zwarts *et al.* 2015).

## METHODS

For a Sahel-wide comparison of grazing and bird numbers we have data at our disposal that were collected in 2144 study sites between 7 and 22°N and between 17°W and 42°E between 2011 and 2019 (Zwarts *et al.* 2023a). At each site, we counted birds and trees in triangular transects with three legs of 300 by 50 m each (Figure 2 in Zwarts *et al.* 2023a); methods are described in detail by Zwarts & Bijlsma (2015). All sites were categorised as woodland, farmland (including fallow) or savannah (including desert, scrubland and woody savannah). This study is based on a selection of savannah sites, excluding those few sites that comprised rocky or stony soil. For the description of the average bird density per rainfall zone and/or longitudinal band, we used only random sites. Unless stated otherwise, we selected data collected in the dry season (20 November – 10 March; most data collection occured in January and early February, but we excluded data from Ethiopia. In the strict sense, the Sahel is the climate zone where the annual rainfall varies between 100 and 600 mm (Figure 5 in Zwarts *et al.* 2023a), but we use the term here in a much wider sense as covering the full transition zone between Sahara in the north and the humid forests in the south.

We visited the western Ferlo more frequently than the rest of the Sahel (January and December 2014, February–March and October 2015 and October 2019), not least to compare the recent situation with the one described in great detail for the 1960s, 1970s and 1990s (Figure 1, Supplementary material; see also Zwarts *et al.* 2018). The average annual rainfall in this region varies between 200 mm in the north (16.5°N) and 400 mm in the south (15°N). The data collected in the western Ferlo are compared to other study sites in sandy savannahs of the 200 to 400 mm rainfall zone between Senegal and Sudan. The average annual rainfall (calculated over the period 1950–2000) per site was taken from Hijmans *et al.* (2005) and does not deviate, on average, from the rainfall during our period of observation (2011–2019). Rainfall (in mm) preceding our visits in the Ferlo and in the dry zone of the rest of the Sahel varied little over the years of our study, except in 2010 (much rain) and 2013 (little rain). The annual rainfall during the four years when we visited the Ferlo did not differ, on average, from the seven years when we did fieldwork in the same rainfall zone elsewhere in the Sahel.

We used various methods to quantify the presence of livestock, the grazing pressure, and its impact on the ground vegetation:

**Photo 2.** In the past, large parts of the Sahelian savannah were left ungrazed by livestock in the dry season due to lack of water. Grazing was limited to river valleys and emerging floodplains and their surroundings, up to a walking distance of 5–10 km from watering points. After the construction of mechanised boreholes (watering points), much larger areas could be grazed in the dry season. This further increased in the 1980s when people started to use donkey carts to transport water to the animals. The photo, taken in the western Ferlo on 30 October 2015, shows that the ground vegetation has already completely disappeared early in the dry season. 1000-litre containers are better for transporting water than using large inner tubes, the method prevalent when donkey carts had become the popular method of water transportation.

(1) To quantify the presence of livestock, we used landscape photos we had taken of the study sites. Regarding the presence of livestock, we consider these images to be unbiased, because our primary purpose was to document per site the landscape and its constituent trees, the latter to validate our field measurements of tree dimensions. For each study site, we noted the presence or absence of livestock (cattle, goats, sheep or dromedaries), enumerating the images in each category; when more than one photo was taken of the same scene, we selected the first one.

(2) To quantify the grazing pressure within the study sites, at each 100 m of transect, we counted the number of small droppings of goats and sheep and cowpats per 4 $m^2$.

(3) To quantify the vegetation cover in the study sites, we estimated the percentage of the soil surface covered by vegetation within a square of 2 × 2 m, irrespective of greenness (including dried vegetation and leftovers from harvest), standing or lying, and crops or natural vegetation. Two by two meter plots were chosen at intervals of c. 100 m, on average 9.7 squares per site.

## RESULTS

### Grazing, vegetation and birds in the Ferlo compared to the rest of the Sahel

GRAZING AND VEGETATION

The photos from our study sites revealed that cattle density in the western Ferlo, averaged for the entire dry season, was quite similar to that elsewhere in the Sahel in the same rainfall zone (200–400 mm/year; 5.1 vs. 4.8% of the pictures; one-way ANOVA: $P > 0.05$, $n = 1754$). However, seasonal differences in the Ferlo were large. In the western Ferlo cattle density was high in the early dry season (livestock visible on 7.4% of the pictures in October–December), declining to 0.8% in February–March ($\chi^2_1 = 4.1$; $P = 0.01$). Elsewhere within the same rainfall zone, the number of cattle visible on the photos remained constant during the dry season. Goats and sheep were more common in the Ferlo than elsewhere (14.8 vs. 9.5%; $\chi^2_1 = 15.4$; $P < 0.001$), with a weak increase between October and March ($P < 0.001$) in the Ferlo ($\chi^2_2 = 15.4$) and elsewhere ($\chi^2_1 = 14.7$).

Counts of cowpats showed that the grazing pressure in the Ferlo, averaged for October–March, was somewhat higher than elsewhere in the rainfall zone of 200–400 mm (2.95 vs. 2.76/4 $m^2$; one-way ANOVA: $P = 0.01$), and significantly different between months (2-way ANOVA: $n = 3036$, $P = 0.006$). Beyond the western Ferlo, the density of cowpats linearly increased from 0.23 in October to 4.43/4 $m^2$ in March. Cowpat density in the Ferlo only increased between October and December; after December, the density of cowpats remained stable. For goats and sheep, the density of their droppings increased non-significantly during the dry season and was higher in the Ferlo than elsewhere (9.83 vs. 8.16/$m^2$; 2-way ANOVA: $n = 1750$, $P = 0.001$).

The vegetation cover declined over the dry season and was overall sparser in the western Ferlo (8.4 vs. 16.2%; Figure 1; see also Photo 1B). The three data sets (pictures, cowpats, vegetation) show the western Ferlo to be more intensively grazed than the rest of our arid study zone. In the western Ferlo, grazing pressure was particularly high in the first months of the dry season (October–December), resulting in a complete loss of ground vegetation. In this area, most herders and their cattle had left by January.

BIRDS

The density of granivorous birds in the western Ferlo was much lower than elsewhere in the arid zone (Table 1). The difference was most striking for Sudan Golden Sparrow *Passer luteus* (0.37/ha in the Ferlo vs. 2.70/ha elsewhere; one-way ANOVA: $n = 255$, $P = 0.02$) and African Silverbill *Euodice cantans* (0.01 vs. 0.20; $P = 0.03$). For several dove species the differences were small (e.g. Namaqua Dove *Oena capensis*: 0.32 vs. 0.40, Laughing Dove *Spilopelia senegalensis*: 0.11 vs. 0.17). The density of insectivorous birds in the Ferlo did not differ from elsewhere in the arid zone. In the Ferlo, bird densities declined during the dry season (Table 1), but no such trend was found elsewhere in the arid zone (based on bird densities averaged for five months between September and March).

### Grazing, vegetation and birds across the Sahel

GRAZING AND VEGETATION

The presence and composition of livestock differed per rainfall zone and longitudinally (Figure 2). In the western Sahel, dromedaries were restricted mostly to the arid zone (<200 mm rainfall/year) while cattle, goats and sheep were more common in the zone with 200–600 mm rainfall/year. In the eastern Sahel, all livestock species roamed extensively across the 200 to 1100 mm rainfall/year zones, but at a lower density. In the western Sahel, cattle and goats+sheep were twice as common as in the eastern Sahel.

The density of cowpats showed a similar trend to livestock presence across the Sahel. In the western

Sahel, cowpat density was three times higher than in the eastern Sahel (Figure 3). The density of droppings of goats and sheep increased from 1.73/4 $m^2$ at <100 mm rainfall/year to 20.5/4 $m^2$ at 200–300 mm, and linearly declined in the more humid zones to 3.5/4 $m^2$ at 900–1000 mm. Rainfall was strongly correlated ($P < 0.001$) to density of droppings; land use, longitude and their interaction terms were not significant (3-way ANOVA: $r^2 = 0.109$; $n = 495$ sites).

BIRDS

The density of ground-foraging birds increased with the rainfall gradient but in the western Sahel lower densities were recorded in the humid zone than in the eastern Sahel (Figure 4). The single exception, recorded in a single grid cell in the western 1000–1100 mm rainfall zone (Figure 4A), refers to high numbers of seedeaters in the Comoé National Park (Côte d'Ivoire) in December, which are unlikely to be representative of the humid zone in West Africa in general. Within the arid zone, bird densities did not differ much between the eastern and western halves of the Sahel (Figure 4). Differences are more pronounced when a comparison is made at species level (Table 2). The Red-billed Quelea *Quelea quelea*, for example, was rare in the Sahel when annual rainfall was less than 500 mm, and also rare in

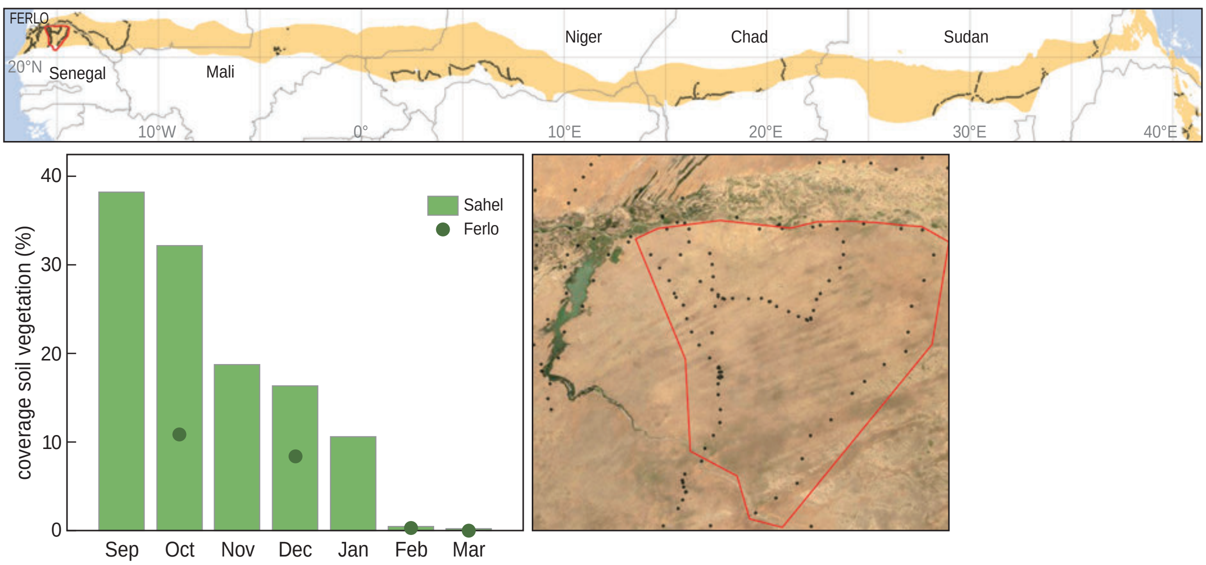


**Figure 1.** Seasonal decline of the vegetation cover (%) of sandy savannah during the dry season, separately for the western Ferlo and all other sites across the Sahel with an average annual rainfall of 200–400 mm/year (2-way ANOVA: season: $P < 0.001$, Ferlo: $P = 0.002$; season×Ferlo: $n = 2183$, $r^2 = 0.103$, $P < 0.001$). The map shows the study sites (•) within the 200–400 rainfall zone (yellow band). The western Ferlo is enclosed by a red line (inset).

**Table 1.** (Left) Average bird density per ha during the dry season (October–March) in the Ferlo and elsewhere in the Sahel on sandy savannah within the 200–400 mm rainfall zones (Figure 1), being significantly different for granivores but not for insectivores (one-way ANOVA; *P* value given in table). (Right) Bird densities of granivores and insectivores significantly declined during the dry season in the Ferlo (one-way ANOVA; *P* value given in table). In the three bird groups, there was no seasonal decline between October and March elsewhere in the arid zone (one-way ANOVA's; results not given). There were no granivorous migrants in the Ferlo and 0.064/ha elsewhere in the arid zone ($P = 0.238$).

| | **Sahel** | **Ferlo** | ***P*** | **Ferlo** | | | ***P*** |
|---|---|---|---|---|---|---|---|
| | Oct–Mar | Oct–Mar | | Sep–Oct | Dec | Feb–Mar | |
| granivorous residents | 4.75 | 1.95 | 0.005 | 3.15 | 2.50 | 1.03 | 0.011 |
| insectivorous residents | 0.72 | 0.80 | N.S. | 1.34 | 1.06 | 0.38 | 0.003 |
| insectivorous migrants | 0.40 | 0.46 | N.S. | 0.79 | 0.51 | 0.29 | 0.014 |
| **Number of sites** | **176** | **79** | | **21** | **19** | **39** | |

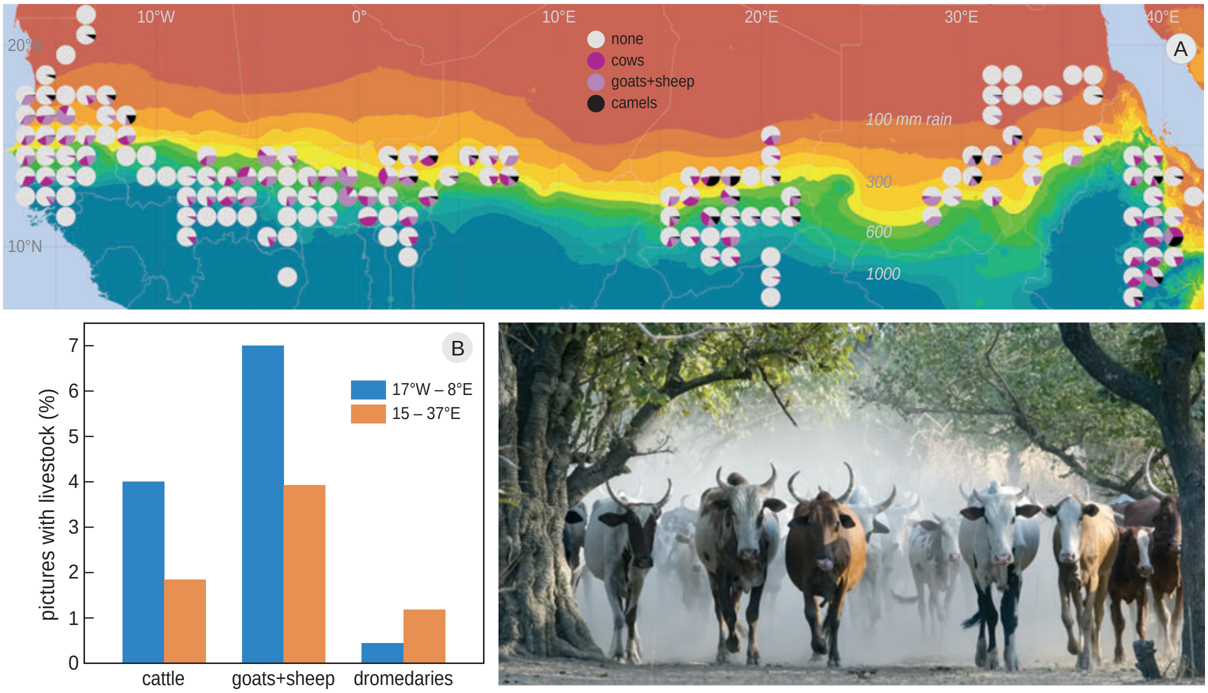


**Figure 2.** (A) The presence of livestock (%) across the Sahel between 20 November and 10 March, scored on 11,883 landscape photos taken in 150 grid cells (excluding woodland sites). Livestock was present on 7% of the photos, on average, and varied for the grid cells between 0 and 33%. To improve the clarity of the pie charts, the maximum percentage of livestock in the grid cells (33.3%) was set at 100%. (B) The presence of livestock on photos (%) in the western and eastern Sahel (annual rainfall <1300 mm, based on 7616 and 2446 photos, respectively. The differences are highly significant (cattle: $\chi^2_1 = 20.8$, goats+sheep: $\chi^2_1 = 22.3$, dromedaries: $\chi^2_1 = 15.59$; $P < 0.0001$).

the more humid zone in the western Sahel. In the eastern Sahel, however, Queleas reached densities of 5.4–6.2 birds/ha in the 700–900 mm rainfall zone. A similar pattern was found for the Red-cheeked Cordon-bleu *Uraeginthus bengalus*, which was uncommon in the western Sahel (<0.8/ha in the 400–800 mm rainfall zone), but common in the eastern Sahel (1.6–2.7/ha in the 500–1000 mm rainfall zone). Very few species showed a reverse pattern of lower densities in the eastern Sahel, notably Cut-throat Finch *Amadina fasciata* (Table 2). The humid zone in the eastern Sahel held many more birds than the same zone in the western Sahel (see last two columns in Table 2). This difference is not just evident for resident bird species, but also for two Wheatear species that reached their highest densities in the west in the zones between 100 and 400 mm of rainfall, and in the east between the 300- and 900-mm-rainfall zones (Figure 5). Woodchat Shrike *Lanius senator* has a more southerly distribution in the east, but the difference with the western Sahel is small. No difference was found in Tawny Pipit *Anthus campestris* (Figure 5).

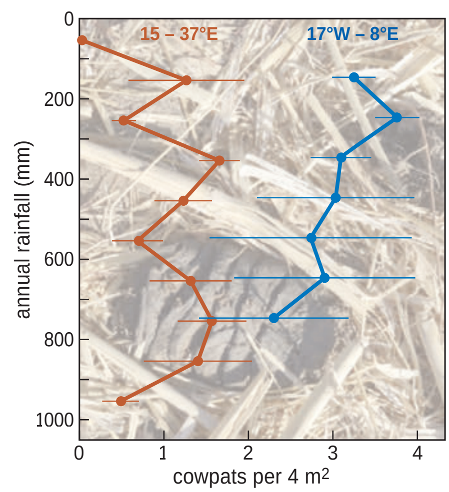


**Figure 3.** The average density of cowpats per 4 m$^2$ (±SE) on sandy savannah in the dry season, given for ten rainfall zones in the western (17°W–8°E) and eastern Sahel (15–37°E). Rainfall, longitude and their interaction term were all significant ($P < 0.001$, 2-way ANOVA: $r^2 = 0.207$, 495 sites). The graph did not change when 269 farmland sites were included; land use was non-significant ($P = 0.157$) in a 3-way ANOVA.

## DISCUSSION

### Decline of ground-foraging birds in the Sahel

Ground-feeding birds showed a large decline in the Ferlo since at least the 1960s, following increased grazing pressure and droughts (Zwarts *et al.* 2018). Two landscape pictures taken at the same site in 1994 and 2011 illustrate how much the savannah in NW Senegal has changed under heavy grazing in a period of just 17 years (Photo 3). Did similar changes occur in Sahelian regions further east, with similar consequences for ground-foraging birds? If so, the overall decline of ground-feeding birds must have been massive. However, the number of livestock (Figure 2) and density of cowpats (Figure 3) showed that the grazing pressure in the western Ferlo in the 2010s was higher than in the corresponding rainfall zone elsewhere in the Sahel. The exceptionally high grazing pressure explains why the ground vegetation in the western Ferlo in October had completely disappeared by December (Figure 1). No such depletion of grassy vegetation was recorded in the eastern Sahel, where

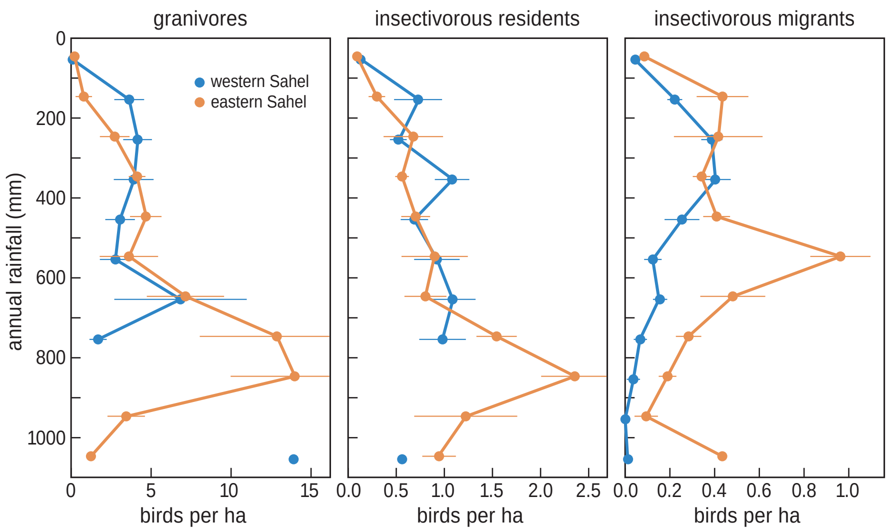


**Figure 4.** Density of three groups of ground-foraging birds per rainfall zone on sandy savannah in the western (17°W–8°E) and eastern Sahel (15–37°E) during winter. The effect of rainfall is significant for all three groups ($P < 0.001$), longitude only in migrants ($P < 0.001$) and the interaction term in granivores ($P = 0.042$) and migrants ($P = 0.003$); $r^2$ is 0.119 in granivores, 0.155 in insectivorous residents and 0.131 in insectivorous migrants (2-way ANOVA; $n = 578$ sites); note that the scales of the horizontal axes vary.

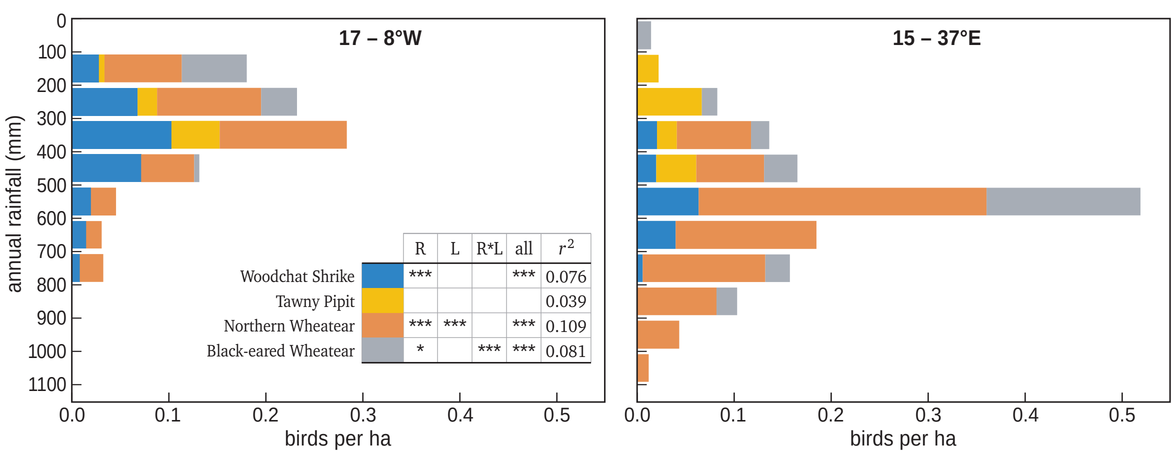


**Figure 5.** Density of four ground-foraging insectivorous migrants on sandy savannah in 11 rainfall zones, given separately for the western (left) and eastern Sahel (right). The density differed significantly per rainfall zone (R; except for Tawny Pipit), non-significantly for longitude (L; except for Northern Wheatear) and for the interaction term (R×L; except for Black-eared Wheatear *Oenanthe melanoleuca*; 2-way ANOVA; $n = 716$ sites; $^{*}P < .05$, $^{**}P < .01$, $^{***}P < .001$).

the grazing pressure was much lower than in the western Ferlo.

The 70% lower density of seed-eating birds in the western Sahel compared to the rest of the arid Sahel can be explained by differences in grazing pressure and therefore by vegetation cover (Table 1). Granivorous birds and ground-foraging insectivorous birds largely left the Ferlo during the dry season (Table 1), unlike elsewhere in the same rainfall zone and in the Ferlo in the 1970s, except in an extremely dry year (Morel & Morel 1974, 1978). As the rainfall during our study period in the Ferlo did not deviate from average (Zwarts *et al.* 2015), the current situation of rapid depletion of the limited food supply will force ground-foraging birds to leave the Ferlo during the dry season, and/or cause high mortality. Our tentative conclusion is that ground-foraging birds in the Ferlo have been more negatively affected by increased grazing pressure than elsewhere in the northern Sahel. It is unlikely that bird numbers in the Sahel in general have declined quite as much as in the Ferlo, at least so far.

**Table 2.** The maximum average density (*n*/ha) per rainfall zone on sandy savannah in the western (W) and eastern (E) Sahel (W = 431 sites; 17°W–8°E and E = 285 sites; 15–37°E). The rainfall zones where the birds reached their maximum densities are shown in the last two columns (0 = rainfall zone 0–100 mm/year, 1 = 100–200 mm, etc.). Granivores are printed in bold. Selection is made of 34 common bird species which occur in both the eastern and western parts of the Sahel.

| Bird species | birds/ha | | rain | |
|---|---|---|---|---|
| | W | E | W | E |
| **African Collared Dove** | 0.120 | 0.207 | 7 | 6 |
| **Vinaceous Dove** | 0.089 | 0.550 | 5 | 7 |
| **Laughing Dove** | 0.231 | 0.186 | 2 | 7 |
| **Black-billed Wood Dove** | 0.017 | 0.166 | 7 | 7 |
| **Namaqua Dove** | 0.463 | 0.264 | 3 | 7 |
| Black-headed Lapwing | 0.209 | 0.222 | 6 | 5 |
| Eurasian Hoopoe | 0.023 | 0.060 | 1 | 7 |
| Northern Red-billed Hornbill | 0.260 | 0.241 | 6 | 5 |
| Abyssinian Roller | 0.067 | 0.058 | 7 | 8 |
| Great Grey Shrike | 0.069 | 0.065 | 1 | 3 |
| Woodchat Shrike | 0.103 | 0.063 | 3 | 5 |
| **Black-crowned Sparrow-Lark** | 0.439 | 0.424 | 1 | 3 |
| **Chestnut-backed Sparrow-Lark** | 0.118 | 0.394 | 6 | 5 |
| **Greater Short-toed Lark** | 0.021 | 2.584 | 0 | 1 |
| Cricket Warbler | 0.144 | 0.172 | 1 | 2 |
| Purple Starling | 0.031 | 0.317 | 3 | 7 |
| Long-tailed Glossy Starling | 0.137 | 0.267 | 7 | 7 |
| Chestnut-bellied Starling | 0.468 | 0.286 | 3 | 4 |
| Black Scrub Robin | 0.115 | 0.184 | 3 | 2 |
| Rufous-tailed Scrub Robin | 0.103 | 0.218 | 6 | 6 |
| Northern Wheatear | 0.131 | 0.297 | 3 | 5 |
| Black-eared Wheatear | 0.067 | 0.159 | 1 | 5 |
| **Sahel Bush Sparrow** | 0.205 | 0.089 | 7 | 6 |
| **Northern Grey-headed Sparrow** | 0.332 | 0.433 | 3 | 6 |
| **Sudan Golden Sparrow** | 2.212 | 2.578 | 2 | 4 |
| **White-billed Buffalo-Weaver** | 0.124 | 0.290 | 3 | 3 |
| **Speckle-fronted Weaver** | 0.308 | 0.928 | 3 | 6 |
| **Vitelline Masked Weaver** | 0.621 | 0.415 | 6 | 6 |
| **Red-billed Quelea** | 1.869 | 6.172 | 6 | 7 |
| **African Silverbill** | 0.341 | 0.173 | 1 | 3 |
| **Black-rumped Waxbill** | 0.185 | 0.741 | 5 | 6 |
| **Cut-throat Finch** | 0.993 | 0.057 | 6 | 5 |
| **Red-cheeked Cordon-bleu** | 0.431 | 2.702 | 5 | 8 |
| **Red-billed Firefinch** | 0.256 | 0.133 | 7 | 6 |

**Seed-eating birds and their food supply**

There are several bird species in the Sahel which cling to grass stems to harvest attached seeds, such as Yellow-fronted Canary *Crithagra mozambica*, Bronze Mannikin *Spermestes cucullata* and various waxbill *Estrilda* species and seedeater *Crithagra* species (Fry & Keith 2004). Other seed-eating bird species may incidentally feed in grass tufts or pull them down to take seeds off the panicle, but most would wait until the plants shed their seeds. From then on, all granivorous birds, including the aforementioned species, forage exclusively on the ground. At first, many seeds are not yet accessible to ground-feeding birds due to the dense vegetation; the tall grasses form a blanket covering the fallen seeds (Ward 1965). By removing the standing grasses and forbs during the early dry season, grazing livestock facilitate seed-eating birds without substantially reducing the total food supply because the seeds have already been shed at the end of the wet season (Hiernaux *et al.* 2009). Timing of grazing has thus far-reaching consequences for the seed supply. Grazing during the wet season reduces seed formation and potential soil seed stocks (Sternberg *et al.* 2003), and consequently the food supply for granivorous birds. In contrast, dry-season grazing by cattle, sheep and goats does not deplete the remaining seed supply.

Our estimates of grazing pressure (counts of cow-pats and droppings, presence of livestock on photos) refer to dry-season grazing and seem – in the light of the above – less relevant to ascertain the local impact of grazing on ground-foraging birds. However, overall cattle density in the western Sahel is much higher than in the eastern part, both during the wet and the dry season. For this reason, we would expect that ground-foraging birds must have declined more severely in the

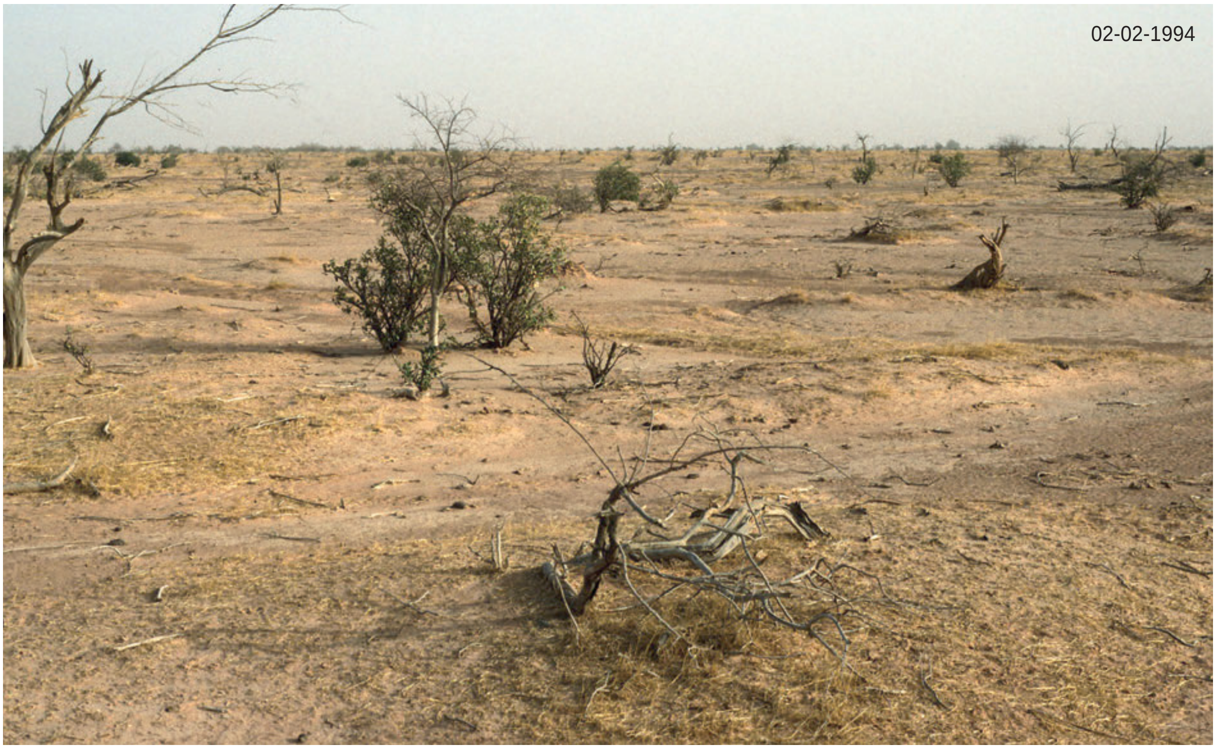



**Photo 3.** Two pictures taken by G. Gray Tappan (U.S. Geological Survey, EROS Center, USA) from exactly the same spot in the Ferlo near Révane (15.6°W, 14.4°N; average annual rainfall 390 mm) during the dry season in 1994 and 2011. The savannah with scattered trees (mainly *Acacia tortilis* and *A. senegal*) had already been transformed into an almost treeless landscape (mainly *Boscia senegalensis* bushes) before 1994 but had become even more desolate 17 years later. The extent of grassy vegetation die-back during the dry season (Figure 1), a process markedly prevalent in February 1994, is much more evident in November 2011; the difference cannot be explained by variation in annual rainfall (the same for both years; Figure 6 in Zwarts *et al.* 2018). See also www.usgs.gov/media/before-after/expansion-degraded-land-ferlo-region-senegal/.

western than in the eastern Sahel. The lack of systematic bird counts from the eastern Sahel in the past prevents any quantified statement to this effect. In the current situation (2010s), insectivorous migrants were 2–8 times more common in most rainfall zones in the eastern than in the western Sahel (Figure 5C). In contrast, insectivorous and granivorous residents were equally common in the (semi) arid zone of the western and eastern Sahel, but in the humid zone reached higher densities in the east than in the west (Figure 5A and 5B).

The 500-mm isohyet in Chad lies some 280 km further south than in Senegal (15°N and 17–18°N, respectively) and the 1000-mm isohyet even further at 780 km (17°N and 9°N, respectively; Figure 4 in Zwarts *et al.* 2023a). Assuming that the distribution of birds is governed by annual rainfall (Figure 13 and 14 in Zwarts *et al.* 2023a), we expected an equally large shift to the south in the distribution of ground-foraging birds in Chad compared to Senegal. The actual shift is larger, in fact, since most of the bird species reach their maximum densities in the eastern Sahel in more humid rainfall zones than the same species in the western Sahel (Table 2, Figure 5 and 6). It is of interest to note that the same applies for the Desert Date *Balanites aegyptiaca* and other characteristic savannah tree species, found in Senegal mostly at 15–17°N (c. 300 mm rain/year) but in Chad at 10–14°N (600–700 mm/year; Figure S3 in Zwarts *et al.* 2023b). The same southward extended distribution was recorded for dromedaries, cattle and sheep and goats (Figure 2).

In sparsely populated Chad and Sudan, the vegetation typical of the savannah zone with an annual rainfall of 500–1000 mm still exists more or less intact, a stark contrast to the densely populated western Sahel (Figure 8 in Zwarts *et al.* 2023a) where the composition of the plant community has changed radically under the influence of mounting grazing pressure. The outlier in West Africa is the high density of many seed-eating birds recorded at >1000 mm rainfall/year (Figure 5), deduced from data collected within the Comoé National Park (11,500 km$^2$). It is unlikely that Comoé NP is representative of the remaining sandy savannah at >1000 mm rainfall in present-day West Africa, given the lack of protection beyond the NP borders. Comoé NP probably is representative of the humid savannahs once typical of West Africa (and still partly found in E Sahel), a glimpse of the past, when huge flocks of seedeaters roamed the savannahs and floodplains to the horror of local farmers (Bruggers & Elliott 1989).

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## SAMENVATTING

Vogeltellingen in de Ferlo, in het noordwesten van Senegal, hadden laten zien dat de dichtheid van vogels die op de grond foerageren, geringer was in begraasde dan in onbegraasde savannes. Het verschil was enorm: 84% minder zaadeters en 64% minder insecteneters. In drie telgebieden in de Ferlo waren zaadeters tussen 1960 en 2010 met 39–97% afgenomen, insecteneters met 61–91%. Deze verliezen werden toegeschreven aan de toegenomen begrazingsdruk van vee. Dat fenomeen beperkt zich niet tot de Ferlo. Overal in de Sahel is de graasdruk toegenomen. Als de bevinding in Senegal algemene geldigheid zou hebben, moeten we voor de afgelopen halve eeuw rekening houden met een verlies van 1,5 miljard vogels in alleen al het aride deel van de Sahel. Helaas is deze rekensom niet te verifiëren, omdat vogeltellingen van een halve eeuw geleden, zoals die er wel zijn voor de Ferlo, ontbreken voor de rest van de Sahel. De verificatie is daarom toegespitst op het recente heden: zijn vogeldichtheid en begrazingsdruk in de Ferlo maatgevend voor de rest van de Sahel? Om die vraag te beantwoorden zijn tussen 2011 en 2019 in 1901 random gekozen vakjes van 4,5 ha, verspreid over de hele regio (van Mauritanië tot Ethiopië), systematisch vogels geteld en is de begrazingsdruk geschat door de dichtheid te meten van koeienvlaaien en schapen- en geitenkeutels. Duizenden landschapsfoto's, genomen tijdens het veldwerk in de onderzochte plotjes, zijn bekeken op de aanwezigheid van vee. Bovendien is in alle vakjes de bedekking van de bodemvegetatie geschat. De begrazingsdruk was in de Ferlo aan het begin van de droge tijd (oktober–november) groter dan elders in de Sahel binnen dezelfde neerslagzone (200–400 mm regen per jaar). Ook de bodemvegetatie was er eerder verdwenen dan elders. In de Ferlo vonden we veel minder zaadeters dan elders. De vogels die er wel waren, verdwenen grotendeels in de loop van het droge seizoen uit het gebied. Elders in de Sahel was de graasdruk minder en bleven de vogels gedurende oktober–maart in dezelfde aantallen aanwezig. In de jaren zestig en zeventig, toen de begrazingsdruk veel kleiner was dan nu, was er in de Ferlo evenmin een afname van de vogels in de loop van het droge seizoen, behalve in extreem droge jaren wanneer veel vogels doodgingen door gebrek aan voedsel. De conclusie moet dan ook zijn dat de graasdruk van vee in de Ferlo veel groter is dan elders in dezelfde regenvalzone. Het is daarom onwaarschijnlijk dat de vogels in de rest van de Sahel even hard zouden zijn afgenomen als in Noord-Senegal. Niettemin blijkt uit een vergelijking van de begrazingsdruk en de vogeldichtheid in alle neerslagzones van de westelijke en oostelijke Sahel dat een toename van de veedichtheid een negatief effect heeft op vogels. De begrazingsdruk van het vee was in het westen groter dan in het oosten en de meeste vogelsoorten die op de grond foerageren, kwamen in het westen minder algemeen voor dan in het oosten. Bovendien foerageerden de meeste van deze vogelsoorten in het westen van de Sahel in de aride en semi-aride savannes, maar hadden zij een veel bredere verspreiding in het oosten, waar ze ook in groten getale aanwezig waren in savannes binnen de humide zone.

## RÉSUMÉ

Des comptages d'oiseaux réalisés dans le Ferlo, au nord-ouest du Sénégal, ont montré que la densité d'oiseaux se nourrissant au sol est plus faible dans les savanes pâturées que dans les savanes non pâturées. La différence est énorme : 84 % de granivores et 64 % d'insectivores en moins. Dans trois secteurs du Ferlo, les populations de granivores ont diminué de 39 à 97 % entre 1960 et 2010, et celles d'insectivores de 61 à 91 %. Ces pertes ont été attribuées à l'intensification de la pression de pâturage due à une augmentation du nombre de têtes de bétail, phénomène qui n'est pas limité au Ferlo, mais généralisé dans tout le Sahel. Si le constat fait au Sénégal se vérifiait partout, alors les populations d'oiseaux dans la seule partie aride du Sahel pourraient avoir diminué d'1,5 milliard d'oiseaux au cours du dernier demi-siècle. Malheureusement, ce calcul n'est pas vérifiable, faute d'anciennes données disponibles. Afin de vérifier si le Ferlo est un cas particulier ou pas, nous avons cherché à vérifier si la densité d'oiseaux et la pression de pâturage dans cette région sont comparables à celles du reste du Sahel. Pour répondre à cette question, nous avons inventorié, entre 2011 et 2019, les oiseaux présents et la couverture végétale dans 1901 parcelles de 4,5 ha sélectionnées aléatoirement dans tout le Sahel, de la Mauritanie à l'Ethiopie. Nous y avons également estimé la pression de pâturage en analysant la présence de bétail sur des milliers de photographies de paysages et en relevant la densité de déjections de vaches, moutons et chèvres. Nos résultats montrent que la pression de pâturage est plus élevée dans le Ferlo au début de la saison sèche (octobre–novembre) que dans les zones de précipitations équivalentes ailleurs au Sahel (200–400 mm de pluie par an) et que la végétation au sol y disparaît plus tôt. La densité d'oiseaux granivores est bien plus faible dans le Ferlo qu'ailleurs, et une bonne partie de ceux qui y sont en disparaissent pendant la saison sèche. Ailleurs dans le Sahel, la pression du pâturage est moindre et la densité d'oiseaux reste stable de septembre à mars. Dans les années 1960 et 1970, lorsque la quantité de bétail était beaucoup plus faible qu'aujourd'hui, la population d'oiseaux ne diminuait pas pendant la saison sèche, sauf lors des années extrêmement sèches où de nombreux oiseaux mourraient par manque de nourriture. La pression de pâturage du bétail dans le Ferlo est donc beaucoup plus importante qu'ailleurs dans la même zone pluviométrique : il est par conséquent peu probable que les oiseaux du reste du Sahel aient décliné autant que ceux du Nord du Sénégal. Néanmoins, la comparaison de la pression de pâturage et de la densité d'oiseaux réalisée pour l'ensemble du Sahel, toutes zones pluviométriques confondues, montre que l'augmentation de la densité du bétail a un effet négatif sur les populations d'oiseaux. La pression de pâturage est plus importante à l'Ouest qu'à l'Est, alors que la densité des espèces d'oiseaux qui se nourrissent au sol est plus faible à l'Ouest qu'à l'Est. De plus, la répartition de la plupart des espèces concernées est restreinte aux savanes (semi-)arides dans le Sahel occidental, alors qu'elle est beaucoup plus large à l'Est, où ces espèces fréquentent également en grand nombre les savanes de la zone humide.

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## SUPPLEMENTARY MATERIAL: Bird counts in the Ferlo, NW Senegal, between 1960 and 2015

The bird counts in Fété Olé and two other sites in the 1960s–1990s were repeated in 2014–2015 in order to investigate the impact of mounting grazing pressure on bird populations (Zwarts *et al.* 2018). At another site, bird density was compared in grazed and ungrazed savannah. All four sites are situated in NW Senegal, a region known as the western or sandy Ferlo (Tappan *et al.* 2004), at about 16.2°N and 15.4°W:

(1) The Fété Olé study area was not grazed by livestock when Morel & Morel (1974, 1992) carried out their bird counts between 1969 and 1976. During the 1970s, bird density during the dry season had peaked at 8.2 birds/ha in a wet year (311 mm/year), declining linearly to 1.9 birds/ha in a very dry year (33 mm/year; Figure 13 in Zwarts *et al.* 2018). The region had been heavily grazed in the months preceding our visit in February 2015. Given the local rainfall of 161 mm/year in 2014/15, 3.52 birds/ha were expected, but only 1.16 birds/ha were present (–67%). Most of the birds counted by Morel & Morel were seedeaters (although no precise data on species were given), which suggests that granivorous birds must have been affected most, given their density of only 0.16/ha in 2015.

(2) When Tréca *et al.* (1996) performed systematic monthly bird counts in 1993/94, livestock were excluded from their study site, but in 2014/15 their site was being grazed. Granivorous ground-feeding birds had declined from 20.89 birds/ha in 1993/94 to only 0.64 in 2014/15 (–97%) and insectivorous ground-feeding birds from 3.69 birds/ha to 1.46 (– 61%; Figure 11 in Zwarts *et al.* 2018).

(3) Livestock were not excluded from the study site of Morel (1968) when he counted birds in 1960–1962, nor during our repeat survey in 2014/15. Granivorous ground-feeding birds had declined from 1.45 birds/ha in 1960–62 to 0.88 in 2014/15 (–39%), and insectivorous ground-feeding birds from 0.91 to 0.06 (–93%; Figure 12 in Zwarts *et al.* 2018).

(4) In the fenced experimental site of Widou Thiengoly (Miehe *et al.* 2010), we counted birds in 2014/15 not only in exclosures that were still intact but also in the adjoining areas that had been heavily grazed (Photo 1B). Granivorous ground-foraging birds were much more common in the ungrazed than in the grazed savannah (18.29 birds/ha vs. 2.92; –84%). That difference was also substantial for insectivorous ground-feeding birds (4.08 birds/ha vs. 1.48; –64%; Figure 14 in Zwarts *et al.* 2018).

The data sets 1–3 show that in the Ferlo granivorous birds declined by 39–97% and insectivorous birds by 61–91% over the last 20–50 years. In data set 4 (Widou Thiengoly) a similarly large difference in bird density was found between ungrazed and grazed habitat. The losses due to grazing are particularly telling because grazed and ungrazed areas were surveyed simultaneously within the same region. In study sites (1) and (2) that were being grazed but had lacked grazing in the past, it is difficult to assign the large loss of birds to grazing, to overall habitat deterioration independent of grazing, or to both. In study site (3), grazed currently and in the past (though probably by fewer livestock), bird loss was also considerable.

**Photo 4.** The Ferlo in the dry season during a sand storm (26 February 2015, 16.264°N, 15.313°W).