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Distribution and relative density of raptors in the sub-Saharan during the dry season

Rob G. Bijlsma^{1,*}, Jan van der Kamp² & Leo Zwarts²

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The sub-Saharan between the Atlantic Ocean and Red Sea and between 5°N (Guinean vegetation zone) and 20°N (southern Sahara) was visited on 466 days during 15 dry seasons (late September – early March) in 1996–2019. Using a combination of field methods, ranging from road counts to surveys of single sites (non-random and random-stratified), a total of 22,696 raptors of 62 species were identified. These were allocated to 1° latitude-longitude grid cells. Palearctic migrants accounted for 13% of the total. Two Afrotropical raptors were by far the most common, Yellow-billed Kite *Milvus aegyptius* (46%) and Hooded Vulture *Necrosyrtes monachus* (25%). Diversity and density were lowest in the arid and semi-arid zones but increased with increasing annual rainfall and vegetation cover. Palearctic migrants almost exclusively occupied the driest zones (100–500 mm rainfall per year), African raptors were commonest in the more humid zones. Migrants were concentrated in the western and eastern sections of the sub-Saharan, in longitudinal agreement with the main crossing points on either side of the Mediterranean for the large majority of Palearctic migrants. Comparatively few migrants were encountered in the central Sahel (Mali-Niger-Chad), suggesting that most Palearctic raptors remained either in West or in East Africa upon entering the continent. Even harriers *Circus* spp., known to cross the full width of the Mediterranean Sea, showed a distinct East Africa bias in their distribution. Afrotropical raptors were more evenly distributed across the width of the sub-Saharan within the 100–1000-mm rainfall zone.

Key words: Sahel, birds of prey, bird distribution, relative density

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The diversity of raptors in Africa is seasonally enriched with tens of Eurasian species. Via the eastern flyway, namely Turkey, Caucasus, Middle East and Arabian Peninsula, several million raptors from Europe and Asia pour into Africa (Jobson *et al.* 2021). The western route via the Iberian Peninsula is a floodgate for migratory raptors from western and northern Europe. A trickle of raptor species with low wing-loading crosses the full width of the Mediterranean in between the two bottlenecks (Panuccio *et al.* 2021). Except for European Honey Buzzard *Pernis apivorus*, which typically winters in humid forests in western and central Africa (Vansteelant *et al.* 2015), and Osprey *Pandion haliaetus*, which winters in coastal and inland wetlands, most common migratory raptor species from Eurasia spend

the non-breeding period in savannah-like ecosystems (including derived savannah) in the sub-Saharan and southern Africa (Thiollay 1978a, Brown *et al.* 1982).

In the recent past, attempts to describe distributional and seasonal patterns in the dry zones of Africa were mostly restricted to analyses of observations of resident ornithologists (e.g. in Nigeria by Elgood *et al.* 1973). Road counts were used to cope more quantitatively with diversity and abundance across large regions, notably in West Africa (Mali, Burkina Faso, Niger and northern Cameroon; Thiollay 1978a, 2006), and in East and southern Africa (with a preliminary overview by Brown 1970: 284–295). Many more road surveys have seen the light of day since then (McClure *et al.* 2021), albeit rather few from the Sahelian-

Sudano-Guinean zone (but see e.g. Rondeau *et al.* 2007, Anadon *et al.* 2010, Buij *et al.* 2013, Angelov & Hashim 2019). The advent of satellite-tracking has fine-tuned distributional patterns and movements within wintering ranges in Africa, especially when concurrent field studies were carried out to quantify habitat use and food resources *in situ* (Schlaich *et al.* 2016). Similarly, ornithologists and birders have not remained idle in the 50 years since Brown's (1970) overview was published. Many open questions regarding biology and ecology of raptors in Africa have been resolved through fieldwork and telemetry. Still, much work on raptors is concentrated on certain species, be they threatened or large, such as vultures, or limited to specific habitats (wetlands, forests) and regions (National Parks; e.g. Smeenk 1974, Thiollay 1998). This leaves much scope for publishing data on raptor guilds, irrespective of conservation directives.

During fieldwork between 1996 and 2019, raptors were routinely recorded across the full width of sub-Saharan Africa north of 5°N. The longitudinal and latitudinal distribution of common Afro-Palaearctic migratory raptors are compared to those of Afro-tropical raptor species (including intra-African migrants). The study complements those covering ground-foraging and arboreal birds, with the caveat that densities per 1° latitude × 1° longitude grid cells used in the present study are relative (rather than absolute, as in Zwarts *et al.* 2023a, 2023b).

METHODS

The material for this overview was collected across the Sahelian-Sudano-Guinean zone between Atlantic Coast and Red Sea in 15 dry seasons (late September – early March) over the years 1996–2019. Three major sources of data were tapped. Raptors were recorded during road trips, stays at a single site (e.g. Bijlsma 2001), and stratified-random plot-sampling (Zwarts *et al.* 2023a). Additionally, raptors were registered whenever encountered and identified during fieldwork. Out of 22,696 raptors observed, 83% were recorded in December–February, i.e. midway through the dry season when within-African displacements are small or non-existent (hence the qualification 'residents' for Afrotropical species).

Road counts were opportunistic, insofar as raptors were identified and counted from the passenger's seat, with or without the help of other passengers, along roads and dirt tracks. Road counts were made on day-long journeys (Mali, Ghana, Nigeria) and on much

shorter trips (usually the 11-km stretches between successive sites forming part of the stratified-random survey of the wider Sahel; Zwarts *et al.* 2023a). Vehicle speed varied substantially between slow-moving and full speed (up to 90 km/h) depending on the terrain. Only rarely were stops made to better examine flocks or individuals. Raptors were categorized as recorded within or further than 100 m from the road or observation site (Table S1, for % recorded at >100 m). Except for the width of the band, counts were not standardized (in terms of McClure *et al.* 2021). The road surveys were probably biased towards large and/or exposed species.

Single site studies were available for Nigeria (Boje-Ebakken, 6.63°N, 9.08°E, 2 × 3 km, 2604 mm rainfall/year near Ikom), Mali (Inner Niger Delta, 15.15°N, 4.23°W, 100 × 50 km), Ghana (Kintampo, 7.97°N, 1.73°W, 1 × 1 km and Damongo, 9.08°N, 1.77°W, 50 ha, respectively, 1351 mm and 1082 mm rainfall/year, averaged over 2001–2011; Ouwehand 2016: 27) and Ivory Coast (Comoé National Park, 8.75°N, 3.78°E, 1 × 1 km, 1000 mm rainfall/year; Ouwehand *et al.* 2023).

The site in Nigeria consisted of rainforest in the foothills of Afi Mountain, where an observation post in a *Pennisetum*-covered gap on the hillside provided an unobstructed view over forest and valley. Systematic daily observations of raptors were performed from elevated positions between 31 January and 21 February 2001 (Bijlsma 2001), and small forest raptors were netted incidentally during the capture of roosting Barn Swallows *Hirundo rustica* in early morning and evening (Bijlsma & van den Brink 2005).

Two study sites in Ghana near Kintampo and Damongo were situated in wooded savannah and consisted of dry forest remnants amidst farmland (for a detailed description, see Ouwehand 2016). Sites were alternately visited for 7–12 days to study European Pied Flycatchers *Ficedula hypoleuca*, and raptors were opportunistically recorded whilst surveying the forest and nearby fields, including occasional captures of small forest raptors during targeted netting of flycatchers (Ouwehand 2016). Prolonged stays at specific sites and where the forest was broken (clearcuts, small fields) achieved better than average detection of secretive raptors in these sites, whether by sight or hearing. In addition, raptor observations were available from several sites across Ghana that were visited between 10 December and 3 January 1996/1997 as part of a survey of Barn Swallow roosts. These included Keta Lagoon, Akuse Dam, Owabi Dam, Bosumtwi and Ayensudo (see van den Brink *et al.* 1998, for a description of sites).

The site in Comoé National Park in Ivory Coast consists of wooded savannah with two small forest islands and gallery forest along the Comoé River. Raptor observations were mostly carried out in the afternoons, whilst walking transects on the savannah, along the Comoé River and in the edges of forest islands. Fieldwork was conducted before the annual burning of savannah grasses was started (in 2018, the first fires were lit by late December).

The sub-Saharan between 7°N and 22°N and between 17°W and 42°E was systematically surveyed between 2007 and 2019 during the dry season from 26 September up to and including 10 March (see Figures 3–4 in Zwartz *et al.* 2023a). We used a stratified random sampling regime, covering a total of 2144 sites of 4.5 ha each (occasionally smaller when they were particularly labour-intensive). The sites were at least 5.5 km, but most often 11 km apart, and located along longitudinal and latitudinal transects traversing 14 countries between the Atlantic Ocean and the Red Sea. The field methods were specifically developed to collect absolute quantitative data from sunrise to sunset on ground-foraging and arboreal birds, while simultaneously obtaining detailed descriptions of the woody vegetation within plots (Zwartz & Bijlsma 2015). This time-consuming approach involved close and prolonged examination of individual trees, rather than scanning the sky. Consequently, many flying raptors, especially when high overhead, must have been overlooked, unlike those residing within the site boundaries of three legs of 300 × 50 m each. When moving by car from one site to the next, raptors were recorded as usual (within and beyond 100 m of the road).

Overall, the observations form a disparate collection based on repeatable (stratified-random) and non-repeatable methods. Of common raptor species (>500 records; Table S1), only a few were frequently observed

beyond 100 m, namely Hooded Vulture *Necrosyrtes monachus* (38%), Black Kite *Milvus migrans* (36%), Yellow-billed Kite *M. aegyptius* (35%) and White-backed Vulture *Gyps africanus* (24%). For the present paper, we combined all observations, irrespective of distance from the observer. The data are condensed into species-specific numbers per 1° latitude × 1° longitude grid cells (111 × c. 104 km), corrected for observer effort (field days spent in grid cells; Figure 1). 83 out of 154 grid cells were visited during just a single day (54%; yellow squares in Figure 1) and only 9 grid cells for more than 10 days (red squares in Figure 1; sometimes across several years, and restricted to Senegal, Mali, Ivory Coast, Ghana and Nigeria). Each raptor observation is also consigned to a site-specific value of mean annual rainfall (based on Hijmans *et al.* 2005). During the 15 dry seasons of observation, rainfall was below or well below the calculated average for 1950–2000 in 1996, 2000, 2004, 2008 and 2011 (dry years), about average in 2003, 2005, 2010 and 2013–2017, and well above in 2018–2019 (wet years; see Supplementary Material 4, in Zwartz *et al.* 2023a).

RESULTS

Species and relative abundance

During 466 field days spent in 14 sub-Saharan countries in 1996–2019 a total of 22,696 raptors of 62 species were recorded (Table S1). Just two species, Yellow-billed Kite (46.0%) and Hooded Vulture (25.2%), accounted for the bulk of the observations. Twenty species were recorded 10 times or fewer, partly because of their secretive life-style, as for several *Accipiter* species and Long-tailed Hawk *Urotriorchis macrourus*, or partly because they had a genuinely rare presence in the sub-Saharan north of 5°N (e.g. White-

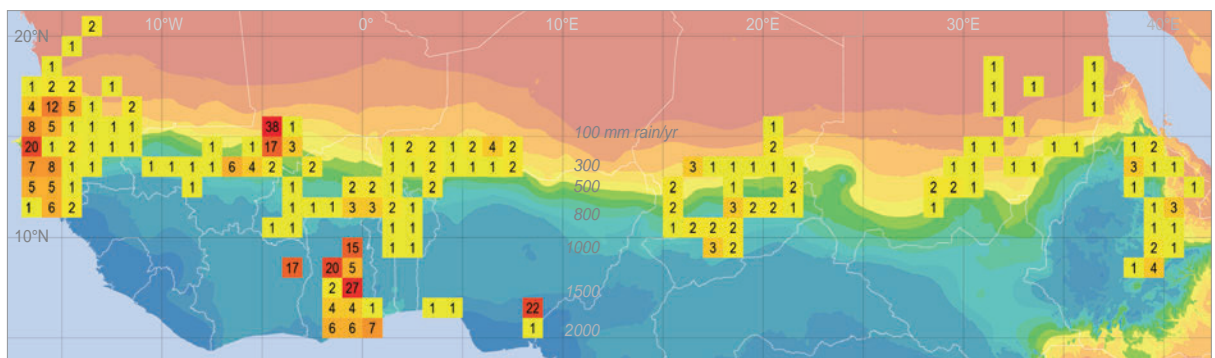


Figure 1. Number of days spent in grid cells (on average 111 × 104 km) across the sub-Saharan in 1996–2019, against a backdrop of rainfall isolines between <100 mm in the north (dark red) and >2000 mm in the south (dark blue).

headed Vulture *Trionocephs occipitalis*, Eastern Imperial Eagle *Aquila heliaca*, Greater Spotted Eagle *Clanga clanga* and Red-footed Falcon *Falco vespertinus*, or because they had a limited distribution (e.g. Bearded Vulture *Gypaetus barbatus* confined to the Ethiopian Highlands). Sparsely recorded raptor species were less frequently encountered than expected within their distributional range than species that were commonly recorded (Figure 2). Overall, migrants were vastly outnumbered by residents (the latter including intra-African migrants), only 13.4% being migrants among the 22,696 raptors recorded.

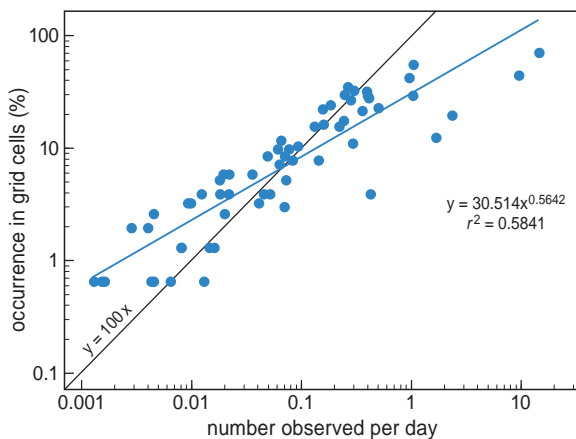


Figure 2. Encounter rate of 62 raptor species (dots) recorded within the grid cells encompassing their distributional range in the sub-Saharan as a function of their abundance, based on data collected in the dry seasons between 1996 and 2019. For raw data see Table S1.

Rainfall and latitudinal variation in distribution

Migratory raptors were mostly concentrated in the driest zones within the sub-Saharan (Table S2). Many species were typically confined to desert (<100 mm rainfall per annum), Sahel and the northern Sudan zone (<500 mm rainfall), notably Montagu's *Circus pygargus* and Pallid Harrier *C. macrourus*, Black Kite, Short-toed Snake Eagle *Circaetus gallicus*, Booted Eagle *Hieraetus pennatus*, Egyptian Vulture *Neophron percnopterus* and Lesser Kestrel *Falco naumanni* (Figure 3). In the arid zones migrants were about as numerous as residents, but they outnumbered Afrotropical species when rainfall was 200 mm per year or less (Figure 4).

Residents covered a wider range of rainfall zones, were scarce in the most arid zones (<200 mm) and were most common when rainfall exceeded 1000 mm. Ecologically closely related species differed in their latitudinal range, with migratory species wintering north

of the residents on average, as in Egyptian Vulture (although those in the East mostly refer to local breeding birds) versus Hooded Vulture, Black Kite versus Yellow-billed Kite and Short-toed Snake Eagle versus Black-chested *Circaetus pectoralis* and Brown Snake Eagle *C. cinereus*.

The highest diversity of raptors was found in the humid Guinean zone, with a mixture of forests, farmland and derived savannah. This diversity was under-recorded given the fact that many species lead a secretive life in cover and are hard to detect. The few raptors observed in deserts and semi-deserts in the dry season were most notably the bird-hunting Lanner Falcon *Falco biarmicus* and the scavenging Egyptian Vulture (mostly in the Afar region in eastern Ethiopia) and Yellow-billed Kite near human settlements, with acridivorous raptors during occasional outbreaks of grasshoppers and locusts (Black Kite and Lesser Kestrel) and species profiting from large floodplains in the Sahel (especially Western Marsh Harrier *Circus aeruginosus*, e.g. in Inner Niger Delta and Lake Chad).

Longitudinal variation in distribution

Migratory raptors within the wider Sahel showed distinct concentrations in the east and west, and least so in the central Sahel (Niger-Chad; Figure 5, Table S3). Overall numbers were highest in the eastern Sahel (notably Montagu's and Pallid Harrier, Short-toed Snake Eagle and Booted Eagle). Black Kite was slightly more common in the west than in the east (Table S3).

Numbers of resident raptor species (including intra-African migrants) were more evenly spread across the width of the sub-Saharan region, except Sudan and Chad where numbers were much smaller. High densities were typically encountered in regions with a dense human population and large cities, as in W Senegal, S Ghana and Ethiopia, where until recently urban scavengers, such as Hooded Vulture and Yellow-billed Kite, abounded.

DISCUSSION

The Gap of Niger-Chad

The vast majority of thermal-using migratory raptors bypass the Mediterranean Sea via Iberia and the Middle and Near East. Species that routinely cross the Mediterranean Sea have low wing loadings, notably harriers, or are powerful fliers (falcons). Facultatively soaring species, such as Osprey and – to a lesser extent – European Honey Buzzard, are known to profit from thermal uplift of the seascape (Duriez *et al.* 2019,

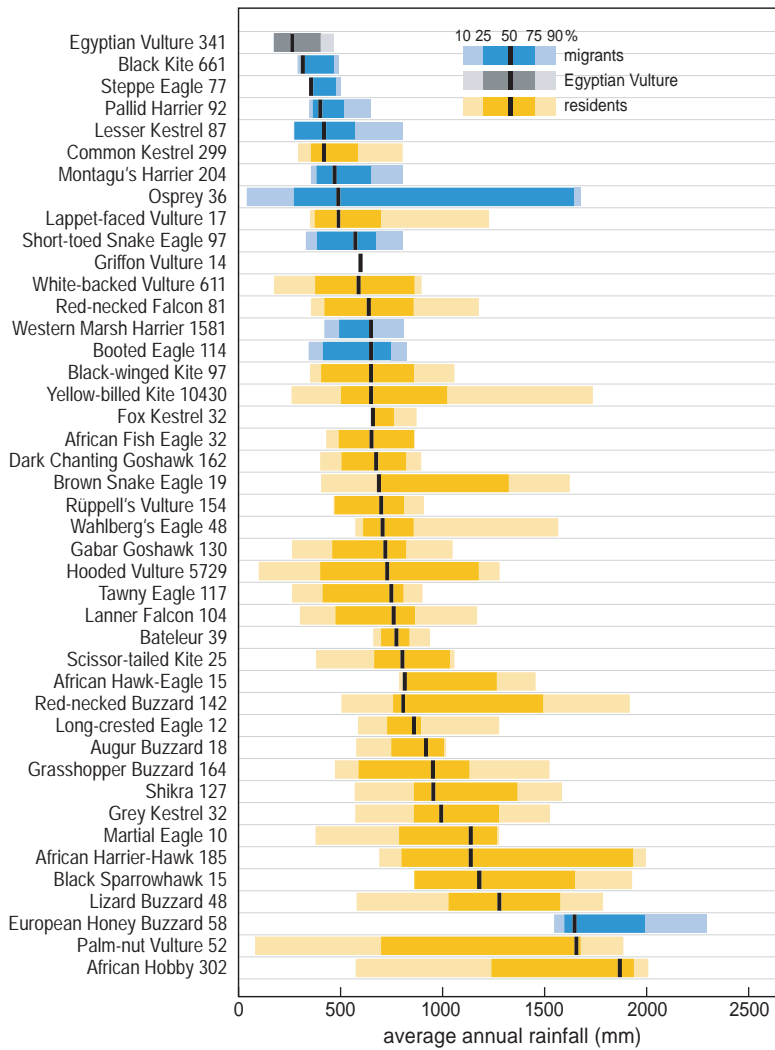


Figure 3. Average annual rainfall for the sites in the sub-Sahara where migratory and resident raptor species (including intra-African migrants) were recorded in this study (with >10 observations in 1996–2019, totals included). Egyptian Vultures are represented by (mostly) residents and some Palearctic migrants.

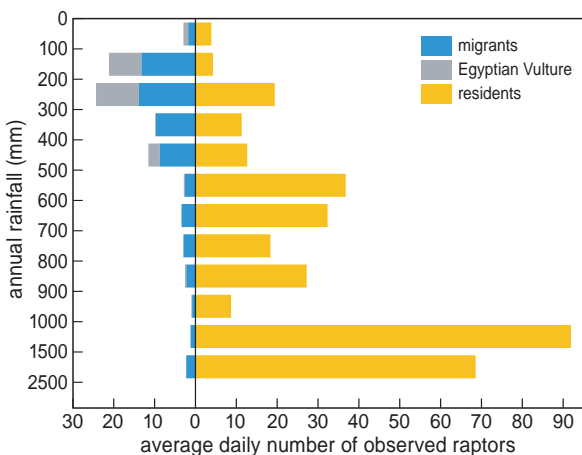


Figure 4. Latitudinal distribution of migratory, intra-African migratory and resident raptors in the dry season in the sub-Sahara (1996–2019), in terms of 100-mm annual rainfall bands (from desert to humid forests), but 500- and 1000-mm bands in the hyper-humid region. Egyptian Vulture mostly relates to residents in Ethiopia), with some Palearctic migrants (mostly in West Africa). Averages based on mean densities in 154 grid cells (Figure 1). ANOVA: migrants NS, $r^2 = 0.09$; Egyptian vulture: NS, $r^2 = 0.09$; residents $r^2 = 0.21$, $P < 0.001$.

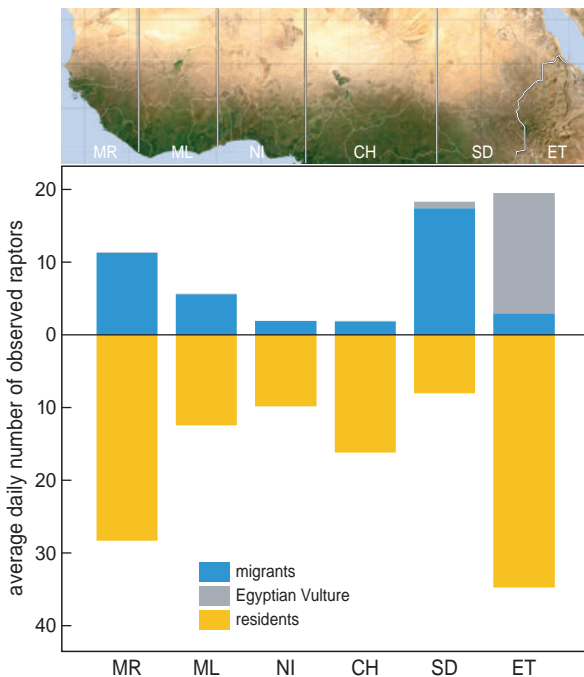


Figure 5. Relative density of migratory and resident raptors across six longitudinal bands in the sub-Saharan (1996–2019); Egyptian Vulture in East Africa mostly refers to local residents. Averages based on mean densities in 118 grid cells where annual rainfall varied between 100 and 1000 mm (Figure 1). ANOVA: migrants $r^2 = 0.11$, $P < 0.02$; Egyptian vulture: $r^2 = 0.21$, $P < 0.001$; residents $r^2 = 0.10$, $P = 0.03$.

Nourani *et al.* 2020) and to perform direct flights across the Central Mediterranean. Soaring raptors using the eastern gateway easily surpass 2 million birds (combining bottlenecks in Caucasus, Middle East and Yemen; Table 1), whereas the western bottleneck in the Gibraltar region probably accounts for less than 400,000 raptors (comprehensive overviews for this site are lacking, or make use of outdated, anecdotal or relative data; e.g. de Juana & Garcia 2015, Panuccio *et al.* 2021).

The higher number of migratory raptors encountered during our surveys in the eastern sub-Saharan compared to the western half, and the relative scarcity of Palearctic raptors in Niger-Chad (as found in passerines; Zwarts *et al.* 2023c), are coincident with the respective hinterlands and general migration pattern. It furthermore suggests that movements from West Africa eastwards or from East Africa westwards are limited in scope. Several species entering Africa in the east continue migration into southern Africa, as do Common Buzzard *Buteo buteo vulpinus*, Lesser Spotted Eagle *Clanga pomarina*, Red-footed Falcon and Lesser Kestrel.

These species – except Lesser Kestrel that has a large wintering population in West Africa (with 24,000 at a single roost in Senegal in 2007; Rodriguez *et al.* 2009) – were sparsely recorded during our surveys.

The discrepancy between the small numbers of Eurasian Egyptian Vultures entering Africa via the eastern bottleneck and the spike in occurrence in eastern Ethiopia hinges on the local population in mainly the Afar region, which numbered at least 1082–1424 birds in 2009–2013 (Arkumarev *et al.* 2014, McGrady *et al.* 2018). In Ethiopia we recorded 261 Egyptian Vultures in 1–24 February 2019, mostly in the region of Mekele-Logya where a single communication tower at 13.315°N and 39.982°E held 83 roosting birds on 17 February. A total of 153 out of 261 birds were aged: 99 (sub)adults, 25 immature (second and third plumage) and 29 juveniles. The proportion of 19% juveniles was much lower than the 32% among c. 1282 (90% age-identified of 1424) birds in the Afar region in 2009–2013 (Arkumarev *et al.* 2014).

The case of the harriers

Raptor species with low wing-loading, notably harriers, are known to cross the Mediterranean Sea in a broad front. An assessment of systematic counts across the northern Mediterranean during autumn migration of Montagu's Harriers suggested a preponderance of migrants crossing via Spain (23%), Aegean Archipelago (22%) and the Middle East (52%), but relatively few taking the Central Mediterranean (Trierweiler & Bijlsma 2010). The combined tracks of 145 birds equipped with transmitters partly confirmed the concentrated passage of western European Montagu's Harriers via SE Spain, but eastern European breeding

Table 1. Maximum count of long-distance migratory raptor species in autumn at bottlenecks in the Western Mediterranean (Gibraltar region) and in the East Mediterranean plus the Arabian Peninsula (Batumi¹, Belen Pass², Suez³, Bab el Mandeb⁴; after Jobson *et al.* 2021, Panuccio *et al.* 2021), known to winter largely in the sub-Saharan excluding humid forests.

| Species | West | East |
|--|---------|------------------------|
| Egyptian Vulture <i>Neophron percnopterus</i> | 4000 | 1000 ³ |
| Short-toed Snake Eagle <i>Circaetus gallicus</i> | 12,000 | 13,000 ² |
| Booted Eagle <i>Hieraetus pennatus</i> | 31,000 | 7370 ¹ |
| Steppe Eagle <i>Aquila nipalensis</i> | 0 | 141,000 ^{3,4} |
| Western Marsh Harrier <i>Circus aeruginosus</i> | 8000 | 6500 ¹ |
| Montagu's Harrier <i>Circus pygargus</i> | 6500 | 7000 ¹ |
| Pallid Harrier <i>Circus macrourus</i> | 0 | 1500 ¹ |
| Black Kite <i>Milvus migrans</i> | 224,000 | 221,000 ¹ |

birds crossed the Mediterranean via Corsica-Sardinia, the Italian mainland and the Aegean Sea. Eastern European birds ended up in the central Sudano-Sahel (with a concentration in the drainage basin of the Sokoto River in northern Nigeria), from where the birds redistributed themselves westwards in the course of the dry season (Schlaich & Klaassen in Panuccio *et al.* 2021: 152–159). Montagu's Harriers have not yet been tagged with transmitters in the Russian breeding range between Belarus and Kazakhstan (birds from Kazakhstan were found to winter in India; Panuccio *et al.* 2021: 155), and their distribution in Africa is not yet clear. Our observations suggest wintering grounds in eastern Africa, without much of a westward redistribution into the central Sudano-Sahel.

Pallid Harriers were largely confined to the eastern Sudano-Sahel (in Chad-Sudan-Ethiopia), as expected from the position of their Central Asian breeding grounds. Although telemetry showed some birds (2 out of 6; Limiñana *et al.* 2015) to shift their midwinter distribution from East to Central Sahel, our data indicate that Pallid Harriers are sparse west of Chad (Table S3). Orthopterans and rodents constitute major food resources, but granivorous birds may become an alternative food when such prey are scarce (Buij 2013). Within the Sudano-Sahel seed-eating birds were found to be most abundant in Chad, but they have declined significantly in West Africa (Zwarts *et al.* 2018, 2023c, 2023d). Numbers of Red-billed Quelea *Quelea quelea*, for example, an important prey of Pallid Harriers in northern Cameroon (Buij 2013), have crashed by 47–85% between the 1960s and 2010s, and other granivorous birds (at least in NW Senegal) by 39–97% (Zwarts *et al.* 2023d). When orthopterans and rodents are scarce, West Africa has not much to offer Pallid Harriers in the form of large flocks of granivorous birds, except locally near wetlands (notably Waza Logone in the Lake Chad Basin, a local magnet for Palearctic raptors; Thiollay 1978b, Buij & Croes 2013).

Western Marsh Harriers were typically concentrated within or near floodplains and other wetlands, especially in the delta and valley of the Senegal River, the Inner Niger Delta in Mali and Keta Lagoon in S Ghana (Zwarts *et al.* 2009). Of sex-identified adult Western Marsh Harriers, 98% of 95 females were recorded in wetlands, compared to 76% of 246 males; the latter were frequently recorded in savannah and cropland. Lake Chad is known to also hold a substantial wintering population (Buij *et al.* 2012), where Western Marsh Harrier is the most common Palearctic raptor species in the inundation zone with a mean dry season abundance of 23 birds per 100 km transect (Buij & Croes 2014).

Latitudinal distribution and rainfall

The latitudinal separation between migrants and residents, with the former residing in the (semi-)arid strata north of the residents, showed little overlap between both groups of raptors (as already noted by Thiollay 1978a, 1989). Our survey methods were inadequate to show seasonal latitudinal movements in the course of the dry season. A gradual southward shift in conjunction with declining food availability in the arid and semi-arid Sahel and Sudan zone has been shown for Montagu's Harrier between September and April (Trierweiler *et al.* 2013, Schlaich *et al.* 2016). Similar shifts have been noted for most Afrotropical and Palearctic raptor species (Brown 1970, Elgood *et al.* 1972). In very poor rainy seasons, as in 1972, birds left the Sahara and Sahel earlier, and their movements extended 200–300 km farther to the south, than in normal years (Thiollay 1978a). During our surveys, mostly in December–February, halfway through the dry season, local Afrotropical raptors had already moved into the more humid regions of the sub-Saharan, so that residents vastly outnumbered migrants south of 500 mm rainfall. Within the zone of overlap, residents were largely confined to urbanized regions (notably Yellow-billed Kite, with smaller numbers attending large wetlands such as the Inner Niger Delta, where breeding had commenced and food consisted of fishes, amphibians, rodents and offal (Bijlsma *et al.* 2005). The migratory Black Kite roamed the savannahs and farmland in small flocks, their movements being itinerant in response to local outbreaks of grasshoppers and locusts. Long-distance displacements were at great height (Thiollay 1978a).

Whether the latitudinal separation hinges on competition for resources between migrants and residents (as alluded to by Thiollay 1978a), or is the result of differences in diet and the concurrent habitat choice, or a combination of these and other factors, is unknown. Local studies showed clear differences in preferred habitats in winter, with Palearctic migrants occupying savannahs and exploiting cropland and rice fields after harvest (rodents and lizards), whereas residents profited from habitat fragmentation in the humid Guinean zones where a wider range of habitats, ecozones and foraging niches are available (Buij *et al.* 2013, Rodrigues *et al.* 2020). The semi-arid regions provide fewer contrasts between habitats, and in terms of food are especially productive regarding seed (attracting seed-eaters, and hence passerine-hunting raptors) and locusts and grasshoppers (attracting acridivorous raptors, like falcons, kites and harriers).

Shifting prospects

In the sub-Saharan, a study period of almost a quarter of a century is sufficiently long for large changes in climate and land use to occur. Well before our study took place, Thiollay (2006) had demonstrated vast declines in most raptor species in the Sudano-Sahelian zone of Mali, Burkina Faso, Niger and N Cameroon between 1969–1973 and 2003–2004. African vultures and eagles showed particularly steep declines in the late 1900s, but smaller African species were also affected (and Palearctic migrants less so). Outside protected zones declines were rampant. This general trend has largely continued unabated in later decades, notably in vultures (Di Vittorio *et al.* 2018, Henriques *et al.* 2020). Our study was not designed to monitor trends, but it is likely that within the quarter of a century covered by our survey raptors have been the

subject of further changes, not just in vultures and eagles but also in medium-sized and small raptor species. Apart from declines, these changes also include some increases related to improving fortunes of some Palearctic raptor species. For example, juveniles and immatures of the booming Iberian population of Griffon Vultures *Gyps fulvus* began to winter in Senegal and at present locally outnumber White-backed Vultures (Ouweneel 2021). Similarly, the population of western Palearctic Osprey has increased from 5500 in the 1980s to 9500–11,500 pairs in the early 2000s (Schmidt-Rothmund *et al.* 2014), which must have resulted in higher numbers wintering in West Africa.

At the same time, several Palearctic raptor species are in the process of shifting their wintering range to the north within Europe and Africa, as evident in Common Buzzard *Buteo buteo*, for example, which de



Outbreaks of locusts, like this flock of *Schistocerca gregaria* alighting from *Acacia tortilis* in semi-arid Mauritania (18.970°N, 15.314°W) on 27 January 2017, and roving grasshopper bands are lodestones to raptors, in this particular instance mostly Black Kites, Eurasian Kestrels and Lesser Kestrels.

facto has ceased to cross the Straits of Gibraltar in spring. This is attributed to a decreased migratory tendency in European breeding birds since the 1970s (Bensusan *et al.* 2007, Holte *et al.* 2017). Shifts are also evident among Palearctic-African migrants which until recently almost exclusively wintered in Africa. Black Kites are now routinely wintering in substantial numbers in southern Europe, although partly consisting of the eastern *Milvus migrans lineatus* (Zwarts *et al.* 2023d), as are Western Marsh Harriers and Booted Eagles (also in substantial numbers, e.g. 180–220 Booted Eagles on just Sicily in winter 2022; Surdo *et al.* 2022). To a smaller extent, the same tendency is noted in Pallid Harrier (Ollé *et al.* 2015) and Osprey (Martín *et al.* 2019).

Of African raptors, apart from vultures and some eagles, much less is known regarding trends, migratory shifts or shifting breeding and wintering ranges. The overall decline among seed-eating passerines in savannah-like habitats, as quantified by Zwarts *et al.* (2018, 2023a, 2023b, 2023d), has resulted in a substantial decline in food supply of bird-eating raptors. On the other hand, the conversion of savannah into farmland and floodplains into rice fields will, temporarily at least, favour rodent-eating raptors (Anadon *et al.* 2010, Buij *et al.* 2012, 2013, Augiron *et al.* 2015, Shaw *et al.* 2019). The overall effect of changing landscapes on raptors in the sub-Saharan, especially on small and medium-sized species, is presently an enigma but in the long run augurs large changes (Amar *et al.* 2018).

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SAMENVATTING

In vijftien winters tussen 1996 en 2019 werden 466 dagen in het veld doorgebracht in veertien landen ten zuiden van de Sahara en ten noorden van 5°N, in regencijfers uitgedrukt van <100 mm tot 2650 mm regenval per jaar. Het onderzoek bestreek de volle breedte van Afrika, van Atlantische Oceaan tot Rode Zee. Het veldwerk was niet per se gericht op roofvogels, maar deze werden niettemin zoveel mogelijk genoteerd tijdens autotochten, *in situ* veldwerk aan andere soorten en tijdens een gestratificeerd-random onderzoek naar bomen en vogels van West- tot Oost-Afrika. Het allegaartje van 22.696 waarnemingen van 62 soorten roofvogels werd ingedikt tot aantal waarnemingen per gradenhok (1° breedte- × 1° lengtegraad, 111 × c. 104 km), omgerekend naar het aantal waargenomen per dag doorgebracht in het betreffende hok. Van 154 hokken was aldus informatie beschikbaar, waarbij in 54% van de hokken slechts één dag werd gekeken (en in negen hokken >10 dagen). In de jaren van onderzoek lag de regenval in de voorafgaande natte tijd acht maal rond het gemiddelde berekend over 1950–2000, vijf maal er (duidelijk) onder en twee maal er duidelijk boven. De verspreiding, dichtheid en diversiteit van roofvogels was mager in de aride en semi-aride gebieden van zuidelijke Sahara, Sahel en Soedanzone. Juist in deze band met <800 mm regenval per jaar zaten verreweg de meeste Palearctische trekvogels. Meer naar het zuiden werden die uitgesproken schaars, en in de meest humide zone (>1500 mm regenval per jaar) werd slechts één Palearctische soort vastgesteld, de Wespendif *Pernis apivorus*. Op het totale aantal waargenomen roofvogels namen de Euraziatische soorten maar 13.4% voor hun rekening (vooral Zwarte Wouw *Milvus migrans* en Bruine Kiekendief *Circus aeruginosus*, die laatste sterk gebonden aan vloedvlaktes, rivierdalen en -delta's); de rest betrof Afrotropische roofvogels inclusief intra-Afrikaanse trekvogels. De Afrikaanse roofvogels waren schaars in de droge gebieden en hun dichtheid en verscheidenheid namen sterk toe naarmate de regenval toenam. De Afrotropische Geelsnavelwouw *Milvus aegyptius* en Kapgier *Necrosyrtes monachus* namen resp. 46.0% en 25.2% van alle roofvogels voor hun rekening. Ook over de breedte van de sub-Sahara bleken roofvogels verre van willekeurig verspreid voor te komen. Palearctische soorten hielden zich vooral in het Westen of Oosten op (binnen de zone met 100 tot 1000 mm regenval), overeenkomend met de twee flessenhalzen die de bulk van de thermiek gebruikende Euraziatische roofvogels gebruiken (resp. Gibraltar en Turkije-Kaukasus-Midden-Oosten en Arabische Schiereiland. De schaarste aan Palearctische roofvogels in de

centrale Sahel (Mali-Niger-Tsjaad-Soedan) laat zien dat verhoudingsgewijs weinig roofvogels zich vanuit het westen of oosten naar het hart van de Sahel bewegen. Bij de Afrikaanse soorten werd een minder prominente 'leegte' in de centrale Sahel opgemerkt. Het materiaal was van onvoldoende kwaliteit om iets te kunnen zeggen over habitatgebruik, invloed van voedselaanbod op verspreiding en dichtheid en aantalsveranderingen in de loop van de tijd. Maar zeker is dat de door ons waargenomen roofvogelfauna een slap aftreksel is van wat de eerste helft van de vorige eeuw heeft laten zien. Ook in de sub-Sahara, net als in het achterland van de aldaar overwinterende Palearctische soorten, gaan de veranderingen snel.

RÉSUMÉ

Pendant les 15 hivers entre 1996 à 2019 et en 466 jours d'observations de terrain effectués dans 14 pays différents au sein de la bande comprise entre le Sud du Sahara et la latitude 5°N, nous n'avons observé qu'une seule espèce d'origine paléarctique : la Bondrée apivore *Pernis apivorus*. Par ailleurs, les espèces paléarctiques n'ont représenté que 13,4% du nombre total de rapaces observés. Il s'agit principalement de Milan noir *Milvus migrans* et du Busard des roseaux *Circus aeruginosus*, ce dernier étant fortement lié aux estrans, aux vallées fluviales et aux deltas. Les rapaces sédentaires et les migrants intra-africains sont donc dominants. Les rapaces africains sont rares dans les zones arides et leur densité et diversité augmentent fortement avec l'accroissement des précipitations. Deux espèces sédentaires, le Milan d'Afrique *Milvus aegyptius* et le Vautour charognard *Necrosyrtes monachus*, représentent respectivement 46,0 % et 25,2 % de tous les rapaces. Nous avons également constaté que la répartition des rapaces est loin d'être aléatoire sous les latitudes subsahariennes. Les espèces paléarctiques sont principalement présentes aux extrémités Ouest et Est de la zone (avec 100 à 1000 mm précipitation per an), ce qui correspond aux deux principaux axes migratoires qui empruntent respectivement le Delta de Gibraltar à l'Ouest, le Caucase et le Moyen-Orient à l'Est. La rareté des rapaces paléarctiques dans le Sahel central (Mali-Niger-Tchad-Soudan) montre que peu d'entre eux se déplacent de l'Ouest ou de l'Est vers le cœur du Sahel. Pour les espèces africaines, la zone de moindre densité dans le centre du Sahel est moins étendue. La qualité des données collectées ne permet pas de tirer de conclusions sur l'utilisation de l'habitat, l'influence de la disponibilité alimentaire sur la répartition des rapaces ou sur l'évolution dans le temps de leur densité et de leur nombre. Mais ce qui est certain, c'est que les populations de rapaces que nous avons observées ne représentent qu'une fraction de ce qu'elles étaient lors de la première moitié du siècle dernier. Les changements sont rapides en Afrique subsaharienne, comme dans les pays d'origine des espèces paléarctiques qui y hivernent.

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SUPPLEMENTARY MATERIAL



Table S1. Number of raptors observed in the sub-Saharan in 15 dry seasons between 1996 and 2019, subdivided in migrants (blue), residents (yellow) and the partly Palearctic Egyptian Vulture (grey), with % observed >100 m, % of 154 grid cells (1° longitude × 1° latitude) occupied, average number observed per field day, average group size and average annual rainfall (mm) for all sites where the species was observed.

| Species | | <i>n</i> | >100m% | % grid | <i>n/day</i> | <i>n/obs</i> | avg. rain |
|----------------------------|--------------------------------|----------|--------|--------|--------------|--------------|-----------|
| Osprey | <i>Pandion haliaetus</i> | 36 | 14 | 12 | 0.07 | 1.0 | 727 |
| Black-winged Kite | <i>Elanus caeruleus</i> | 97 | 5 | 27 | 0.28 | 1.4 | 769 |
| Scissor-tailed Kite | <i>Chelictinia riocourii</i> | 25 | 16 | 8 | 0.08 | 1.2 | 602 |
| African Harrier-Hawk | <i>Polyboroides typus</i> | 185 | 3 | 16 | 0.16 | 1.3 | 1575 |
| Palm-nut Vulture | <i>Gypohierax angolensis</i> | 52 | 4 | 8 | 0.05 | 1.3 | 1501 |
| Bearded Vulture | <i>Gypaetus barbatus</i> | 4 | 0 | 1 | 0.02 | 1.3 | 943 |
| Egyptian Vulture | <i>Neophron percnopterus</i> | 341 | 3 | 12 | 1.69 | 3.7 | 310 |
| European Honey Buzzard | <i>Pernis apivorus</i> | 58 | 12 | 6 | 0.04 | 1.1 | 1613 |
| African Cuckoo-Hawk | <i>Aviceda cuculoides</i> | 8 | 0 | 4 | 0.01 | 1.1 | 1158 |
| Hooded Vulture | <i>Necrosyrtes monachus</i> | 5729 | 38 | 44 | 9.60 | 11.5 | 1169 |
| White-backed Vulture | <i>Gyps africanus</i> | 611 | 24 | 29 | 1.04 | 3.5 | 632 |
| Rüppell's Vulture | <i>Gyps rueppelli</i> | 154 | 48 | 11 | 0.30 | 2.9 | 629 |
| Griffon Vulture | <i>Gyps fulvus</i> | 14 | 14 | 1 | 0.00 | 4.7 | 588 |
| White-headed Vulture | <i>Trigonoceps occipitalis</i> | 9 | 0 | 4 | 0.02 | 1.5 | 720 |
| Lappet-faced Vulture | <i>Torgos tracheliotos</i> | 17 | 12 | 6 | 0.02 | 1.5 | 638 |
| Short-toed Snake Eagle | <i>Circaetus gallicus</i> | 97 | 13 | 30 | 0.25 | 1.1 | 606 |
| Beaudouin's Snake Eagle | <i>Circaetus beaudouini</i> | 6 | 0 | 4 | 0.02 | 1.0 | 816 |
| Black-chested Snake Eagle | <i>Circaetus pectoralis</i> | 2 | 100 | 1 | 0.01 | 1.0 | 802 |
| Brown Snake Eagle | <i>Circaetus cinereus</i> | 19 | 21 | 10 | 0.08 | 1.0 | 876 |
| Western Banded Snake Eagle | <i>Circaetus cinerascens</i> | 6 | 0 | 2 | 0.00 | 1.2 | 1356 |
| Bateleur | <i>Terathopius ecaudatus</i> | 39 | 11 | 10 | 0.09 | 1.2 | 891 |
| Martial Eagle | <i>Polemaetus bellicosus</i> | 10 | 10 | 3 | 0.01 | 1.1 | 1029 |
| Long-crested Eagle | <i>Lophaetus occipitalis</i> | 12 | 8 | 5 | 0.02 | 1.0 | 995 |
| Lesser Spotted Eagle | <i>Clanga pomarina</i> | 6 | 33 | 1 | 0.01 | 2.0 | 738 |
| Greater Spotted Eagle | <i>Clanga clanga</i> | 2 | 50 | 1 | 0.01 | 1.0 | 545 |
| Wahlberg's Eagle | <i>Hieraetus wahlbergi</i> | 48 | 16 | 8 | 0.07 | 1.4 | 1278 |
| Booted Eagle | <i>Hieraetus pennatus</i> | 114 | 6 | 32 | 0.30 | 1.1 | 585 |
| Tawny Eagle | <i>Aquila rapax</i> | 117 | 21 | 23 | 0.50 | 1.4 | 729 |
| Steppe Eagle | <i>Aquila nipalensis</i> | 77 | 25 | 4 | 0.43 | 2.8 | 454 |
| Eastern Imperial Eagle | <i>Aquila heliaca</i> | 1 | 0 | 1 | 0.01 | 1.0 | 750 |
| Verreaux's Eagle | <i>Aquila verreauxii</i> | 2 | 0 | 1 | 0.01 | 2.0 | 574 |



Table S1. Continued.

| Species | | <i>n</i> | >100m% | % grid | <i>n/day</i> | <i>n/obs</i> | avg. rain |
|-------------------------|---------------------------------|----------|--------|--------|--------------|--------------|-----------|
| African Hawk-Eagle | <i>Aquila spilogaster</i> | 15 | 20 | 7 | 0.06 | 1.2 | 1034 |
| Lizard Buzzard | <i>Kaupifalco monogrammicus</i> | 48 | 0 | 10 | 0.06 | 1.2 | 1184 |
| Gabar Goshawk | <i>Micronisus gabar</i> | 130 | 2 | 32 | 0.40 | 1.1 | 704 |
| Dark Chanting Goshawk | <i>Melierax metabates</i> | 162 | 3 | 28 | 0.41 | 1.1 | 664 |
| Long-tailed Hawk | <i>Urotriorchis macrourus</i> | 1 | 0 | 1 | 0.00 | 1.0 | 1170 |
| African Goshawk | <i>Accipiter tachiro</i> | 7 | 0 | 3 | 0.01 | 1.0 | 1406 |
| Shikra | <i>Accipiter badius</i> | 127 | 2 | 24 | 0.18 | 1.2 | 1063 |
| Red-thighed Sparrowhawk | <i>Accipiter erythropus</i> | 4 | 0 | 1 | 0.00 | 1.0 | 1059 |
| Ovambo Sparrowhawk | <i>Accipiter ovampensis</i> | 8 | 0 | 4 | 0.05 | 1.1 | 898 |
| Eurasian Sparrowhawk | <i>Accipiter nisus</i> | 1 | 0 | 1 | 0.00 | 1.0 | 706 |
| Black Sparrowhawk | <i>Accipiter melanoleucus</i> | 15 | 0 | 3 | 0.00 | 1.1 | 1650 |
| Western Marsh Harrier | <i>Circus aeruginosus</i> | 1581 | 2 | 42 | 0.96 | 2.2 | 425 |
| Pallid Harrier | <i>Circus macrourus</i> | 92 | 12 | 21 | 0.36 | 1.0 | 456 |
| Montagu's Harrier | <i>Circus pygargus</i> | 204 | 3 | 29 | 0.40 | 1.1 | 509 |
| Black Kite | <i>Milvus migrans</i> | 661 | 36 | 19 | 2.37 | 5.2 | 463 |
| Yellow-billed Kite | <i>Milvus aegyptius</i> | 10430 | 35 | 70 | 14.60 | 10.3 | 802 |
| African Fish Eagle | <i>Haliaeetus vocifer</i> | 32 | 9 | 6 | 0.02 | 1.2 | 689 |
| Grasshopper Buzzard | <i>Butastur rufipennis</i> | 164 | 3 | 18 | 0.24 | 1.8 | 1027 |
| Long-legged Buzzard | <i>Buteo rufinus</i> | 7 | 14 | 3 | 0.04 | 1.0 | 405 |
| Common Buzzard | <i>Buteo buteo vulpinus</i> | 5 | 0 | 3 | 0.02 | 1.0 | 703 |
| Red-necked Buzzard | <i>Buteo auguralis</i> | 142 | 3 | 16 | 0.13 | 1.3 | 1491 |
| Augur Buzzard | <i>Buteo augur</i> | 18 | 39 | 5 | 0.07 | 1.0 | 833 |
| Lesser Kestrel | <i>Falco naumanni</i> | 87 | 18 | 16 | 0.22 | 1.0 | 560 |
| Common Kestrel | <i>Falco tinnunculus</i> | 299 | 5 | 55 | 1.05 | 1.9 | 482 |
| Fox Kestrel | <i>Falco alopex</i> | 32 | 6 | 4 | 0.05 | 1.1 | 620 |
| Grey Kestrel | <i>Falco ardosiaceus</i> | 32 | 3 | 3 | 0.07 | 1.5 | 1233 |
| Red-necked Falcon | <i>Falco chicquera</i> | 81 | 0 | 22 | 0.16 | 1.2 | 596 |
| Red-footed Falcon | <i>Falco vespertinus</i> | 4 | 0 | 1 | 0.00 | 1.5 | 1050 |
| African Hobby | <i>Falco cuvierii</i> | 302 | 1 | 8 | 0.14 | 1.2 | 1758 |
| Lanner Falcon | <i>Falco biarmicus</i> | 104 | 2 | 35 | 0.27 | 1.2 | 837 |
| Peregrine Falcon | <i>Falco peregrinus</i> | 3 | 0 | 2 | 0.00 | 1.0 | 640 |

Table S2. Number of raptors observed per day (for species with >10 records) in the sub-Saharan subdivided per 100-mm rainfall zones (0 = 0–100 mm ... 1000 = 1000–1500, 1500 = 1500–2500/annum). Palearctic migrants in yellow, African species in blue and Egyptian Vulture in grey (mixture of both). The last line gives the average number of species observed per day. *P* = statistical significance of the difference between the twelve rainfall zones: **P* < 0.05, ***P* < 0.01, ****P* < 0.001 (one-way ANOVA).

| Species | 0 | 100 | 200 | 300 | 400 | 500 | 600 | 700 | 800 | 900 | 1000 | 1500 | avg | <i>P</i> |
|------------------------|-----|------|------|------|------|------|------|------|------|-----|------|------|------|----------|
| Osprey | 0.1 | 0.0 | 0.1 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.6 | 0.1 | *** |
| Black-winged Kite | 0.0 | 0.0 | 0.4 | 0.2 | 0.4 | 0.1 | 0.2 | 0.1 | 0.6 | 0.0 | 0.7 | 0.0 | 0.3 | |
| Scissor-tailed Kite | 0.0 | 0.0 | 0.0 | 0.2 | 0.0 | 0.1 | 0.4 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | |
| African Harrier-Hawk | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.3 | 0.2 | 0.3 | 0.0 | 0.5 | 0.8 | 0.2 | * |
| Egyptian Vulture | 1.1 | 7.9 | 10.6 | 0.1 | 2.7 | 0.3 | 0.0 | 0.1 | 0.3 | 0.2 | 0.0 | 0.0 | 1.7 | |
| Hooded Vulture | 0.0 | 0.8 | 0.1 | 0.8 | 1.2 | 5.8 | 11.2 | 2.8 | 9.3 | 0.6 | 44.8 | 20.9 | 9.6 | *** |
| White-backed Vulture | 0.1 | 0.5 | 0.6 | 1.7 | 0.7 | 2.0 | 0.9 | 1.6 | 1.5 | 0.3 | 0.7 | 0.9 | 1.0 | |
| Rüppell's Vulture | 0.0 | 0.0 | 0.0 | 0.1 | 0.4 | 0.3 | 0.0 | 1.1 | 0.7 | 0.0 | 0.1 | 0.0 | 0.3 | |
| Short-toed Snake Eagle | 0.0 | 0.1 | 0.3 | 0.6 | 0.2 | 0.4 | 0.9 | 0.1 | 0.3 | 0.0 | 0.0 | 0.1 | 0.2 | *** |
| Brown Snake Eagle | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.2 | 0.1 | 0.4 | 0.0 | 0.0 | 0.1 | 0.1 | |
| Bateleur | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.4 | 0.3 | 0.3 | 0.1 | 0.0 | 0.0 | 0.1 | |
| Wahlberg's Eagle | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.4 | 0.2 | 0.0 | 0.1 | 0.0 | 0.1 | 0.1 | ** |
| Booted Eagle | 0.1 | 0.0 | 0.1 | 0.5 | 0.7 | 0.2 | 0.6 | 0.2 | 0.4 | 0.0 | 0.1 | 0.1 | 0.3 | ** |
| Tawny Eagle | 0.0 | 0.1 | 0.0 | 0.2 | 0.3 | 0.4 | 0.2 | 1.3 | 2.4 | 0.0 | 0.1 | 0.0 | 0.5 | * |
| Steppe Eagle | 0.0 | 0.0 | 0.0 | 2.3 | 0.8 | 0.0 | 0.0 | 0.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.4 | |
| African Hawk-Eagle | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.2 | 0.1 | 0.0 | 0.0 | 0.3 | 0.1 | |
| Gabar Goshawk | 0.1 | 0.0 | 0.1 | 0.1 | 0.4 | 0.8 | 1.5 | 0.2 | 0.7 | 1.1 | 0.3 | 0.0 | 0.4 | *** |
| Dark Chanting Goshawk | 0.0 | 0.0 | 0.1 | 0.3 | 0.4 | 0.7 | 0.6 | 0.7 | 1.2 | 0.1 | 0.2 | 0.0 | 0.4 | * |
| Shikra | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.1 | 0.1 | 0.4 | 0.8 | 0.6 | 0.0 | 0.2 | *** |
| Western Marsh Harrier | 0.0 | 0.3 | 1.0 | 2.7 | 1.0 | 0.7 | 1.3 | 0.4 | 1.2 | 0.4 | 0.5 | 0.9 | 1.0 | |
| Pallid Harrier | 0.0 | 0.1 | 0.5 | 1.3 | 0.8 | 0.4 | 0.1 | 0.1 | 0.2 | 0.0 | 0.0 | 0.0 | 0.4 | ** |
| Montagu's Harrier | 0.0 | 0.4 | 0.3 | 1.6 | 0.4 | 0.3 | 0.3 | 0.2 | 0.1 | 0.1 | 0.2 | 0.1 | 0.4 | *** |
| Black Kite | 1.3 | 11.8 | 11.2 | 0.2 | 4.4 | 0.3 | 0.0 | 1.0 | 0.0 | 0.4 | 0.2 | 0.0 | 2.4 | |
| Yellow-billed Kite | 3.3 | 1.0 | 16.9 | 4.7 | 6.1 | 25.4 | 14.5 | 7.7 | 7.8 | 4.5 | 41.4 | 42.1 | 14.6 | * |
| African Fish Eagle | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | |
| Grasshopper Buzzard | 0.1 | 0.0 | 0.1 | 0.0 | 0.1 | 0.1 | 0.1 | 0.4 | 0.2 | 0.5 | 1.0 | 0.0 | 0.2 | |
| Red-necked Buzzard | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.1 | 0.0 | 0.2 | 0.1 | 0.0 | 0.4 | 0.5 | 0.1 | |
| Augur Buzzard | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.2 | 0.0 | 0.1 | 0.1 | 0.2 | 0.2 | 0.0 | 0.1 | |
| Lesser Kestrel | 0.3 | 0.6 | 0.2 | 0.3 | 0.5 | 0.2 | 0.2 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.2 | |
| Common Kestrel | 0.3 | 1.4 | 1.1 | 2.4 | 2.2 | 0.4 | 1.2 | 0.6 | 0.4 | 0.4 | 0.3 | 0.2 | 1.1 | *** |
| Fox Kestrel | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.1 | 0.2 | 0.2 | 0.0 | 0.0 | 0.0 | 0.1 | |
| Red-necked Falcon | 0.0 | 0.0 | 0.1 | 0.2 | 0.2 | 0.1 | 0.3 | 0.2 | 0.2 | 0.0 | 0.2 | 0.1 | 0.2 | |
| African Hobby | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.3 | 2.0 | 0.1 | * |
| Lanner Falcon | 0.1 | 0.4 | 0.0 | 0.2 | 0.1 | 0.2 | 0.4 | 0.4 | 0.3 | 0.2 | 0.4 | 0.1 | 0.3 | |
| Residents | 3.9 | 4.3 | 19.4 | 11.4 | 12.7 | 36.8 | 32.4 | 18.4 | 27.2 | 8.8 | 92.0 | 68.6 | 29.9 | *** |
| Migrants | 1.8 | 13.3 | 13.8 | 9.7 | 8.9 | 2.6 | 3.4 | 3.0 | 2.3 | 0.9 | 1.2 | 2.2 | 5.5 | |
| no. of species | 2.4 | 3.5 | 7.2 | 8.3 | 7.3 | 8.7 | 9.8 | 9.8 | 10.1 | 5.5 | 12.0 | 7.7 | 8.4 | *** |



Table S3. Number of raptors observed per day (species with >10 records) in the sub-Sahara subdivided per longitudinal zone (Mauritania, Mali, Niger, Chad, Sudan, Ethiopia; see Figure 4). Palearctic migrants in orange, African species in blue and Egyptian Vulture in grey (mixture of both). The last line gives the average number of species observed per day. *P* = statistical significance of the difference between the six zones: **P* < 0.05, ***P* < 0.01, ****P* < 0.001 (one-way ANOVA).

| Species | MR | ML | NI | CH | SD | ET | Total | <i>P</i> |
|------------------------|------|------|------|------|------|------|-------|----------|
| Osprey | 0.2 | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.1 | |
| Black-winged Kite | 0.2 | 0.3 | 0.5 | 0.1 | 0.3 | 0.2 | 0.3 | |
| Scissor-tailed Kite | 0.0 | 0.2 | 0.1 | 0.1 | 0.0 | 0.0 | 0.1 | |
| African Harrier-Hawk | 0.2 | 0.2 | 0.2 | 0.2 | 0.0 | 0.1 | 0.2 | |
| Egyptian Vulture | 0.1 | 0.1 | 0.0 | 0.1 | 1.1 | 15.4 | 1.7 | *** |
| Hooded Vulture | 11.6 | 23.8 | 7.2 | 2.3 | 0.5 | 5.8 | 9.6 | |
| White-backed Vulture | 1.7 | 0.2 | 0.2 | 2.8 | 0.2 | 1.4 | 1.0 | *** |
| Rüppell's Vulture | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 2.6 | 0.3 | *** |
| Short-toed Snake Eagle | 0.3 | 0.3 | 0.1 | 0.2 | 0.5 | 0.2 | 0.2 | |
| Brown Snake Eagle | 0.1 | 0.0 | 0.1 | 0.2 | 0.1 | 0.0 | 0.1 | |
| Bateleur | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.1 | *** |
| Wahlberg's Eagle | 0.0 | 0.0 | 0.1 | 0.3 | 0.0 | 0.1 | 0.1 | * |
| Booted Eagle | 0.1 | 0.3 | 0.3 | 0.2 | 0.5 | 0.5 | 0.3 | |
| Tawny Eagle | 1.0 | 0.1 | 0.0 | 0.8 | 0.0 | 1.6 | 0.5 | * |
| Steppe Eagle | 0.0 | 0.0 | 0.0 | 0.0 | 3.0 | 0.4 | 0.4 | * |
| African Hawk-Eagle | 0.2 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.1 | |
| Gabar Goshawk | 0.3 | 0.6 | 0.3 | 0.8 | 0.3 | 0.1 | 0.4 | |
| Dark Chanting Goshawk | 0.3 | 0.2 | 0.2 | 1.3 | 0.0 | 0.9 | 0.4 | *** |
| Shikra | 0.1 | 0.3 | 0.2 | 0.4 | 0.1 | 0.0 | 0.2 | |
| Western Marsh Harrier | 1.0 | 2.5 | 0.6 | 0.2 | 0.5 | 0.5 | 1.0 | * |
| Pallid Harrier | 0.1 | 0.0 | 0.0 | 0.4 | 1.8 | 0.4 | 0.4 | *** |
| Montagu's Harrier | 0.3 | 0.2 | 0.3 | 0.2 | 1.4 | 0.2 | 0.4 | *** |
| Black Kite | 7.2 | 0.1 | 0.1 | 0.2 | 4.5 | 0.3 | 2.4 | |
| Yellow-billed Kite | 14.0 | 21.9 | 18.3 | 4.4 | 4.4 | 23.2 | 14.6 | |
| African Fish Eagle | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | |
| Grasshopper Buzzard | 0.2 | 0.6 | 0.2 | 0.2 | 0.1 | 0.0 | 0.2 | |
| Red-necked Buzzard | 0.1 | 0.3 | 0.2 | 0.1 | 0.0 | 0.0 | 0.1 | |
| Augur Buzzard | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.7 | 0.1 | *** |
| Lesser Kestrel | 0.4 | 0.0 | 0.1 | 0.3 | 0.6 | 0.0 | 0.2 | |
| Common Kestrel | 0.8 | 0.1 | 1.5 | 1.6 | 1.6 | 1.0 | 1.1 | *** |
| Fox Kestrel | 0.0 | 0.0 | 0.1 | 0.1 | 0.0 | 0.1 | 0.1 | |
| Red-necked Falcon | 0.1 | 0.2 | 0.3 | 0.2 | 0.1 | 0.0 | 0.2 | |
| African Hobby | 0.0 | 0.1 | 0.6 | 0.0 | 0.0 | 0.0 | 0.1 | |
| Lanner Falcon | 0.1 | 0.6 | 0.3 | 0.2 | 0.2 | 0.2 | 0.3 | ** |
| Residents | 31.4 | 49.0 | 30.3 | 16.2 | 7.6 | 38.6 | 29.9 | * |
| Migrants | 9.4 | 3.7 | 1.6 | 1.8 | 13.2 | 2.9 | 5.5 | ** |
| no. of species | 9.0 | 10.4 | 6.3 | 9.0 | 5.6 | 10.2 | 8.4 | |

