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Granivorous birds in the Sahel: is seed supply limiting bird numbers?

Leo Zwarts^{1,*}, Rob G. Bijlsma² & Jan van der Kamp¹

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During the dry season four billion African and European granivorous birds in the Sahel consume, by grand average, 15 g seeds/ha/day, equivalent to an average annual consumption of 4.5 kg/ha. This represents only 4–15% of the estimated average total soil seed bank of some 30–100 kg/ha in the early dry season. Despite this apparent abundance of food, there are many reasons to presume that the number of seed-eating birds is limited by their food supply. First, the birds have to share the seed supply with rodents and insects that eat more seeds than all the birds combined. Second, granivorous birds are constrained by foraging time available to them. They avoid foraging during the midday heat and feeding time is mostly restricted to the early morning and late afternoon, totalling about 4 h per day. This forces them to achieve high intake rates and thus to select feeding sites where the available seeds can be handled quickly and/or are so abundant that the encounter rate is high. Third, only a proportion of the seeds lies on the surface where they are easy to find. Most grass seeds are tiny and even small birds need to eat thousands per day. Because they have so little time to look for food, they cannot afford to search for seeds hidden in the sand. Doves rapidly swallow seeds whole, but all smaller seedeaters have to separate the husk from the seed, a process that takes time too. Fourth, seed-eating birds in the Sahel discriminate between seeds. They ignore 'empty seeds' (husks) and also avoid feeding on common graminoids whose seeds have long awns (*Aristida*) or spines (*Cenchrus*) and which are time-consuming to process. Occasionally, granivorous birds may select seeds from forbs, but these, being low in digestibility, are not the preferred choice. Granivorous birds prefer the seeds of *Panicum* grass and other grass species with highly soluble carbohydrate fractions. Birds switch to marginal seed types at the end of the dry season, when the seed bank of the preferred species is depleted. Fifth, soil seed bank of preferred grass species is much reduced in dry years. *Panicum* and other preferred annual grasses are found mostly on riverine floodplains and in depressions that are prone to ephemeral flooding during the rainy season. Such sites attract many seed-eating birds, but the total surface area of floodplains is relatively small compared to the extensive drylands, on top of being very much smaller in dry years, circumstances that account for high mortality among seed-eating birds in drought years. The final argument for food-limitation is that the mounting grazing pressure of livestock over the last decades has severely reduced the annual soil seed bank and changed the plant community (preferred grass species replaced by non-preferred grasses and forbs). The combination of these factors caused a very large decline of seed-eating bird populations in the Sahel between the 1970s and 2010, including a handful of Eurasian species. The Sahel is still home to some four billion granivorous birds during the dry season, but just half a century ago the numbers must have been much higher.

Key words: granivorous birds, prey depletion, Sahel

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Eurasian bird species spending the northern winter in Africa leave their breeding grounds in August–September and do not usually return until April–May. Most insectivorous birds have no choice but to leave the temperate zone in late summer when their arthropod food supply dwindles. In contrast, seed-eating birds have the option not to migrate because seed stocks remain available throughout winter, albeit in decreasing amounts. This inference is generally valid. Very few granivorous species from the temperate zone cross the Sahara to winter in the tropics (Alerstam 1990: 192–193). Apart from omnivorous waterbirds that also take seeds (i.e. ducks and waders), five Eurasian granivorous bird species winter south of the Sahara: Common Quail *Coturnix coturnix*, European Turtle Dove *Streptopelia turtur*, Greater Short-toed Lark *Calandrella brachydactyla*, Ortolan Bunting *Emberiza hortulana* and Cretzschmar's Bunting *Emberiza caesia* (Moreau 1972). Breeding populations of each of these species are declining (BirdLife International 2021). The Pan-European decline of European Turtle Dove (–84%) and Ortolan (–69%) in 1980–2009 is larger than in any insectivorous migrant species (Vickery *et al.* 2014).

In less than half a century, European Turtle Dove, once a common bird in Europe, has become rare, experiencing a >90% decline at the northwestern fringe of the breeding range between the 1970s and 2010 in Great-Britain (Browne & Aebischer 2004, Woodward *et al.* 2020) and in The Netherlands (de Vries *et al.* 2022). The species is also declining in the core breeding range (e.g. –37% between 1996 and 2018 in Spain; Moreno-Zarate *et al.* 2019). The population crash is associated with habitat loss and declining food supplies on the breeding grounds (Browne & Aebischer 2003, Moreno-Zarate *et al.* 2019, Dunn 2021) and to intense hunting during migration (Hirschfeld *et al.* 2019, Lormée *et al.* 2020). Changes in seed availability and hunting are probably important players also in their African wintering areas (Eraud *et al.* 2009, Zwarts *et al.* 2009).

Ortolan Buntings have declined by 88% in Europe between 1980 and 2015 (Jiguet *et al.* 2016) due to habitat changes on the breeding grounds (Vepsäläinen *et al.* 2005, Berg 2008), exacerbated by hunting during migration (Jiguet *et al.* 2019). The overall decline is larger, as the sparse data from older sources show that the species was already in decline in the 1950s (Stolt 1993). Whether the long-term decline involves changes in the African wintering grounds, as suggested by Stolt (1993), is still in question. Cretzschmar's Bunting has declined in SE Europe and probably also in Turkey where most breed (Keller *et al.* 2020).

Recent bird counts in the Sahel suggest crashing wintering populations of the Greater Short-toed Lark and Common Quail between about 1980 and 2020 (Zwarts *et al.* 2023a,c). Greater Short-toed Larks have declined in Europe, including a contraction of the breeding range. Most birds breed in Spain, where there was a decline of perhaps >30% between 1990 and 2000 (de Juana *et al.* 2020). Fluctuations in numbers of Common Quail on the breeding grounds have been linked to variations in rainfall and to farming practices, but numbers appeared to be rather stable at the turn of the century (Puigcerver *et al.* 2012). Declines of the Common Quail have been attributed to increased hunting pressure during migration (Zuckerbrod *et al.* 1980, Caruana-Galizia & Fenech 2016, Eason *et al.* 2016), but a negative impact of reduced food supply in the Sahel is also implicated, as suggested for European Turtle Dove (Eraud *et al.* 2009).

These five Afro-Palaearctic seedeaters together amount to a few hundred million birds that overwinter in a wide band between the Sahara and tropical woodland in the northern half of Africa (estimates based on BirdLife International 2021). This number pales into insignificance compared to the four billion granivorous Afro-tropical birds in the same region (Zwarts *et al.* 2023a). Is the long-term decline of seed-eating migrants an indication of deteriorating conditions in the Sahel and if so, is it a corollary of a massive undocumented decline in Afro-tropical seedeaters? Bird counts in NW Senegal in the 2010s suggest that African granivorous passerines were much less common than in the 1970s and 1980s, a decline attributed to the mounting grazing pressure from livestock (Zwarts *et al.* 2018). Livestock has increased in all Sahelian countries, and seedeaters therefore face grazing-related problems across the entire Sahel (Zwarts *et al.* 2023c). This paper reviews the available literature to determine whether seed-eating birds in the Sahel suffer from a decline in their food supply. We focus our analysis on four topics, embedded in our own data from bird counts in random sites in tropical northern Africa between 7 and 22°N (see Zwarts *et al.* 2023a):

- (1) What is known about the food supply of seed-eating birds in the Sahel?
- (2) Which seeds are selected (and ignored), and why?
- (3) Has the increase in livestock numbers resulted in a decline of the food supply for seed-eating birds?
- (4) Is the population size of seed-eating birds limited by the annual seed production of preferred plant species?

METHODS

In the strictest sense, the Sahel is the climate zone where annual rainfall varies between 100 and 600 mm (Figure 5 in Zwarts *et al.* 2023a), but we use the term here in a wider sense as the transition zone between the Sahara in the north and the humid forests in the south. This region covers several vegetation and climate zones.

We derived the average seed predation by seed-eaters in the Sahel from the average bird density of granivorous bird species (Zwarts *et al.* 2023a,b,c) and the estimated daily consumption per species. To estimate seed consumption, we took body mass values of seed-eating birds given by Urban *et al.* (1986), Keith *et al.* (1992) and Fry & Keith (2004) and derived the daily food consumption from the relationship between daily seed consumption (DSC, g dry weight) and body mass (BM, g; Figure 1):

$$\text{DSC} = 0.473\text{BM}^{0.657} \quad (1)$$

Using equation (1), the daily seed consumption would vary between 1.9 g/day for the smallest seed-eater in the Sahel, Common Waxbill *Estrilda astrild* (8 g), to 25.6 g/day for the largest, Double-spurred Spurrow *Pternistis bicalcaratus* (440 g). From these data, and using the bird density counts from Zwarts *et al.* (2023a), we calculated for each 4.5-ha study site and for each granivorous bird species the daily seed consumption per ha.

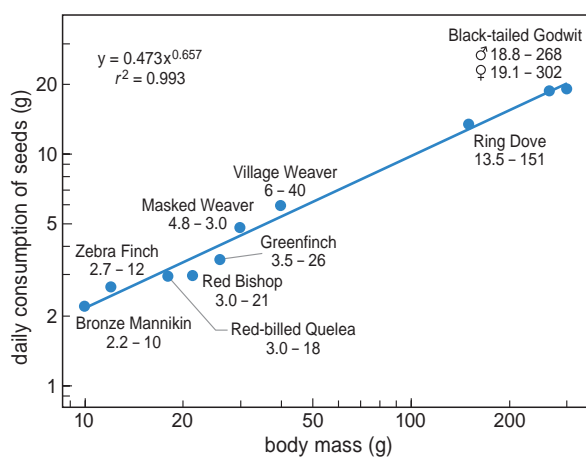


Figure 1. Daily food consumption (g unhusked seed) of nine bird species (captive birds in thermo-neutral conditions) as a function of body mass (g); y - and x -values given below the bird names. Sources: Woodall (1975), Gillespie (1982), Da Camara-Smeets & Manikowski (1981), Brisbin (1969), Meijer *et al.* (1996), Whittington-Jones 2001 and Santiago-Quesada *et al.* (2009).

In our study sites, we measured on 1226 occasions the soil temperature at the surface between November and March (accuracy 0.1°C, not calibrated), during every hour of the daylight period, always in the full sun, and simultaneously on 682 of these occasions the soil temperature in a shady spot in the immediate surroundings. The average rainfall data (determined over the period 1950–2000) were taken from Hijmans *et al.* (2005).

RESULTS

Food supply and seed selection by granivorous birds in the Sahel

FOOD SUPPLY

The vegetation in Africa in the dry belt of the northern tropics reflects the transition from the bare Sahara to savannah grasslands. When less than 100 mm rain/year, herbaceous vegetation is absent. The annual above-ground primary production (dry biomass) of herbaceous vegetation in the 100–200 mm rainfall zone of 0.4 ton/ha increases to 2–3 ton/ha in the 200–400 mm rainfall zone (Le Houérou 1980). Breman & de Wit (1983) provided somewhat higher average annual values: 1 ton/ha at 200 mm of rainfall, increasing linearly to 4 ton/ha at 1000 mm rainfall. Grouzis (1988) measured lower average annual values: 0.2–0.3 ton/ha at 100 mm of rainfall linearly increasing to 1.2–1.8 ton/ha at 600 mm of rainfall. Adding spatial and temporal variation, estimates differ substantially per region and between years depending on annual rainfall. For example, the primary production of the herbaceous layer in Fété-Olé (Senegal, see Figure 2A; 289 mm rainfall/year on average) was measured between 1969 and 1975. The annual rainfall varied between 33 mm (1972) and 450 mm (1969) and the respective annual biomass production between 0 and 1.0 ton/ha on sandy dunes and between 0.02 and 4.1 tons/ha in the valleys (Bille 1977). An equally large variation was measured around Lake Oursi (Burkina Faso, see Figure 2A; 374 mm rainfall/year), with 0.3 tons on sandy dunes and 3.5 tons in low-lying areas with loamy soil (Grouzis 1988). In four African floodplains (Inner Niger Delta, Logone, Kafue and Sudd), the above-ground biomass increased with maximum flood depth (Scholte 2007). The semi-aquatic perennial grasses *Echinochloa stagnina* and *Vossia cuspidata* reached biomass values of 30 to 80 dry tons per ha when the maximum flood depth was 4–8 m (Leauthaud *et al.* 2019). Floodplains are very productive when compared to Sahelian drylands.

Some 1500 plant species occur in the Sahel, but only 15–30 species (often fewer than 5) usually occur within a randomly chosen homogenous site of some hundreds of m² (Hiernaux & Le Houérou 2006). Within the Sahel, the vegetation is dominated by annual grasses, except on the floodplains where perennial grasses are more common. The total annual seed production ranges from 6 to 30% of the annual above-ground primary biomass production (Grouzis 1988). Seedfall occurs at the end of the rainy season (September). Seed densities can be high. For example, near Kaédi (Mauritania, see Figure 2) 176,000 seeds per m² were recorded, mainly *Panicum laetum* (Carrière 1989). With such a density, and with *Panicum* seeds measuring 1 × 2 mm, more than one third of the surface would have been covered by seeds, though a proportion of the seeds lies buried in the soil. Even so, at this site seeds represented a very large, potential food supply of 167 g/m² for granivores.

The variation in seed production on the Sahelian savannah is considerable (Table 1). Exceptionally high seed biomass values (1457–2238 kg/ha) were recorded in years with above-average rainfall in temporarily flooded areas covered mainly by *Panicum*. In Maltam, along the Chari River (Chad, see Figure 2A), seed production varied from 2236 kg/ha in a wet year to 206 kg/ha in a dry year (Gaston 1976); the latter value is higher than seed production during wet years in

drylands. In contrast, very low seed biomass was found on sandy dunes covered by vegetation of *Aristida* species (awngrass) and Sandbur *Cenchrus biflorus* (known in West Africa as cram-cram), especially in dry years. In the drought year of 1972, sandy dunes in Fété-Olé were devoid of herbaceous vegetation and the few seeds present were leftovers from the previous year (Bille 1977).

We do not know whether the cited studies distinguished between viable ('full') and non-viable ('empty') seeds and, if not, to what extent the seed density may have been overestimated by including empty seeds without nutritional values for birds. On the other hand, by counting 'fallen seed on the ground', total seed production is underestimated, because birds also take seeds from the panicles (Price & Joyner 1997, Fry & Keith 2004) and livestock consume grass including seeds. Seed density on the soil declines gradually during the dry season due to consumption by birds, rodents and insects. For instance, from the 20,000 (in 1973) or 120,000 (in 1975) seeds/m² present in the study area of Gaston (1976) during the early dry season, less than 2000 were left 10 months later in April and May, presumably mainly due to heavy predation by Red-billed Quelea *Quelea quelea*.

The large variation in seed production (Table 1) may relate to how seed density was measured (e.g. depth of top layer of the soil being sampled, varying

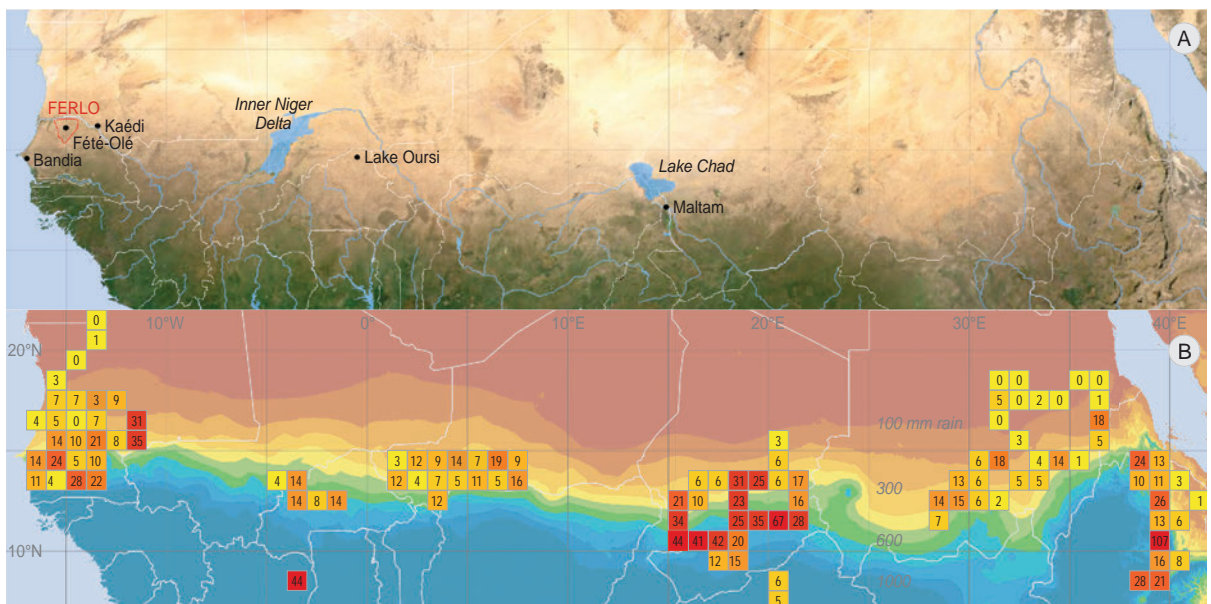


Figure 2. (A) Study areas and large wetlands mentioned in the text. (B) Estimated daily seed consumption (g/ha) by granivorous bird species during the dry season (20 November – 10 March) on savannah or farmland, averaged for 111 grid cells of 1° latitude × 1° longitude.

between 0.5 cm (Bille 1977) to 8 cm (Carrière 1989) and whether 'empty' seeds were included or not. We assume that methodological variations were small compared to the large differences found in seed production between areas and between years. Within the Fété-Olé site, seed production in the valleys was 184 kg/ha, 5.3 times higher than on the surrounding drylands (34 kg/ha). The five study sites of Grouzis (1988) around Lake Oursi had highest seed biomass (1457 kg/ha) on the floodplain and the lowest (77 kg/ha) on the extensive drylands surrounding the lake. From this we tentatively conclude that the initial biomass of the soil seed bank in the early dry season amounted to, on average, 30 to 100 kg/ha on drylands, but much less in a dry year. These values are equal to seed resource levels in North American drylands (Pulliam & Dunning 1987, Desmond *et al.* 2008). However, the seed production can reach 1000–2000 kg/ha after floodplains and valleys become inundated in the rainy season, but such highly productive areas comprise but a small part of the Sahel.

SEED CONSUMPTION

Gaston (1976) suggested that seed density in his Chad study site declined by 100,000 seeds/m² within several months due to heavy predation by Red-billed Queleas. This figure seems realistic given the feeding ecology of Red-billed Queleas. Red-billed Queleas weigh 18 g and their daily consumption of unhusked seeds is estimated at 3.0 g (Figure 1), or 32,000 seeds of 0.95 mg, per individual. To achieve Gaston's claimed consumption rate (100,000 seeds/m², each seed weighing just 0.95 mg), requires 3.1 queleas foraging on a square metre each day the species was present. Extrapolating this to

a 1.0-ha site, requires 31,000 Queleas, or 3100 Queleas feeding for 10 days on a single ha. Queleas are known to occur locally in the millions (Crook & Ward 1968) and have evolved efficient foraging techniques in large groups, including a 'roller feeding' strategy for dense flocks of hundreds or thousands of Queleas sweeping across the plains (Ward 1965). Birds in front of the group take so many seeds that fewer remain for the birds at the back. Once the seeds available to the rear rank become too sparse, the rear rank leapfrogs forwards to form a new front rank, a fluid and regular process. Ward (1965) did not quantify seed depletion, but suggests that dense flocks can reduce local seed density very quickly.

Bird density counts in our study sites (Zwarts *et al.* 2023a) and estimated daily consumption per bird species derived from their body weight (Figure 1) were used to calculate the average seed consumption per grid cell of 1° latitude × 1° longitude (Figure 2B). Seed consumption was very low in the desert and increased with rainfall, reaching higher levels in Chad than in West Africa.

On our study sites, but excluding desert (rainfall < 100 mm/year) and woodland sites, the average daily consumption of all seed-eating birds was estimated at 15 g/ha/day. The variation, however, was large, as no granivores were recorded in 22.5% of the sites. For other sites daily seed consumption levels of over 100 g/ha were calculated (Figure 3). The maximum estimated daily seed consumption (1197 g/ha) was not calculated for a typical Sahel site, but referred to one at the edge of the Danakil Desert (eastern Ethiopia), an area where larger seed-eating bird species were still common (sandgrouse and francolins, nowadays rare

Table 1. Seed (kg/ha) present in the soil during the early dry season in five study areas, with 1–5 vegetation types in a single year (but over five years in Oursi in Burkina Faso). Annual rainfall (mm/year) calculated for the 1950–2000 period (data from the nearest meteorological stations or from Hijmans *et al.* 2005); rainfall during year(s) of observation is given as percent deviation from this 50-year average.

Site	Coordinates	Rainfall/year		Year	Vegetation types	kg/ha	Source
		avg.	dev.%				
Fété-Olé, Senegal	15.01°W, 16.10°N	289	–30	1971	3	34–184	Bille 1977
Fété-Olé, Senegal	15.01°W, 16.10°N	289	–89	1972	3	24–171	Bille 1977
Kaédi, Mauritania	13.43°W, 16.19°N	298	–3	1986	7	268–2170	Carrière 1989
Oursi, Burkina Faso	0.50°W, 14.58°N	374	–10	'77–81	5	77–1475	Grouzis 1988
Maltam, Chad	14.88°E, 12.15°N	466	–32	1973	1	206	Gaston 1976
Maltam, Chad	14.88°E, 12.15°N	466	62	1975	1	2238	Gaston 1976
Bandia, Senegal	16.97°W, 14.57°N	540	14	1978	1	1061	Gillon <i>et al.</i> 1983
Bandia, Senegal	16.97°W, 14.57°N	540	10	1979	1	286	Gillon <i>et al.</i> 1983
Bandia, Senegal	16.97°W, 15.57°N	540	–35	1980	1	803	Gillon <i>et al.</i> 1983

elsewhere in the Sahel). The large variation in seed consumption hinges on several factors, including the large variation in seed density (Table 1), the avoidance by seedeaters of sites lacking seeds and the tendency of granivorous birds to congregate in feeding flocks. Flocking birds cause sampling problems (Figure 12 in Zwarts *et al.* 2023a), and particularly so when sites are visited only once (as in our survey).

The estimated daily seed consumption is based on bird counts during the first half of the dry season. To estimate the total annual seed consumption, we assumed that the birds remained strictly granivorous during 300 days of the year (switching to insect food during the July–September rainy season; Ward 1965, Da Camara-Smeets & Manikowski 1981, Adegoke 1983). An average daily consumption of 15 g/ha/day equates to an annual consumption of 4.5 kg/ha/year, which represents only 4–15% of the estimated total seed supply present on the soil in the early dry season (30–100 kg/ha). Does this mean that food is always plentiful for Sahel's granivores? And are all seeds equally attractive to all seedeaters?

DIET

'The Birds of Africa' (Urban *et al.* 1986, Keith *et al.* 1992, Fry & Keith 2004) and additional sources (Table 2) provided a baseline for seeds taken by African bird species. A comparison with the original papers (e.g.

Morel & Morel 1972, Morel 1987) showed that the information in 'The Birds of Africa' concerned a selection of the most commonly eaten seeds. A seed species omitted from Table 2 does therefore not necessarily equate with absence of that seed in a species' diet. The body masses of the 34 bird species in Table 2 vary between 8 and 440 g, but most are in the 10–20 g range. Seed-eating bird species in Africa showed a preference for a limited number of grass genera. *Panicum* grasses were a main food item for 27 of the 34 bird species: *P. turgidum* in the arid zone (Black-crowned Sparrow-Lark *Eremopterix nigriceps*), *P. laetum* mainly in the Sahel and *P. maximum* also elsewhere in Africa. Seeds of other millet genera were taken relatively often (lines marked blue in Table 2). Some genera of very common grasses were hardly ever mentioned as being part of avian diets. For example, *Aristida* spp. (awn-grass) belong to the most common grass species in the arid and semi-arid zone (Rattray 1968, Le Houérou 1980, Breman & de Wit 1983, Hiernaux *et al.* 2009a), but were taken only by the Desert Sparrow *Passer simplex*. Another very common grass species from the arid and semi-arid region, *Schoenefeldia gracilis*, is mentioned only as food for Red-billed Quelea (Ward 1965), and the even more common and widespread *Cenchrus biflorus* is absent from the literature on avian diets (with one exception; see below).

Seeds of African grasses mostly weigh about 1 mg, varying between 0.07 mg (*Sporobolus*) and 14 mg (Wild Rice *Oryza barthii*). The seeds of cultivars are heavier: rice 17.5 mg, *Sorghum* 19.5 mg, *Pennisetum* (millet) 25 mg and still higher in two species rarely found in the arid and semi-arid zone: *Hordeum* (barley) 35 mg and *Zea* (maize) 262 mg. Two crops in the Sahel have minute seeds: Fonio *Digitaria exilis* (0.5 mg) and Tef *Eragrostis tef* (0.3 mg; Table 2). The selection of seeds according to mass differs for large and small seedeaters, but the overlap is considerable (Table 2). Large seeds, such as those of cultivated rice (17.5 mg), are selected as often by small as by large bird species. Even a bird like the Bronze Mannikin *Spermestes cucullata* (10 g) feeds on rice grains. Very small grass seeds (≤ 0.1 mg), e.g. *Sporobolus* and *Cymbopogon*, are not mentioned in diets of bird species with body masses of >64 g, but seeds that are only slightly less small (≥ 0.25 mg) are important for larger bird species as well.

Seeds may be 'empty', consisting of a hull only, but it is unknown whether they were included in published density counts of seeds present on the surface and in the soil. Seedeaters are known to reject empty seeds. A Common Woodpigeon *Columba palumbus* stomach

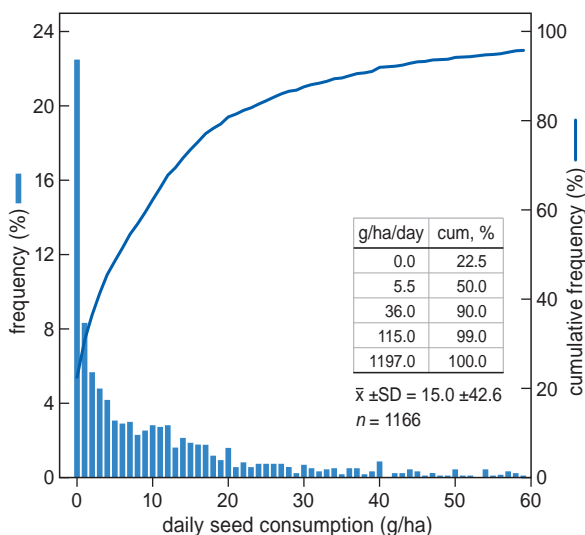


Figure 3. Frequency (% left) and cumulative frequency distribution (% right) of the calculated daily seed consumption (g/ha), derived from bird counts in 1166 sites during the dry season in the grid cells shown in Figure 2. Selection made of random sites with an annual rainfall >100 mm not covered by woodland.

Table 2. Thirty grass genera and six forb genera recorded in the diets of 34 seed-eating bird species occurring in the Sahel and elsewhere in Africa. Diet data extracted from ‘The Birds of Africa’ (Urban *et al.* 1986, Keith *et al.* 1992, Fry & Keith 2004), with supplementary data from Da Camera-Smeets & Manikowski (1981), Adegoke (1983), Badenhorst & Kerley (1996) and <https://birdsoftheworld.org/bow/home>. Body mass of bird species (g; after English names, top of the table) are from ‘The Birds of Africa’ and Tieleman *et al.* (2003) for Dunn’s Lark. Mass of grass seeds (mg; after scientific names of genera on left of the table) are taken mainly from Bille (1977), but also from Ward (1965), Grouzis (1988), Gallinato *et al.* (1999), Peco *et al.* (2013), Török *et al.* (2013), Jedmoski *et al.* (2015), Titulaer *et al.* (2018) and Musso *et al.* (2019). Grasses with awned seeds are marked grey when all, or at least most, species within the genus have awns (Clayton *et al.* 2021). For instance, within *Oryza* (rice) the wild species *O. barthii* has awns but not the cultivated *O. sativa* and *O. glaberrima*. Birds predate 11 millet genera (all awnless, marked blue) three times more often on average than other grasses.

Genus seed mg	Common Quail 110	Double-spurred Spurrow 440	Speckled Pigeon 300	European Turtle Dove 172	African Collared Dove 126	Mourning Collared Dove 149	Vinaceous Dove 110	Laughing Dove 91	Black-billed Wood Dove 66	Namaqua Dove 36	Black-crowned Sparrow-Lark 14	Greater Short-toed Lark 20	Dunn’s Lark 20	Desert Sparrow 19	Sudan Golden Sparrow 13	Village Weaver 40	Red-headed Quelea 19	Red-billed Quelea 20	yellow-crowned Bishop 15	Black-winged Bishop 23	Northern Red Bishop 17	Fan-tailed Widowbird 28	Pin-tailed Whydah 16	Red-collared Widowbird 23	Bronze Mannikin 10	Common Waxbill 8	Cut-throat Finch 20	Green-winged Pytilia 15	Red-billed Firefinch 9	Village Indigobird 12	Cameroon Indigobird 12	White-rumped Seedeater 11	Yellow-fronted Canary 13	Golden-breasted Bunting 19				
Grass genera																																						
<i>Andropogon</i> 3.6																	•								•													
<i>Aristida</i> 0.64													•																									
<i>Brachiaria</i> 1.2							•		•							•			•						•													
<i>Chloris</i> 0.37–0.51																										•	•			•						•		
<i>Cymbopogon</i> 0.1																			•																	•		
<i>Cynodon</i> 0.26																										•							•					
<i>Dactyloctenium</i> 0.25	•					•			•	•								•	•												•	•						
<i>Digitaria</i> 0.3																•		•	•			•	•		•	•				•	•	•	•		•			
<i>Echinochloa</i> 1.94	•																•	•	•			•	•		•	•				•	•	•	•		•			
<i>Eleusine</i> 0.3								•		•		•												•		•												
<i>Eragrostis</i> 0.33			•							•		•				•		•							•	•											•	
<i>Hordeum</i> 35	•	•																																				
<i>Hyparrhenia</i> 0.77																					•			•		•	•	•										
<i>Hyperthelia</i> ?																				•						•												
<i>Ischaemum</i> 0.7																		•																				
<i>Melinis</i> 0.65																											•											
<i>Oryza</i> 14–17.5										•	•						•	•	•		•	•	•		•	•												
<i>Panicum</i> 0.95	•	•		•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	
<i>Paspalum</i> 1.08																		•					•		•	•												
<i>Pennisetum</i> 2.3–25			•						•	•	•			•	•	•	•	•	•			•			•	•									•			
<i>Phalaris</i> 0.6																																					•	
<i>Poa</i> 0.15								•																													•	
<i>Rottboellia</i> 10.6																	•	•			•																•	
<i>Schoenefeldia</i> 0.11																			•																			
<i>Setaria</i> 0.75				•								•							•	•			•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	
<i>Sorghum</i> 19.5	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	
<i>Sporobolus</i> 0.07																				•					•	•												
<i>Tricholaena</i> ?																																						
<i>Urochloa</i> 1.3																		•						•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Zea</i> 262			•						•								•	•			•	•			•	•												
Forb genera																																						
<i>Arachis</i> 500					•	•	•	•																														
<i>Alysicarpus</i> 3.6										•																												
<i>Citrullus</i> 55					•	•	•	•																														
<i>Gisekia</i> 0.26					•	•	•	•		•																												
<i>Tribulus</i> 6.4		•	•	•	•	•	•	•																														
<i>Zornia</i> 1.9							•	•								•																						

contained full beechnuts only (average weight 0.17 g, compared to 0.08 g for a random sample), whereas 11% of the nuts available on its foraging patch had been empty (Bijlsma 1995). Another study, on Black-tailed Godwits *Limosa limosa* feeding on rice grains in Portuguese farmland (Blomert & Zwarts unpubl. data), found that available rice grains varied in weight between 2 and 27 mg. The godwits ignored all grains <8 mg, took some of 9–11 mg, but preferred to take the larger grains of which 80% of the mass was digestible (against <20% for all grains <8 mg). The fraction of empty rice grains in the field was high (34%), probably not much different from that in Sahelian grass and forb species (Hérault & Hiernaux 2004).

Most granivorous birds in the Sahel predominantly feed on seeds of annual grasses, but they also take the seeds of some forbs, from the very small (*Mollugo* and *Cleome*; 0.1 mg) to the very large (*Citrullus colocynthis*; 55 mg and *Arachis*; 500 mg). The latter two are taken by Speckled Pigeon *Columba guinea* and by four of the larger dove species (91–300 g body mass) but not by Namaqua Dove *Oena capensis* (36 g) which preferred the small *Mollugo* and *Cleome* seeds that were ignored by the larger doves (Morel & Morel 1972b).

We combined the data summarised in Table 2 to test whether the selection of seed by mass differs for small and large birds. Although the smallest seeds are not taken by the largest birds, the overlap in seed size between small and large granivorous species is nearly complete because the smaller bird species also take the larger seeds ($\chi^2_{24} = 14.7$, $P = 0.93$; bird species in weight classes of 7–10, 11–15, 16–20, 35–91 and 110–440 g, and seeds in weight classes of 0.07–0.1, 0.11–0.37, 0.64–1.4, 1.94–5 and 14–500 mg). A similar large overlap in seed size was found for seed-eating bird species of the Monte Desert, Argentina (Cueto *et al.* 2006, Marone *et al.* 2008, Camín *et al.* 2015, Marone *et al.* 2022).

The grass species often mentioned in diets of granivorous bird species have awnless seeds, whereas grass species infrequently reported as food have awns (Table 2). Some very common grass species with awned (*Diheteropogon*, *Loudetia*) or spiny seeds (*Cenchrus*) are not mentioned at all as bird food. The exception is queleas feeding their young with *Cenchrus* seeds in September (Morel *et al.* 1957), when the seeds are still soft. Once these seeds have hardened, the spines can even injure livestock and humans. Another very common food resource, the awned seed of *Aristida*, is ignored as food by birds in Africa and N America (Pulliam & Brand 1975, Titulaer *et al.* 2017, Desmond

et al. 2008) and ignored by small, but not by large seed-eating birds in S America (Marone *et al.* 2008, 2017). Granivorous bird species are able to husk most seeds (Kear 1962, Newton 1967, Pulliam 1985), even some that are large or hardy (van der Meij & Bout 2004, 2007). They are also able to separate awns (up to 7 cm long) from seeds, but some awned seeds are more difficult to handle than others (Pulliam & Brand 1975, Titulaer *et al.* 2018). Overall, birds prefer seeds that are easier to handle, to make their foraging strategy as profitable as possible (Hrabar & Perrin 2002, Soobramoney & Perrin 2007, Marone *et al.* 2022).

Seed masses as cited in Table 2 refer to total dry mass including hull and awns, the standard way of expressing seed mass in studies of birds' seed selection. These values are a far cry from the mass and energy content of the digestible fraction of the seed when the indigestible husks, awns and hairs are excluded. The seed hull consists of crude fibre and is indigestible by birds. The indigestible fraction can be as high as 50–70% in seeds with a heavy hull and/or with large awns or many hairs, but in grasses mostly comprises 20–30% and in grass seeds lacking hairs or awns even less (Kear 1962, Hespenheide 1966, Pulliam 1985, Hrabar & Perrin 2002). Most grass seeds are easy to handle by birds due to their soft and thin hull, in contrast to the seeds of forbs that are often equipped with a sturdy seed coat. Puncture Vine *Tribulus terrestris*, for instance, has nutlets (37 mg) containing 3 seeds (6.4 mg, only partly digestible due to its thick hull; Bille 1977, Grouzis 1988, Morel 1987), so more than half of the nutlet is indigestible. Most granivorous bird species in the Sahel are unable to crack the nutlet, but five larger pigeon and dove species swallow the nutlets whole (Morel & Morel 1972b), much to the surprise of Morel (1987) that these birds were able to process nutlets with such hard spines. In the light of these findings it is not surprising that savannah birds take grass seeds relatively more often than forb seeds (Cueto *et al.* 2006, Marone *et al.* 2008, Díos *et al.* 2012a, Camín *et al.* 2015, Marone *et al.* 2017, 2022), in addition to the fact that some forb seeds are (slightly) toxic (Díos *et al.* 2012a,b), such as *Senna tora* which contains phytohaemagglutinins (Gillon *et al.* 1983). *Senna tora* is locally a very common forb in West Africa which produces a lot of large seeds (19 mg) that are eaten by insects but refused by birds.

Apart from mass, the energy content of seed kernels also varies greatly, i.e. between 17 and 30 kJ/g. Energy content is higher in fat seeds (e.g. sunflower, rape) but only 17–19 kJ in most grass seeds (Willson 1971, Willson & Harmeson 1973, Hrabar & Perrin 2002,

Soobramoney & Perrin 2006). Birds, rodents and insects prefer highly nutritional seeds with a high soluble carbohydrate fraction that are easy to digest (Kelrick *et al.* 1986). The carbohydrate fraction is particularly high in *Panicum* and other millet species' seeds (*Echinochloa*, *Eleusine*, *Paspalum*; Kelrick *et al.* 1986, Gupta *et al.* 2014), which may encourage their selection by seed-eating birds (Ríos *et al.* 2012a), also in Africa (Table 2).

Heat stress at midday

Seed-eating birds in the Sahel roost communally at night (e.g. Ward 1985) and forage only during daylight hours (12 h a day available). However, the middle of the day is usually too hot to exploit for foraging. Even in a desert-dwelling species, such as Dune Lark *Calendulauda erythrochlamys*, heat stress manifested itself in a change of behaviour (searching for shade or remaining immobile) when sand temperatures exceeded some 35°C (Wolf *et al.* 1996, Cox 1983, Williams 2001). Soil temperature in our study sites in the Sahel increased from an average of 15°C in the early morning to a maximum of 46.5°C between 11:30 and 13:30, after which it cooled down to 27°C at sunset (Figure 4). These are average values, with daily maxima sometimes exceeding 50°C or even 60°C on clear sunny days. On dusty days when the sun was scarcely visible, maximum temperatures may not rise above 30°C, however. Temperatures varied in the course of the dry season from late November to early March, with surface temperatures around midday (11:30–13:30) increasing from an average of 44.8°C ± 0.8 (±SE) in December (*n* = 37), to 45.6°C ± 0.5 in January (*n* = 68), 46.9°C ± 1.2 in February (*n* = 42) and

50.8°C ± 1.3 in early March (*n* = 17; sunny days only). The threshold of a maximum temperature of 35°C at ground level for seedeaters would limit the foraging windows to 3 h in the morning and 1.5 h in the late afternoon. We lack quantitative data to confirm this threshold for ground-foraging birds, but it fits the observation of Ward (1965) that Red-billed Queleas feed 2–3 h in the early morning and about 2 h in the late afternoon, later revised to two hours in each period (Ward 1978).

Non-feeding birds were often seen resting in the shadow, where it was always cooler even when still on the ground. The soil temperature in the shadow was, on average, 4.7°C lower than in the sun, but the difference increased at high temperatures, to 6.2°C when soil temperature in the sun exceeded 35°C, with a linear relationship between soil temperature in the shadow and in the sun:

$$T_{\text{shadow}} (\text{°C}) = 2.82 + 0.79T_{\text{sun}} \quad (2)$$

based on 682 simultaneous measurements of soil temperature in the sun and a shady spot in the immediate surrounding; $r^2 = 0.88$; range 8.8–56.8°C (T_{sun}) and 7.9–50.2°C (T_{shadow}).

In arid and semi-arid savannahs, the presence of solitary trees and pockets of trees may extend the duration of foraging bouts for ground-foraging birds at high temperatures, but we lack empirical data on this subject. Trees can also act as 'thermal refugia' in a heat-stressed environment, as suggested for arboreal and, especially, ground-foraging birds (in the Kalahari; Martin *et al.* 2015).

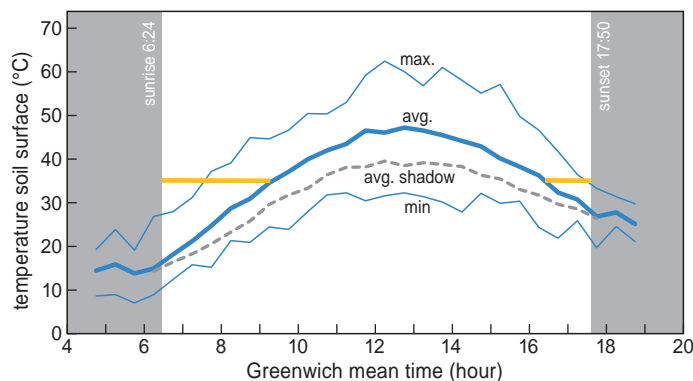


Figure 4. Diurnal variation in the average, maximum and minimum temperature of the exposed soil surface, and the average temperature of soil surface in the shadow, between 20 November and 10 March. Based on 1226 measurements in the region shown in Figure 2 (but excluding Ethiopia) from three time zones converted to Greenwich mean time. The horizontal yellow lines indicate the feeding periods of seedeaters during daylight, assuming birds avoid foraging when average soil temperature is >35°C, yellow time slots cover 6:24–9:20 h and 16:20–17:50 h.

Intermezzo: Foraging theory applied to Sahelian granivores

A reduction of foraging time has consequences for the intake rate needed to meet the daily energy requirements. The daily food consumption is determined by five variables: energy content of the prey (E), handling time per prey (H), searching time per prey (S), number of prey and total daily foraging time, where E/H is the profitability (intake rate during handling the prey) and E/(H+S) the intake rate during feeding.

INTAKE RATE

When the available foraging time is restricted, birds need to raise their intake rate to meet the required daily food consumption. Assuming seed-eating birds in the Sahel have to meet their energy demand during a foraging period of 4 h per day (avoiding heat stress), instead of the full daylight period of 12 h (Figure 4), their intake rate must be three times higher. The required intake rate during feeding can be derived from the daily consumption as determined by body mass (Figure 1; Eq. 1), assuming they forage nonstop in the time (4 h) available:

$$\text{intake rate} = 0.0328\text{bm}^{0.657}, \quad (3)$$

where intake rate = mg dry mass/s feeding and bm = body mass of the bird (g).

HANDLING TIME

Seeds may be ignored when they take too much handling time and intake rate during prey handling becomes lower than the intake rate during feeding. Most seed-eating birds husk the seeds to get rid of indigestible material, but doves and waders swallow seeds whole. Swallowing a seed whole takes 0.3–1.2 s, depending on size and dimensions of the seed relative to the gape width of the bird (Pulliam 1985, Hrabar & Perrin 2002, Zwarts & Wanink 1993, Marone *et al.* 2022). To crack and husk seeds takes additional time. Husking canary grass *Phalaris* seeds (7 mg) and hemp *Cannabis* seeds (18.5 mg) amounts to 2–4 seconds of handling time in birds with a body mass of >25 g but varies in smaller birds between 3 and 16 s (van der Meij & Bout 2004, 2006). We found 13 studies where seed mass (for 38 species) and seed handling time by birds (in 48 species) were given in detail (full list of handling times given in Supplementary Material). The handling time varies per bird species, depending on bill size, bill shape, biting force, seed handling method (with or without husking) and seed species (e.g. size, shape, hardness of the husk, presence of awns or stiff

spines). An analysis of the pooled data showed that handling time depends mainly on seed mass, and to a lesser degree on body mass of the bird and width and depth of its bill. It also makes a difference whether or not husk and kernel are separated. For seeds swallowed whole, the expected decrease of handling time with body size and increase with seed mass is small and far from significant. In contrast, the relationship is highly significant for husked seeds. Handling time is a function of seed mass, body mass, bill width and bill depth with all (log-transformed) variables being highly significant ($r^2 = 0.74$, $n = 151$; multiple regression analysis). However, heavier bird species have a sturdier bill ($r = +0.66$ for bill depth vs. body mass and $r = +0.50$ for bill width vs. body mass) which complicates the interpretation of handling time. Bill dimensions are known for only a few Sahelian seed-eating birds. Therefore, we disregard bill dimensions in the equation for handling time:

$$\text{ht} = \exp(1.188 \pm 0.419 + 0.609 \pm 0.038 \times \ln(\text{sm}) - 0.211 \pm 0.139 \times \ln(\text{bm})), \quad (4)$$

where ht = handling time (s), sm = seed mass (mg \pm SE; $P < 0.001$), bm = body mass of bird species (g \pm SE; $P = 0.131$), $r^2 = 0.59$, $n = 192$; raw data in Supplementary Material.

SEARCH TIME

Equation 3 gives the required intake rate of birds assuming they forage 4 h a day and equation 4 gives the handling time of birds feeding on seeds varying in

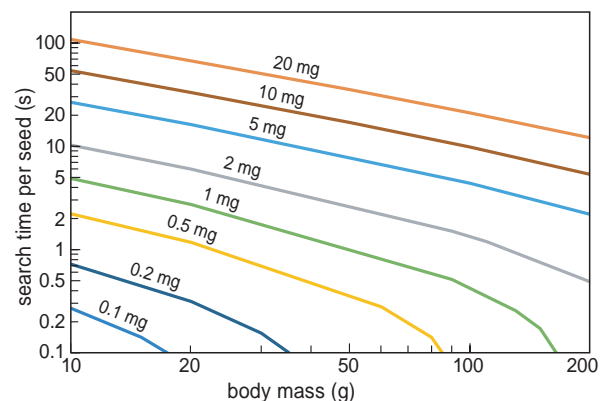


Figure 5. The search time needed per seed, varying in mass between 0.1 and 20 mg, as a function of the body mass of bird species feeding on those seeds. The prediction is based on the assumption that birds have to meet their daily food demand (Figure 1) in 4 h (Figure 4) and intake rate and handling times of seeds are according to equation 3 and 4, respectively.

mass. To estimate the search time per seed as a function of seed mass and body mass of the bird species we subtracted estimated handling time from the total time needed to find and handle a seed (Equation 3). The estimation of search time (Figure 5) was based on the assumption that the birds foraged continuously during the available daily foraging time of 4 h. In practice, foraging times will be shorter as birds have to spend time searching for rich feeding sites, meanwhile dealing with disturbances, experiencing interactions with other birds and resorting to comfort behaviour. According to Figure 5, seeds of 0.1 mg, and even of 0.2 mg, would be worthwhile to take by only the smallest bird species. This prediction refers to birds that husk the seeds. Doves swallowing seeds whole have shorter handling times, allowing them the valuable option of feeding also on small seeds that are unprofitable for husking seedeaters.

PROFITABILITY

A bird as small as a Bronze Mannikin (10 g) has to take 2.15 g seeds per day (Figure 1) and therefore needs to find 154 rice grains (14 mg each). Given an available foraging period of 4 h (Figure 4), mannikins have to find one rice grain per 94 s. The much larger Double-spurred Spurfowl (440 g) needs to take a rice grain every 7.6 s which seems feasible at high seed density. But if the same species had to feed on seeds of 1 mg, it would have to take a seed every 0.5 s which would only be possible at a very high encounter rate. Most seed-eating birds in the Sahel weigh 10–20 g. For a 4-hour

feeding time, the bird's search time per seed would vary between 0.2 s for a seed of 0.1 mg taken by a bird of 20 g to 4.6 s for a bird of 10 g feeding on seeds of 1 mg (Figure 5). Obviously, seed-eating birds in (hot) Sahelian drylands feeding on small seeds cannot spend a long time searching for each and every seed and therefore must be dependent on sites where seeds are abundant. The available studies clearly show the impact of seed density on birds' intake rates and feeding density (Green 1978, Bock & Bock 1999, Whittingham & Markland 2001, Moorcroft *et al.* 2002, Stephens *et al.* 2003, Tsurim *et al.* 2007). The intake rate increases with seed density but levels off when the density is high enough to reduce search time effectively to zero: the maximal intake rate is determined by the profitability, i.e. the intake rate while handling the prey. When the birds face reduced foraging times, they must increase their intake rate by selecting profitable prey and sites where seed density is high (Figure 6A). However, when they are forced to feed on unprofitable prey, their foraging time may be too short even when the seed density is very high (Figure 6B).

DISCUSSION

Searching for visible seeds

Seed-eating birds in the Sahel, being time-constrained in their search for small grass seeds (Figure 5), also have the problem that not all seeds are accessible at the surface and, when accessible, are not always visible. 30

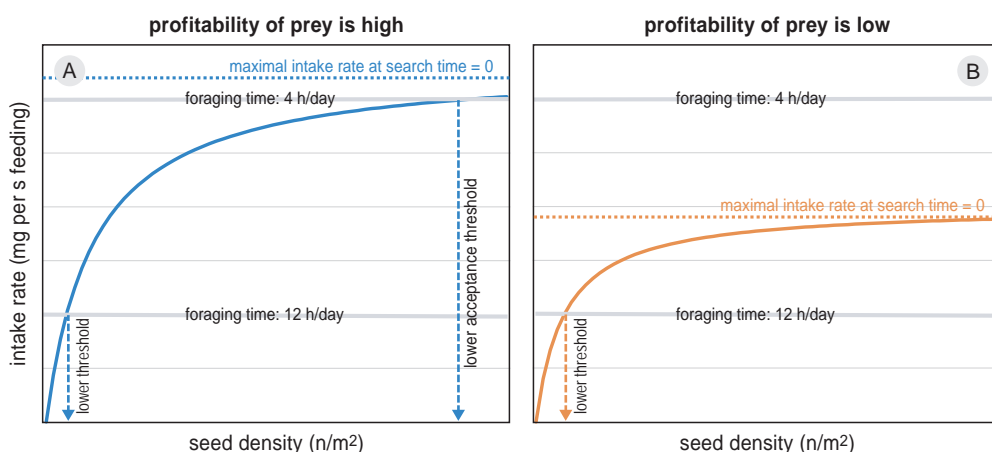


Figure 6. Functional response, the expected relationship between intake rate and seed density when the prey has (A) a high or (B) a low profitability. The dashed lines show the threshold values below which the seed density becomes too low to achieve the intake rate required to survive at a daily foraging time of 4 or 12 h/day. In a restricted foraging time period, birds need a higher intake rate and so will select sites where the search time per seed is less. In this example, birds foraging on seeds with a low profitability cannot meet their energy requirement when the feeding time is only 4 hours a day, even if seeds are so abundant that the search time is 0 (dotted line).

to 40% of the seeds of savannah grasses are buried more than 1 cm below the surface, but as the dry season progresses this proportion increased to about 50% (Carrière 1989). This increase may be a consequence of selective predation of shallow seeds, but if so, larger declines would be expected for grass species that are eaten more often. This difference was not evident from the data in Carrière (1989), but nevertheless such depletions of shallow seeds may well occur, given that experiments with captive birds showed that birds focused on visible seeds. Three finch species and a sparrow species had to search for seeds both on the surface and buried at different depths. When there were no visible seeds, the birds opted for the shallowest seeds (Cueto *et al.* 2013). Some bird species such as indigobirds and whydahs may scratch the soil in search of more deeply buried seeds (Fry & Keith 2004, Whalen & Watts 2010), but most seed-eating birds do not, likely because it would be too time-consuming. When the ground is covered by a blanket of (dead) vegetation, any seeds present on the soil surface are more difficult to detect. Indeed, the intake rate of seed-eating canaries in captivity was 36% higher on bare ground than on grass-covered ground (Whittingham & Markland 2002). Most of the soil in the Sahel is bare in the dry season, but in the humid zone a large part of the ground is covered by (dead) vegetation, unless it has been burned (Zwarts *et al.* 2023d).

Is heat stress at midday a constraint for ground-foraging birds?

Morel *et al.* (1957), Morel (1968) and Morel & Morel (1978a) noted that the length of the midday roosting period was reduced at lower temperatures, but extended when food was abundantly available (e.g. after rice had been harvested). However, bird species apparently differ in their susceptibility to heat stress; larger species tolerate higher air temperatures (Whitfield *et al.* 2015). Drinking regularly is also important (e.g. Morel 1975). Curry (1974) noted that European Turtle Doves, in contrast to African dove species, continued to feed throughout the day on the floodplains of the Inner Niger Delta, probably because water was always nearby, and also because moist areas on floodplains were not as hot as the surrounding drylands; Nobel & Geller (1987) showed that on dry and wet desert soils daily peak temperatures reached 56 and 28°C, respectively.

If birds are forced to forsake foraging during the hottest parts of days, several predictions can be made. First, due to the daily variation in midday temperatures, the reduced food consumption rate of ground-

foraging birds in effect makes that resource less predictable. Birds may adopt the compensatory behaviour of enhancing their consumption during cooler days, so that their fat deposits tide them over the hot spells (e.g. Bednekoff & Krebs 1995). Second, the length of the overall daily feeding period will fluctuate more during the hot season (March–May) than during the cooler season (December–January), particularly apparent in the (hot) arid zone rather than in the (less hot) humid zone. Body mass should show a corresponding day-to-day-variation. The fat content of Red-billed Weavers amounted to 5–6% relative to their total body mass during the dry season (Ward 1965), but whether the ‘lean-season fat’ varies in relation to temperature remained unexamined. If the temperatures in the Sahel keep rising, having already increased in April–May by an average of 1.8°C between 1950 and 2010 (Barbier *et al.* 2018), more research is surely warranted on whether midday temperatures are an increasing constraint for ground-foraging birds.

Significance of temporary wetlands in the dry Sahel

The Fété-Olé site in NW Senegal consists of low sandy dunes where small valleys are temporarily inundated during the wet season (Photo 1). Seed biomass was 2.32 g/m² on the dunes, but in depressions was five times higher: 11.97 g/m² (Bille & Poupon 1974). However, when the seeds not taken by birds are excluded (*Aristida*, *Cenchrus*, *Diheteropogon* and *Schoenefeldia*), seed biomass on the dunes was 74% lower at 0.61 g/m², but in depressions only 4% lower, at 11.46 g/m². As a result, density of preferred seeds in depressions was 19 times greater than on dry land. Floodplains and depressions (often with a clayish soil) accordingly attract seedeaters because (1) they are much more productive and (2) awnless grass species typical of seasonal ephemeral wetlands are preferred by all seedeaters, *Panicum* being first choice, followed by *Echinochloa*. The opposite applies to the arid savannah’s commonest grass species (such as *Aristida* and *Cenchrus*), which are ignored.

The third reason why temporary wetlands are attractive to seedeaters is the lower soil temperatures in wet terrain, enabling European Turtle Dove to continue feeding during the middle of the day (Curry 1974). The total daily seed consumption of the European Turtle Dove (body mass: 156 g) may be estimated at 13.1 g (Figure 1). When the doves feed on *Panicum* seeds (0.95 mg), they need 12,400 seeds/day. Before their departure in April, they increase their body mass up to >190 g (Morel 1986); to attain this mass, an increase of the daily consumption is required. Indeed, Morel

(1987) found in March up to 15,000 *Panicum* seeds (14 g) in the gullet and gizzard (an underestimate of total daily intake, since seeds eaten hours before had already been digested). Handling a seed of the size of a *Panicum* would take a Turtle Dove 0.5–1.0 s (Anne-Marie Blomert pers. comm.), and so just to handle 15,000 seeds would take 125–250 minutes. Data are lacking on encounter rates of seeds by doves in the Sahel, but assuming that birds need at least 1 s to find a *Panicum* seed, they have to forage at least 6.2 to 8.3 h to consume 15,000 *Panicum* seeds. It would be much more difficult for European Turtle Doves to fuel up in drylands where soil temperature in March is still higher than in the preceding months (Figure 4).

Red-billed Queleas in NE Nigeria were concentrated in the inundation zone around Lake Chad, where they fed on a large variety of seeds from cereals (rice, sorghum) and wild grasses (especially *Echinochloa* and *Panicum*; Ward 1975, Conert 1987). On the low-lying areas of fertile alluvial soil of the dry zone, they fed on their preferred *Panicum* seed (Ward 1975). In North Senegal the queleas concentrated on floodplains along the Senegal River, where they took the same grass

species as their congeners in NE Nigeria, *Echinochloa*, *Panicum* and Wild Rice, and later on in the dry season also *Chloris* and *Dactyloctenium* (Morel & Morel 1978a, 1980, 1992). This supports Ward's conclusion that food supply in drylands is insufficient to feed the many millions of queleas, hence the large gatherings of queleas in floodplains along the Rivers Senegal, Niger, Chari and Logone, and in comparable areas elsewhere in Africa. However, in dry years, seed-rich floodplains are not as extensive as in wet years (Zwarts *et al.* 2009) and far fewer ephemeral lakes can be found in the drylands. Consequently, grass species restricted to these habitats, such as *Panicum* and *Echinochloa*, will be thin on the ground, forcing seed-eating birds to switch to seeds of other graminoids or to disperse to other feeding areas.

Impact of grazing

Wet-season grazing has a large negative impact on seed-dependent birds during the dry season (Pol *et al.* 2014). Soil seed banks are reduced if livestock graze the swards before seed has fallen on the ground (Sternberg *et al.* 2003). The impact of grazing becomes



Photo 1. The landscape of the Ferlo, N Senegal, is flat, but subtle differences in elevation produce a mosaic of vegetations. The lower areas retain water for some time after the short rainy season and are covered by a dense mat of annual grasses, mainly *Panicum* and *Echinochloa*, preferred by seed-eating birds. Other grass species (e.g. *Aristida* and *Cenchrus*), ignored by birds, dominate the surrounding low dunes. The photo, taken by G. Gray Tappan (U.S. Geological Survey, EROS Center, USA) in the early dry season, shows these low depressions as green spots, often speckled with trees and shrubs, among light brown drylands.

greater still if heavy grazing leads to a change in the herbaceous community and birds' preferred seed plants are reduced or eliminated, leading to the predominance of grasses whose seeds are mostly ignored by birds. This vegetational shift is not unexpected because the softer seeds preferred by birds do not survive digestion by livestock, whereas the seeds ignored by birds, do (Gardener *et al.* 1993). Long-term studies in the Sahel are in agreement of changes in plant communities in the wake of increased grazing pressure. At a site in Niger (annual rainfall 575 mm) most plant species that benefited from grazing (*Aristida*, *Cenchrus*, *Schoenefeldia*) are not taken by birds, or may be taken as a last resort (*Zornia glochidiata*; 1.92 mg) when other seeds are no longer present (Hiernaux 1998). At elevated grazing pressure near Niono, Mali (570 mm rain/year) *Andropogon gayanus* was replaced by the annual herb *Zornia glochidiata* (Breman & Cissé 1977). A long history of heavy grazing and trampling at Gourma, Mali (200–500 mm rain/year) promoted an increase of the perennial *Tribulus* and the short-cycle annual *Zornia* (Hiernaux *et al.* 2009a). Heavy grazing impinges on the composition of the vegetation (Hiernaux *et al.* 2016), which in the long run will create plant communities consisting of grasses and forbs that birds dislike or avoid. The result equates a year-round qualitative and quantitative degradation of the food supply for granivorous birds (but not necessarily for livestock). In the Sahel, this scenario is based on sparse evidence as far as birds are concerned, but it corresponds with the results from detailed research in the Monte Desert of Argentina (Pol *et al.* 2014, Marone *et al.* 2017, Marone & Pol 2021, Sagario *et al.* 2020).

The impact of pastoralism on the savannah ecosystem is particularly evident in the vicinity of natural and man-made watering points. Within the heavily grazed first km from the watering points in NW Senegal, the soil vegetation was dominated by species with non-preferred seeds: *Dactyloctenium* (a grass with minute seeds) and *Zornia* (Poissenet *et al.* 1992). At 1–2.5 km from the watering points the situation was much the same, the vegetation being dominated by *Zornia* and two grasses whose seeds are not taken by birds (*Aristida* and *Cenchrus*). At a distance of more than 4 km grass diversity became greater, with four species taken by birds (*Chloris*, *Digitaria*, *Eragrostis*, *Panicum*) and one species less favoured (*Schoenefeldia*). The density of seed-eating birds increased with distance from watering points in NW Senegal, but trends were not significant (Zwarts *et al.* 2018). These counts, however, referred to all birds present in the study sites, partly feeding on the ground but mostly roosting in

trees, including those near watering points. Seed-eating birds are known to drink regularly (Morel 1975) and watering points are therefore magnets for seed-eating birds, obscuring any trend of expected increase of density of seed-eating birds with increasing distances from the watering points.

The heavy grazing pressure of livestock on Sahelian drylands makes floodplains and depressions even more important as refuges for seed-eating birds. It is therefore of relevance to establish the impact of grazing livestock on the herbaceous vegetation in temporary wetlands. In the absence of grazing in the low-lying parts around Lake Oursi, *Panicum* was replaced by *Aeschynomene indica* (Grouzis 1988), a tall legume with toxic seeds (7.5 mg) and probably not taken by seed-eating birds. Grazing on low-lying wet soils in this particular region helped to create and maintain an abundant food resource for seed-eating birds (but probably with negatively effects on birds like Sedge Warbler *Acrocephalus schoenobaenus*, which reaches high densities in dense vegetation of *Aeschynomene*; own unpubl. data). And exclusion of cattle from the floodplains of the Somone River in the Bandia reserve (W Senegal) resulted within a few years in the colonization of grasslands by Red Acacia *Acacia seyal* (Hejcmanová *et al.* 2009; Photo 1D in Zwarts *et al.* 2023c). Similarly, exclosures in the Inner Niger Delta (Mali) led to the establishment of flooded forests of *Acacia kirkii* (Beintema *et al.* 2007). Hence, and contrasting with drylands, seed-eating birds lose foraging habitat in Sahelian floodplains and depressions when grazing is completely absent. It is evident that seed-eating birds on the savannahs and floodplains profit from light or moderate grazing regimes, but not from the heavy grazing which is becoming the standard across the Sahel and which reduces the soil seed bank of selected plant species.

Does the available food supply limit the number of seed-eating birds?

Savannahs, at first sight perhaps perceived as simple ecosystems, are in reality complex webs with many actors on various trophic levels. This complexity is stressed again and again by plant ecologists with a long history of research in Sahelian ecosystems (e.g. Hiernaux *et al.* 2016). In the words of Peter Ward (1965) "Only those who have never seen tropical grasslands or savannah in the dry-season could suppose that there were no seasonal variations in food supply. Certainly, queleas experience a time of severe shortage of food at the onset of the rains and evidence has been given that considerable mortality occurs at this time.

Allee & Schmidt (1951) stated that in the African grassland “With the first rains, the vicissitudes of the dry season are over...”, but as far as *Quelea* is concerned, nothing could be further from the truth.” In fact, ‘*Quelea*’ in this quotation can be substituted for any seed-eating bird species.

During the early dry season, Red-billed *Quelea* in NE Nigeria took mainly small seeds (*Panicum*, *Echinochloa*), but later in the season they switched to minute (*Digitaria*, *Dactyloctenium*) and large seeds (sorghum, wild rice), presumably because the small seeds were depleted (Ward 1965). Morel & Morel (1978a) agreed that queleas in the late dry season in NW Senegal began to take minute seeds (*Chloris* and *Dactyloctenium*; <0.5 mg). Variation in dietary choices is typical in seasonal habitats, as evident in European Turtle Doves in N Senegal, which fed mainly on *Panicum* in August–November, on wild and cultivated rice in December–February and on the forb *Tribulus* in March–July (Morel & Morel 1979). Six Afro-tropical dove species studied by Morel & Morel (1972b) also took *Panicum* in the early dry season but forb seeds such as *Tribulus*, *Gisekia pharnaceoides* (0.26 mg) and *Zornia* in the late dry season.

The seed supply varies from year to year but is always lower in dry years (Table 1). Ward (1965) concluded that for queleas the food shortage at the end of the dry season was larger in a dry than in a wet year. In NW Senegal, seven dove species mainly fed on *Panicum* in a wet year but switched to forb seeds (*Gisekia*, *Tribulus* and *Zornia*) and small grass seeds (*Dactyloctenium*) which were normally taken only at the end of the dry season when their preferred seeds had been depleted (Morel & Morel 1972b, Urban *et al.* 1986). In the Fété-Olé study site, the density of ground-foraging birds remained stable at about 7 birds/ha between July and February in a year with a normal rainfall, but in a dry year, the numbers declined to 2–3 birds/ha in November–February (Morel & Morel 1974). The larger decline in the dry year may be due to birds leaving the area, but also to high mortality. The birds that survived the dry season were in such a poor condition that they refrained from breeding (Morel & Morel 1978b, 1992). Seed supply declines during the dry season, and much more so in years with little rain. Seeds of *Tribulus* and *Zornia*, taken during periods of food shortage, are inadequate replacements of preferred seeds, possibly due to their low digestible fraction.

Morel & Morel (1972a) estimated that in the Fété-Olé study site seed-eating birds took 2.6 g/ha in a dry year and 4.3 g/ha in a wet year, which equates to 7% of the total annual seed production (40–60 g/ha; Bille

et al. 1972). Seed-eating birds ignored the seeds of *Aristida*, *Cenchrus*, *Diheteropogon* and *Schoenefeldia* (Morel & Morel 1972b), representing a staggering 64% of the total seed biomass (Bille & Poupon 1974). Predation pressure on the seeds of the remaining species is estimated at 20%. It must have been much higher in *Panicum* (1.8 g/ha), considering that the total annual seed consumption by birds amounted to 2.6–4.3 g/ha and *Panicum* being the main prey for seed-eating bird species. Other studies indeed found that seed-eating animals depleted the food supply during the dry season (or during winter in the temperate zone) by 50–90% and for this reason populations of seed-eating birds are often considered as limited by food (Noy-Meir 1979, Dunning & Brown 1982, Pulliam 1985, Robinson & Sutherland 1999, Gonnet 2001, Robinson *et al.* 2004, Desmond *et al.* 2008, Siriwardena *et al.* 2008, Pol *et al.* 2014, Marone *et al.* 2017). This is no different in the Sahelian savannahs.

Which leads to the conclusion, following the initial questions asked, that (1) food supply of seedeaters in the Sahel is declining, (2) seedeaters in the Sahel are highly selective in their seed choice, (3) heavy grazing has in general a negative impact on the food resources in the Sahel, and (4) present overall conditions in the Sahel are indeed limiting numbers of granivorous birds to the extent of causing steep declines in populations of most species involved, including the few species breeding in Eurasia.

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SAMENVATTING

Zaadetende vogels eten in de Sahel dagelijks met zijn alle gemiddeld ongeveer 15 gram zaad per ha. Dat is berekend aan de hand van systematische tellingen van vogels in vakjes van 4,5 ha en een geschatte dagelijkse voedselconsumptie afgeleid van hun lichaamsgewicht. Gedurende de korte regentijd stappen veel zaadeters over op ander voedsel. Als we daarmee rekening houden, zouden zaadetende vogels jaarlijks gemiddeld 4,5 kg zaad per ha consumeren. Het gaat daarbij om zaden van kruiden en grassen, vooral eenjarige soorten die aan het eind van de regentijd afsterven. Hoeveel zaad er dan op de grond ligt, verschilt naar locatie. Voor de gehele Sahel zal de gemiddelde zaadproductie tussen 30 en 100 kg per ha liggen. Als deze schattingen juist zijn, zouden zaadetende vogels niet meer dan 4 tot 15% van de jaarlijkse zaadvoorraad opeten, ogenschijnlijk geen aanwijzing voor voedselschaarste. Toch zijn er diverse redenen om aan te nemen dat het aantal zaadetende vogels wordt beperkt door hun voedselaanbod. Ten eerste moeten de vogels de zaadvoorraad delen met knaagdieren en insecten die bij elkaar meer zaden eten dan alle vogels samen. Ten tweede hebben de vogels per dag niet veel tijd om te foerageren, omdat ze ermee stoppen als de bodemtemperatuur

boven 35°C stijgt. Midden op de dag kan de bodemtemperatuur, zonder schaduw, oplopen tot 50°C of hoger. Dat is de belangrijkste reden dat grondfoeragerende vogels grosso modo vooral in de vroege ochtend en de late middag naar voedsel zoeken, in totaal ongeveer 4 uur per dag. Dit beperkte tijdvak zou in de toekomst nog verder kunnen worden ingeperkt; tussen 1950 en 2010 zijn de temperaturen in de Sahel in de heetste maanden april en mei al met 1,8° C gestegen. Hittestress dwingt vogels ertoe om in weinig tijd veel te eten. Ze zijn daardoor afhankelijk van plekken waar de beschikbare zaden zo talrijk zijn dat ze gemakkelijk kunnen worden gevonden (korte zoektijd). Maar de zaden moeten ook heel snel kunnen worden verwerkt (korte hannestijd). Duiven slikken de zaden in één keer in en dat gaat heel snel. Maar alle kleinere zaadeters scheiden eerst het kaf van het zaadje en dat kost meer tijd. Een derde reden om te denken dat het voedselaanbod beperkt is, heeft te maken met het feit dat slechts een deel van de zaden aan het oppervlak ligt en daardoor gemakkelijk te vinden is. De meeste graszaden liggen verborgen in het zand en zijn ook nog eens heel klein. Zo klein dat zelfs vogels van minder dan 10 gram er duizenden per dag moeten eten om rond te komen. Maar omdat ze zo weinig tijd hebben om voedsel te zoeken, kunnen ze het zich niet permitteren om te zoeken naar zaden die onder het zand verborgen liggen. Zelfs in overvloed kan voedsel toch onbereikbaar zijn. Ten vierde laten vogels in de Sahel veel zaad links liggen. Ze weigeren 'lege zaden' (zaden bestaande uit alleen het onverteerbaar kafje, dus zonder inhoud). Ook de zaden van juist de meest voorkomende grassoorten worden vermeden, zoals van *Aristida* waar aan de zaden lange naalden zitten of van *Cenchrus*, een soort kleeftkruid met keiharde stekels. Deze zaden worden waarschijnlijk niet gegeten omdat het te veel hannestijd zou kosten om ze naar binnen te kunnen werken. Sommige zaden van kruidachtigen worden wel gegeten, maar genieten niet de voorkeur, waarschijnlijk vanwege hun geringe verteerbaarheid. Zaadetende vogels eten het liefst de zaden van het gras *Panicum* en andere wilde gierstsoorten die geen naalden of stekels hebben en gemakkelijk verteerbaar zijn. Vogels schakelen pas over op marginale zaadsoorten wanneer, aan het einde van de droge tijd, de zaadvoorraad van de voorkeurssoorten is uitgeput. Ten vijfde worden *Panicum* en andere preferente eenjarige grassen meestal aangetroffen op vloedvlakten en lage plekken die tijdens het regenseizoen tijdelijk onder water komen te staan. Deze gebieden trekken veel zaadetende vogels aan, maar de totale oppervlakte van vochtige foerageergebieden is relatief klein vergeleken met de uitgestrekte droge gebieden. En nog veel kleiner in droge jaren, waaraan geen gebrek was in de afgelopen ruim halve eeuw. In dergelijke jaren is de sterfte onder zaadetende vogels enorm. Het zesde en laatste argument voor beperkt voedselaanbod is dat de hoeveelheid zaad op de bodem is geslonken door de gestegen begrazingsdruk van vee die met het gras ook de zaden opeten. De hogere graasdruk heeft er tevens voor gezorgd dat de voor zaadetende vogels favoriete grassoorten zijn vervangen door niet-preferente grassen en kruiden die beter bestand zijn tegen graasdruk of daar zelfs van profiteren. Al deze factoren tezamen hebben bijgedragen aan de fenomenale achteruitgang van zaadetende vogels in de Sahel tussen 1970 en 2010. Het zijn er nu nog vier miljard, maar een halve eeuw geleden moeten dat er miljarden meer zijn geweest. Ook het handjevol Euraziatische zaadeters dat in de Sahel overwintert kan daarover meespreken.

RÉSUMÉ

Les oiseaux granivores du Sahel mangent en moyenne environ 15 grammes de graines par hectare. Ce chiffre a été calculé à partir de comptages systématiques des oiseaux dans des parcelles de 4,5 ha et d'une estimation de la consommation alimentaire quotidienne dérivée de leur poids corporel. Pendant la courte saison des pluies, de nombreux oiseaux granivores se tournent vers d'autres aliments. Compte tenu de ce facteur, les oiseaux granivores consommeraient en moyenne 4,5 kg de graines par ha et par an. Il s'agit de graines d'herbes et de graminées, en particulier d'espèces annuelles qui meurent à la fin de la saison des pluies. La quantité de semences laissée sur le sol varie alors d'un endroit à l'autre. Pour l'ensemble du Sahel, la production moyenne de semences se situera entre 30 et 100 kg par ha. Si correcte, les oiseaux granivores ne mangeraient pas plus de 4 à 15% de l'approvisionnement annuel en graines. Cependant, il y a plusieurs raisons de supposer que le nombre d'oiseaux granivores est limité par leur nourriture. (1) Les oiseaux doivent partager l'approvisionnement en graines avec les rongeurs et les insectes qui, ensemble, mangent plus de graines que tous les oiseaux réunis. (2) Les oiseaux n'ont pas beaucoup de temps par jour pour fourrager car ils s'arrêtent lorsque la température du sol dépasse 35°C. Au milieu de la journée, sans ombre, la température du sol peut atteindre 50 ou 60°C. C'est la principale raison pour laquelle les oiseaux butinant au sol ne s'alimentent qu'en début de matinée et en fin d'après-midi, pour un total d'environ 4 heures par jour. Le stress thermique oblige les oiseaux à manger beaucoup en peu de temps. Ils dépendent donc des endroits où les graines disponibles sont si abondantes qu'elles peuvent être trouvées facilement (temps de recherche court). Mais il faut aussi que les graines soient traitées très rapidement (temps d'accrochage court). Les pigeons avalent les graines d'un seul coup et très rapidement. Mais tous les petits mangeurs de graines séparent d'abord l'enveloppe de la graine et cela prend plus de temps. (3) Seules certaines des graines sont à la surface et donc faciles à trouver. La plupart des graines d'herbe, très petites, sont cachées dans le sable. Si petites que même les oiseaux pesant moins de 10 grammes doivent en manger des milliers par jour pour joindre les deux bouts. Mais comme ils ont si peu de temps pour se nourrir, ils ne peuvent pas se permettre de chercher des graines cachées sous le sable. Même en abondance, la nourriture peut encore être inaccessible. (4) Les oiseaux du Sahel ignorent de nombreuses graines. Ils refusent les "graines vides" (graines constituées uniquement de l'enveloppe indigeste, donc sans contenu). Ils évitent également les graines des espèces de graminées les plus courantes, telles que l'*Aristide*, dont les graines sont munies de longues aiguilles, ou le *Cenchrus*, un type de gaillet gratteron aux épines très dures. Ces graines ne sont probablement pas consommées car il faudrait une trop grande envie pour les ingérer. Certaines graines d'herbacées sont consommées, mais ne sont pas préférées, probablement en raison de leur faible digestibilité. Les oiseaux granivores préfèrent les graines de l'herbe *Panicum* et d'autres espèces de millet sauvage qui n'ont pas d'aiguilles ou d'épines et sont faciles à digérer. Les oiseaux ne passent à des espèces marginales que lorsque, à la fin de la saison sèche, les réserves de graines de l'espèce préférée sont épuisées. (5) Le *Panicum* et d'autres herbes annuelles préférées se trouvent généralement dans les plaines inondables. Ces zones attirent de nombreux oiseaux

granivores, mais la superficie totale de ces zones est relativement faible par rapport aux vastes zones sèches. Et encore moins pendant les années sèches, qui n'ont pas manqué au cours du dernier demi-siècle. Ces années-là, la mortalité des oiseaux granivores est énorme. (6) La quantité de graines sur le sol a diminué en raison de la pression accrue du bétail, qui mange les graines en même temps que l'herbe. La pression de pâturage plus élevée a également entraîné le remplacement des espèces de graminées favorisées par les oiseaux granivores par

des graminées et des herbes non préférées qui sont plus résistantes à la pression de pâturage, voire qui en bénéficient. Tous ces facteurs ont contribué au déclin phénoménal des oiseaux granivores du Sahel entre 1970 et 2010. Aujourd'hui, ils sont encore quatre milliards, mais il y a un demi-siècle, ils devaient être beaucoup plus nombreux.

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SUPPLEMENTARY MATERIAL: Handling time in seed-eating birds

Table S1. The handling time in seconds (ht), defined as the time needed to husk and ingest a seed, for 48 seed-eating bird species with body masses (bm) varying between 9.6 and 70 g, and for 38 seed species varying between 0.1 and 146 mg. A selection is made for seeds that are husked (thus excluding seeds swallowed whole, as typical of doves and waterbirds). The 197 handling times and seed weights are taken from 13 sources (#): (1) Carrillo et al. 2007, (2) Goldstein & Baker 1984, (3) Hespeneheide 1966, (4) Hrabar & Perrin 2002, (5) Kear 1962, (6) Marone et al. 2022, (7) Pulliam 1985, (8) Soobramoney & Perrin 2007, (9) Titulaer 2018, (10) van der Meij & Bout 2004, (11) van der Meij & Bout 2006, (12) Willson 1971 and (13) Willson & Harmeson 1973.

Bird species	bm	Seed species	seed (mg)	ht	#	Bird species	bm	Seed species	seed (mg)	ht	#
Fischer's Lovebird	46.6	<i>Echinochloa frumentacea</i>	3.5	6.0	4	White-rumped Munia	13.6	<i>Echinochloa frumentacea</i>	3.3	3.7	8
Fischer's Lovebird	46.6	<i>Panicum maximum</i>	5.6	6.6	4	White-rumped Munia	13.6	<i>Guizotia abyssinica</i>	2.9	4.5	8
Fischer's Lovebird	46.6	<i>Phalaris canariensis</i>	7.0	5.3	4	White-rumped Munia	13.6	<i>Panicum maximum</i>	3.6	2.3	8
Fischer's Lovebird	46.6	<i>Setaria italica</i>	5.4	7.1	4	White-rumped Munia	13.6	<i>Phalaris canariensis</i>	7.0	6.7	8
Cape Sparrow	24.6	<i>Echinochloa frumentacea</i>	3.3	2.2	8	White-rumped Munia	13.6	<i>Setaria italica</i>	5.1	5.9	8
Cape Sparrow	24.6	<i>Guizotia abyssinica</i>	2.9	7.1	8	White-rumped Munia	13.6	<i>Sorghum bicolor</i>	20.8	29.7	8
Cape Sparrow	24.6	<i>Panicum maximum</i>	3.6	3.1	8	Gouldian Finch	15.2	<i>Phalaris canariensis</i>	7.0	12.5	11
Cape Sparrow	24.6	<i>Phalaris canariensis</i>	7.0	2.7	8	Blue-faced Parrotfinch	13.1	<i>Phalaris canariensis</i>	7.0	7.8	11
Cape Sparrow	24.6	<i>Setaria italica</i>	5.1	2.9	8	Cut-throat Finch	18.5	<i>Phalaris canariensis</i>	7.0	5.4	11
Cape Sparrow	24.6	<i>Sorghum bicolor</i>	20.8	22.3	8	Common Chaffinch	22.0	<i>Brassica napus</i>	5.3	2.4	5
Thick-billed Weaver	43.9	<i>Echinochloa frumentacea</i>	3.3	5.9	8	Common Chaffinch	22.0	<i>Cannabis sativa</i>	25.0	5.0	5
Thick-billed Weaver	43.9	<i>Guizotia abyssinica</i>	2.9	8.3	8	Common Chaffinch	22.0	<i>Helianthus annuus</i>	143.0	41.0	5
Thick-billed Weaver	43.9	<i>Panicum maximum</i>	3.6	6.4	8	Common Chaffinch	22.0	<i>Linum usitatissimum</i>	7.8	6.5	5
Thick-billed Weaver	43.9	<i>Phalaris canariensis</i>	7.0	4.7	8	Common Chaffinch	22.0	<i>Phalaris canariensis</i>	11.0	2.8	5
Thick-billed Weaver	43.9	<i>Setaria italica</i>	5.1	7.3	8	Common Chaffinch	22.0	<i>Setaria italica</i>	4.9	3.2	5
Thick-billed Weaver	43.9	<i>Sorghum bicolor</i>	20.8	16.5	8	Collared Grosbeak	70.0	<i>Phalaris canariensis</i>	7.0	2.4	11
Black-winged Red Bishop	22.0	<i>Cannabis sativa</i>	18.5	5.5	10	Evening Grosbeak	55.0	<i>Cannabis sativa</i>	25.0	2.3	5
Southern Red Bishop	21.1	<i>Echinochloa frumentacea</i>	3.3	3.2	8	Evening Grosbeak	55.0	<i>Helianthus annuus</i>	143.0	4.3	5
Southern Red Bishop	21.1	<i>Guizotia abyssinica</i>	2.9	6.4	8	Hawfinch	21.8	<i>Cannabis sativa</i>	25.0	3.1	5
Southern Red Bishop	21.1	<i>Panicum maximum</i>	3.6	2.7	8	Hawfinch	21.8	<i>Helianthus annuus</i>	143.0	4.3	5
Southern Red Bishop	21.1	<i>Phalaris canariensis</i>	7.0	3.5	8	Hawfinch	21.8	<i>Linum usitatissimum</i>	7.8	5.6	5
Southern Red Bishop	21.1	<i>Setaria italica</i>	5.1	4.1	8	Hawfinch	21.8	<i>Phalaris canariensis</i>	11.0	2.8	5
Southern Red Bishop	21.1	<i>Sorghum bicolor</i>	20.8	24.5	8	Chinese Grosbeak	52.0	<i>Phalaris canariensis</i>	7.0	2.1	11
Sunda Zebra Finch	22.7	<i>Phalaris canariensis</i>	7.0	16.0	11	Eurasian Bullfinch	20.9	<i>Phalaris canariensis</i>	7.0	4.9	11
Bronze Mannikin	9.6	<i>Echinochloa frumentacea</i>	3.3	5.0	8	Trumpeter Finch	19.2	<i>Avena sativa</i>	16.0	11.9	1
Bronze Mannikin	9.6	<i>Guizotia abyssinica</i>	2.9	5.8	8	Trumpeter Finch	19.2	<i>Brassica napus</i>	4.0	2.3	1
Bronze Mannikin	9.6	<i>Panicum maximum</i>	3.6	1.6	8	Trumpeter Finch	19.2	<i>Linum usitatissimum</i>	4.8	4.3	1
Bronze Mannikin	9.6	<i>Phalaris canariensis</i>	7.0	8.9	8	Trumpeter Finch	19.2	<i>Phalaris canariensis</i>	6.5	2.8	1
Bronze Mannikin	9.6	<i>Setaria italica</i>	5.1	6.4	8	Trumpeter Finch	19.2	<i>Setaria italica</i>	6.7	6.3	1
Bronze Mannikin	9.6	<i>Sorghum bicolor</i>	20.8	32.2	8	Common Rosefinch	21.6	<i>Phalaris canariensis</i>	7.0	3.4	11
Magpie Mannikin	16.2	<i>Phalaris canariensis</i>	7.0	7.9	11	European Greenfinch	25.1	<i>Cannabis sativa</i>	25.0	2.8	5
Java Sparrow	30.4	<i>Cannabis sativa</i>	18.5	4.1	10	European Greenfinch	28.3	<i>Cannabis sativa</i>	18.5	2.2	10
Java Sparrow	26.9	<i>Echinochloa frumentacea</i>	3.5	2.3	4	European Greenfinch	25.1	<i>Helianthus annuus</i>	143.0	5.9	5
Java Sparrow	26.9	<i>Panicum maximum</i>	5.6	2.7	4	European Greenfinch	25.1	<i>Linum usitatissimum</i>	7.8	4.8	5
Java Sparrow	26.9	<i>Phalaris canariensis</i>	7.0	2.6	4	European Greenfinch	25.1	<i>Phalaris canariensis</i>	11.0	2.8	5
Java Sparrow	30.4	<i>Phalaris canariensis</i>	7.0	2.6	11	European Greenfinch	28.3	<i>Phalaris canariensis</i>	7.0	2.6	11
Java Sparrow	26.9	<i>Setaria italica</i>	5.4	3.1	4	Grey-capped Greenfinch	20.0	<i>Phalaris canariensis</i>	7.0	2.9	11
Scaly-breasted Munia	12.4	<i>Phalaris canariensis</i>	7.0	11.6	11	Desert Finch	22.5	<i>Phalaris canariensis</i>	7.0	4.0	11

Table S1. Continued.

Bird species	bm	Seed species	seed (mg)	ht	#	Bird species	bm	Seed species	seed (mg)	ht	#
Yellow-fronted Canary	12.0	<i>Cannabis sativa</i>	18.5	12.6	10	Rufous-collared Sparrow	19.2	<i>Pappophorum</i> spp.	1.45	0.7	6
Yellow-fronted Canary	12.0	<i>Phalaris canariensis</i>	7.0	12.6	11	Rufous-collared Sparrow	19.2	<i>Setaria leucopila</i>	2.05	0.8	6
Common Redpoll	12.6	<i>Phalaris canariensis</i>	7.0	9.8	11	White-crowned Sparrow	27.0	<i>Aristida divaricata</i>	1.0	1.4	7
Red Crossbill	44.0	<i>Phalaris canariensis</i>	7.0	3.7	11	White-crowned Sparrow	27.0	<i>Aristida hamulosa</i>	0.8	2.2	7
Atlantic Canary	24.9	<i>Brassica napus</i>	5.3	2.3	5	White-crowned Sparrow	27.0	<i>Aristida ternipes</i>	1.0	2.0	7
Atlantic Canary	24.9	<i>Cannabis sativa</i>	25.0	4.6	5	White-crowned Sparrow	27.0	<i>Bouteloua aristidoides</i>	0.8	1.0	7
Atlantic Canary	24.9	<i>Linum usitatissimum</i>	7.8	8.3	5	White-crowned Sparrow	27.0	<i>Bouteloua hirsuta</i>	0.7	1.1	7
Atlantic Canary	24.9	<i>Phalaris canariensis</i>	11.0	3.3	5	White-crowned Sparrow	23.2	<i>Helianthus annuus</i>	86.0	72.0	3
Atlantic Canary	24.9	<i>Setaria italica</i>	4.9	3.3	5	White-crowned Sparrow	27.0	<i>Lycurus phleoides</i>	0.2	0.8	7
Eurasian Siskin	13.0	<i>Phalaris canariensis</i>	7.0	9.2	11	White-throated Sparrow	23.2	<i>Avena sativa</i>	29.6	13.2	12
Yellowhammer	25.0	<i>Cannabis sativa</i>	18.5	4.8	10	White-throated Sparrow	23.2	<i>Cannabis sativa</i>	16.8	13.9	12
Grasshopper Sparrow	16.6	<i>Bouteloua aristidoides</i>	0.3	0.4	9	White-throated Sparrow	23.2	<i>Guizotia abyssinica</i>	2.9	4.8	12
Grasshopper Sparrow	16.6	<i>Bouteloua curtipendula</i>	2.4	0.4	9	White-throated Sparrow	23.2	<i>Helianthus annuus</i>	93.0	103.0	3
Grasshopper Sparrow	16.6	<i>Cenchrus ciliaris</i>	2.9	0.9	9	White-throated Sparrow	23.2	<i>Helianthus annuus</i>	122.0	121.0	3
Grasshopper Sparrow	16.6	<i>Disakisperma dubium</i>	0.6	0.7	9	White-throated Sparrow	23.2	<i>Helianthus annuus</i>	146.0	158.0	3
Grasshopper Sparrow	16.6	<i>Eragrostis lehmanniana</i>	0.1	0.5	9	White-throated Sparrow	23.2	<i>Phalaris canariensis</i>	6.5	3.3	12
Grasshopper Sparrow	16.6	<i>Melinis repens</i>	0.7	0.3	9	White-throated Sparrow	23.2	<i>Setaria italica</i>	3.4	4.9	12
Chipping Sparrow	12.6	<i>Aristida divaricata</i>	1.0	3.2	7	Baird's Sparrow	17.5	<i>Bouteloua aristidoides</i>	0.3	0.5	9
Chipping Sparrow	12.6	<i>Aristida hamulosa</i>	0.8	2.8	7	Baird's Sparrow	17.5	<i>Bouteloua curtipendula</i>	2.4	0.8	9
Chipping Sparrow	12.6	<i>Aristida ternipes</i>	1.0	4.4	7	Baird's Sparrow	17.5	<i>Cenchrus ciliaris</i>	2.9	0.8	9
Chipping Sparrow	12.6	<i>Bidens leptoccephala</i>	1.2	6.3	7	Baird's Sparrow	17.5	<i>Disakisperma dubium</i>	0.6	0.6	9
Chipping Sparrow	12.6	<i>Bouteloua aristidoides</i>	0.8	1.3	7	Baird's Sparrow	17.5	<i>Eragrostis lehmanniana</i>	0.1	0.5	9
Chipping Sparrow	12.6	<i>Bouteloua curtipendula</i>	0.8	1.4	7	Baird's Sparrow	17.5	<i>Melinis repens</i>	0.7	0.3	9
Chipping Sparrow	12.6	<i>Bouteloua hirsuta</i>	0.7	1.5	7	Savannah sparrow	16.5	<i>Bouteloua aristidoides</i>	0.3	0.7	9
Chipping Sparrow	12.6	<i>Digitaria californica</i>	0.6	2.3	7	Savannah sparrow	16.5	<i>Bouteloua curtipendula</i>	2.4	1.1	9
Chipping Sparrow	12.6	<i>Disakisperma dubium</i>	0.7	1.2	7	Savannah sparrow	16.5	<i>Disakisperma dubium</i>	0.6	0.7	9
Chipping Sparrow	12.6	<i>Eragrostis lehmanniana</i>	0.1	0.6	7	Savannah sparrow	16.5	<i>Melinis repens</i>	0.7	0.3	9
Chipping Sparrow	12.6	<i>Glinus oppositifolius</i>	0.1	0.1	7	Song Sparrow	25.0	<i>Amaranthus retroflexus</i>	0.3	2.2	13
Chipping Sparrow	12.6	<i>Hexasepalum teres</i>	4.1	5.9	7	Song Sparrow	25.0	<i>Cannabis sativa</i>	16.8	12.8	12
Chipping Sparrow	12.6	<i>Hopia obtusum</i>	1.8	4.5	7	Song Sparrow	25.0	<i>Cannabis sativa</i>	7.0	11.4	13
Chipping Sparrow	12.6	<i>Lycurus phleoides</i>	0.2	0.9	7	Song Sparrow	25.0	<i>Guizotia abyssinica</i>	2.9	4.5	12
Chipping Sparrow	12.6	<i>Portulaca oleracea</i>	0.1	0.9	7	Song Sparrow	25.0	<i>Persicaria bungeana</i>	4.8	10.1	13
Chipping Sparrow	12.6	<i>Portulaca oleracea</i>	0.2	0.6	7	Song Sparrow	25.0	<i>Phalaris canariensis</i>	6.5	3.5	12
Chipping Sparrow	12.6	<i>Schkuhria pinnata</i>	3.1	4.7	7	Song Sparrow	25.0	<i>Setaria faberi</i>	1.2	2.0	13
Chipping Sparrow	12.6	<i>Sida abutilifolia</i>	1.6	5.5	7	Song Sparrow	25.0	<i>Setaria italica</i>	3.4	2.9	12
Field Sparrow	13.1	<i>Setaria italica</i>	3.4	3.2	12	Swamp Sparrow	16.0	<i>Guizotia abyssinica</i>	2.9	3.1	12
Red Fox Sparrow	31.0	<i>Cannabis sativa</i>	16.8	8.1	12	Swamp Sparrow	16.0	<i>Phalaris canariensis</i>	6.5	3.5	12
Red Fox Sparrow	31.0	<i>Guizotia abyssinica</i>	2.9	2.0	12	Swamp Sparrow	16.0	<i>Setaria italica</i>	3.4	2.8	12
Red Fox Sparrow	31.0	<i>Linum usitatissimum</i>	5.5	6.2	12	Northern Cardinal	44.0	<i>Ambrosia trifida</i>	35.7	80.7	13
Red Fox Sparrow	31.0	<i>Phalaris canariensis</i>	6.5	2.8	12	Northern Cardinal	44.0	<i>Ambrosia trifida</i>	35.7	43.6	13
Red Fox Sparrow	31.0	<i>Setaria italica</i>	3.4	4.0	12	Northern Cardinal	44.0	<i>Avena sativa</i>	29.6	28.9	12
American Tree Sparrow	17.8	<i>Cannabis sativa</i>	16.8	19.0	12	Northern Cardinal	44.0	<i>Cannabis sativa</i>	16.8	13.5	12
American Tree Sparrow	17.8	<i>Guizotia abyssinica</i>	2.9	4.6	12	Northern Cardinal	44.0	<i>Cannabis sativa</i>	7.0	5.5	13
American Tree Sparrow	17.8	<i>Phalaris canariensis</i>	6.5	4.4	12	Northern Cardinal	44.0	<i>Guizotia abyssinica</i>	2.9	2.7	12
American Tree Sparrow	17.8	<i>Setaria italica</i>	3.4	1.6	12	Northern Cardinal	44.0	<i>Helianthus annuus</i>	120.0	36.8	12
Dark-eyed Junco	19.8	<i>Aristida hamulosa</i>	0.8	2.5	7	Northern Cardinal	44.0	<i>Persicaria bungeana</i>	4.8	11.7	13
Dark-eyed Junco	21.0	<i>Cannabis sativa</i>	16.8	30.3	12	Northern Cardinal	44.0	<i>Phalaris canariensis</i>	6.5	4.3	12
Dark-eyed Junco	19.8	<i>Digitaria californica</i>	0.6	1.3	7	Northern Cardinal	44.0	<i>Setaria faberi</i>	1.2	3.0	13
Dark-eyed Junco	19.8	<i>Disakisperma dubium</i>	0.7	1.0	7	Northern Cardinal	44.0	<i>Setaria italica</i>	3.4	5.4	12
Dark-eyed Junco	19.8	<i>Eriochloa acuminata</i>		4.1	7	Many-colored Chaco Finch	22.4	<i>Digitaria californica</i>	1.32	0.4	6
Dark-eyed Junco	19.8	<i>Guizotia abyssinica</i>	3.1	4.9	2	Many-colored Chaco Finch	22.4	<i>Parthenium hysterophorus</i>	2.28	0.4	6
Dark-eyed Junco	21.0	<i>Guizotia abyssinica</i>	2.9	3.4	12	Many-colored Chaco Finch	22.4	<i>Pappophorum</i> spp.	1.59	0.7	6
Dark-eyed Junco	21.1	<i>Helianthus annuus</i>	86.0	228.0	3	Many-colored Chaco Finch	22.4	<i>Setaria leucopila</i>	2.13	0.8	6
Dark-eyed Junco	21.1	<i>Helianthus annuus</i>	93.0	166.0	3	Cinnamon Warbling Finch	12.7	<i>Digitaria californica</i>	1.33	0.4	6
Dark-eyed Junco	21.0	<i>Linum usitatissimum</i>	5.5	7.8	12	Cinnamon Warbling Finch	12.7	<i>Parthenium hysterophorus</i>	1.89	0.4	6
Dark-eyed Junco	19.8	<i>Lycurus phleoides</i>	0.2	0.7	7	Cinnamon Warbling Finch	12.7	<i>Pappophorum</i> spp.	1.7	0.7	6
Dark-eyed Junco	19.8	<i>Phalaris canariensis</i>	7.0	5.9	2	Cinnamon Warbling Finch	19.2	<i>Setaria leucopila</i>	3.09	0.8	6
Dark-eyed Junco	21.0	<i>Phalaris canariensis</i>	6.5	5.3	12	Diuca Finch	25.0	<i>Digitaria californica</i>	1.72	0.4	6
Dark-eyed Junco	21.0	<i>Setaria italica</i>	3.4	3.9	12	Diuca Finch	25.0	<i>Parthenium hysterophorus</i>	1.63	0.4	6
Rufous-collared Sparrow	19.2	<i>Digitaria californica</i>	1.52	0.4	6	Diuca Finch	25.0	<i>Pappophorum</i> spp.	3.86	0.7	6
Rufous-collared Sparrow	19.2	<i>Parthenium hysterophorus</i>	1.85	0.4	6	Diuca Finch	25.0	<i>Setaria leucopila</i>	1.04	0.8	6