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Temporal and spatial distribution, and flight directions of migratory birds in Tsavo West National Park, Kenya: a comparison of radar and ringing data

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Summary

From 1 November 2013 to 30 April 2014 an avian radar system was operated in Tsavo West National Park, Kenya. The aim of this research was to study the temporal and spatial distribution of migrating birds over Ngulia Safari Lodge and to compare radar data with catching results of grounded birds. Additionally, the general pattern of flight directions during the six-month season is shown. From 25 November to 12 December 2013 more than 21 000 birds of 29 species were caught and ringed under misty conditions, supported by floodlights and sound luring (Pearson 2013). A total of 8564 individuals (41%) were caught during the night. The majority of the birds were Marsh Warblers *Acrocephalus palustris* (4442 ringed) and Thrush Nightingales *Luscinia luscinia* (2719). Radar data of bird migration intensities (migration traffic rates, MTR = birds/km/h) show an increase in late November to December, decreasing towards February and rising again in March and April when birds are migrating north to their breeding grounds in Eurasia. These MTRs correlate very well with the numbers of birds on the ground. They also show that birds are still migrating under clear, mist-free conditions, when no attempts were undertaken to catch birds. As expected, the flight directions changed from south in the autumn, to north in March and April. The support of the wind is optimal for migrating birds. At the lower altitudes the wind direction changes from northeast (November – January) to southeast (March, April), thus supporting migrating birds with optimal tailwinds. This means that birds are not obliged to change their flight altitude between seasons. The wind support originated in the calm Intertropical Convergence Zone and is optimal throughout the season from November to April. To our knowledge this is the first time that a study has shown the magnitude of bird migration in eastern Africa and the temporal and spatial distribution for half a year.

Keywords Palaearctic migration, radar, Kenya

Introduction

The catching and ringing of birds during the migratory season has been used to indicate the intensity of day-by-day migration and the seasonal phenology (Jenni 1984, Karlsson *et al.* 2002, Korner-Nievergelt *et al.* 2007). The number of birds caught is often used to monitor population size and demographic parameters (Baillie *et al.* 1999,

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Spina 1999, Peach *et al.* 1999, Dunn & Ralph 2004). Variation in numbers of long-term ringing programmes and the involved phenology have often been assessed in the literature over the years with the aim of examining the effect of climate change on bird migration (Hüppop & Hüppop 2003, Jenni & Kery 2003, Vickery *et al.* 2007, Hušek & Adamík 2008). Numbers caught, however, have limitations because of biases in sampling methods. When assessing daily migration intensity by looking at the numbers caught, it is assumed that the number of birds caught is a quantitatively representative sample of the birds migrating over the netting site. A close relationship between the numbers caught and the migration intensity in the air above may be more likely at sites where birds are caught from active migration, for example on an alpine pass with virtually no stopover possibilities (Komenda-Zehnder *et al.* 2010). However, a less close relationship might be found at stopover sites where birds stay in appropriate habitats to refuel for several days, as found at the Lake Constance reed beds in northeastern Switzerland (Stark *et al.* in prep.). It is nevertheless still an open question whether the numbers of migrants caught reflect the numbers passing over. Birds typically fly at far higher altitudes than the height of mist nets. Until now, few studies have investigated whether numbers captured and ringed are quantitatively representative of migration intensities (Peckford & Taylor 2008). At Falsterbo, in southern Sweden, Zehnder & Karlsson (2001) found a good correlation between daily numbers caught and nocturnal migratory intensity of the preceding night. These were measured with an infrared system at the Falsterbo Bird Observatory. Simons *et al.* (2004) found a correlation of migratory peaks observed by weather surveillance radar, mist netting and morning censuses at the north coast of the Gulf of Mexico, USA, while Peckford & Taylor (2008) reported a positive correlation between ground counts and numbers of birds tracked with radar the night before at a coastal site in Nova Scotia, eastern Canada.

To our knowledge, until now, all studies comparing catching data with migration intensities have been performed at coastal sites. Furthermore, in these studies the comparisons were restricted to nocturnal counts of flying birds and diurnal captures or counts on the ground. However, appearances of grounded birds are not always a good reflection of the strength of migration overhead and it is unlikely that large scale movements out of Ethiopia, for example, would be much influenced by local conditions many hundreds of kilometres to the south (Pearson 1990).

Bird migration south of the equator is dominated by a small number of Palaearctic species. Forty-four passerine species commonly reach the equator and 21 of these extend their migrations further, to winter mainly, or in part, from 5° S to 25° S (Pearson *et al.* 1988), thus effectively following the intertropical rain belt and benefitting from humid conditions during most of their stay on the continent. These migrations, between the Palaearctic and southern Africa, typically with an approximate distance between 6000 and 10 000 km, include some of the longest passerine journeys known. In our study we compared the numbers of birds ringed in Tsavo West National Park, Kenya, with the migration intensity determined simultaneously by radar. The ringing station and the radar station were situated at the Ngulia Safari Lodge. Thus, it was possible to see whether or not catching numbers correlate with migration intensity or not, and this is crucial in the analysis and interpretation of this huge data set. Moreover, at this site, actively migrating birds are caught mainly during the night and morning hours, and there is, in general, no netting during the afternoon.

Study site, methods and materials

This study was conducted at Ngulia Safari Lodge (3°00′S, 38°13′E, altitude 920 m) in Tsavo West National Park (Fig. 1) from 1 November 2013 to 30 April 2014. Ngulia Lodge is sited above a 300-m escarpment overlooking plains to the east and backed to the south by the Ngulia ridge (rising to 1821 m). This site was chosen because on misty nights, from late October to January, thousands of night-migrating birds, which have nested in Europe and Asia on their way to destinations further south, are attracted to the lodge's bright game-viewing lights (Pearson & Backhurst 1976). The attraction of the lights is lessened when the moon is up. The 'lighthouse effect' of Ngulia was discovered in 1969, soon after the lodge was built, and since then a team of ornithologists, the Ngulia Ringing Group (NRG), has come to Ngulia each year to study the phenomenon using ringing and other techniques. If there is mist and little or no moonlight, night migrants are attracted in their thousands to strong flood lamps around the lodge. Sometimes huge 'falls' remain at dawn, especially if drizzle or showers occur at night. To our knowledge, this is the first study to involve a bird radar south of the equator. This radar system is automatically operated and provides the opportunity to examine temporal and spatial bird migration.

Throughout this paper, the seasonal terms 'spring', 'summer', 'autumn' and 'winter', refer to the boreal seasons.

Figure 1. Location of Ngulia Safari Lodge in Tsavo West National Park, Kenya.

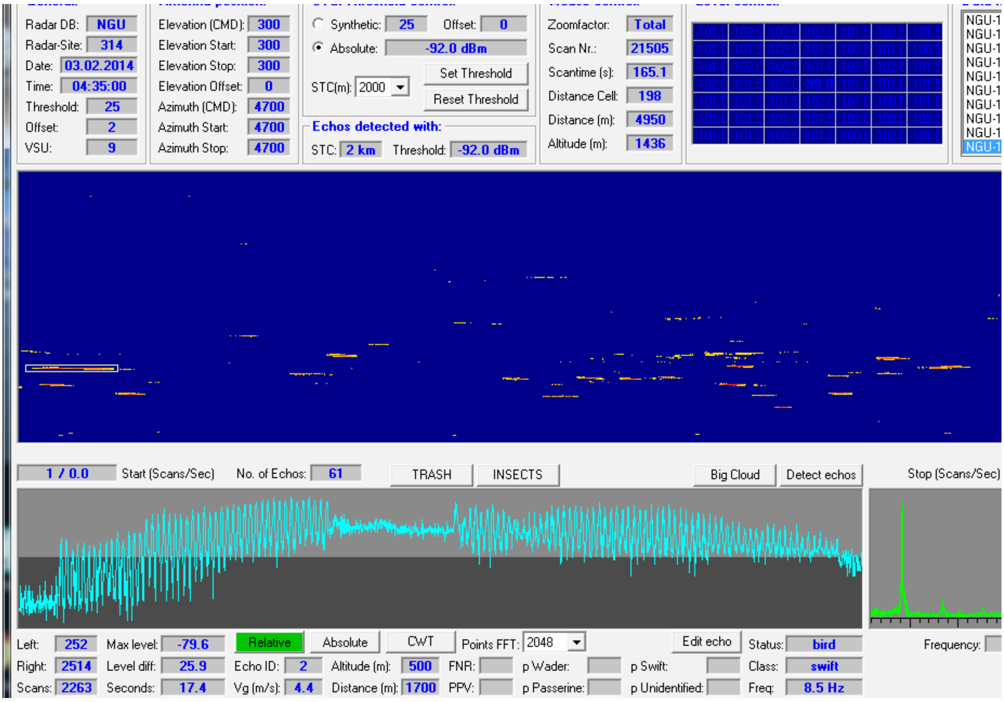
Based on a marine radar, the Swiss Ornithological Institute (SOI) has developed a bird radar (Fig. 2) with a parabolic dish which produces a very narrow beam with an opening angle of just 2 degrees. The antenna can be positioned at different elevations (0 to 85 degrees) and also in the azimuth within a certain range (0 to 270 degrees). The radar was operated at 25 kW in short pulse mode. Every moving item crossing this beam produces an echo and is registered in the database.

The direction of bird migration in Tsavo West NP is expected to be north–south in the Palaearctic autumn and vice versa in the Palaearctic spring. To scan a maximum number of birds, the radar beam should be directed nearly perpendicular to the expected flight direction of the birds. For this reason, and also for avoiding clutter from landscape structures, the radar beam was directed in two directions, 95° east and 45° northeast. For each azimuth, alternating every half hour, six elevations (11°, 17°, 28°, 34°, 45° and 68°) were used to monitor bird movements.

Figure 2. Fixed-beam radar: Birdscan MT1 at the Ngulia Safari Lodge (photo: M. Schaad).

Tailor-made software, Fixbeam, was used for the evaluation of the collected radar data, but the following points need to be taken into account:

1. All clouds from rain or heavy fog have to be extracted manually. This was done continuously during the fieldwork.
2. The software automatically detects all echoes. These data are then entered into a Microsoft Access database.
3. A training dataset had to be established manually to program the software to be able to differentiate between bird echoes and echoes resulting from clutter.
4. With this training dataset, the software then verified all sampled echoes and classified them into four groups: passerines, waders, swifts or unidentified birds (see Fig. 3 to Fig. 6).
5. With these classified bird echoes, the migration traffic rate (MTR) was then calculated by MS Access, which subsequently showed how many birds cross a line of 1 km in one hour. These MTR values form the basis of the following analysis related to the temporal and spatial distribution of migrating birds over Tsavo West National Park.



Radar DB: NGU
Radar-Site: 314
Date: 03.02.2014
Time: 04:35:00
Threshold: 25
Offset: 2
VSU: 9

Elevation (CMD): 300
Elevation Start: 300
Elevation Stop: 300
Elevation Offset: 0
Azimuth (CMD): 4700
Azimuth Start: 4700
Azimuth Stop: 4700

○ Synthetic: 25 Offset: 0
● Absolute: -92.0 dBm
STC(m): 2000

Echos detected with:
STC: 2 km Threshold: -92.0 dBm

Zoomfactor: Total
Scan Nr.: 21505
Scantime (s): 165.1
Distance Cell: 198
Distance (m): 4950
Altitude (m): 1436

1 / 0.0 Start (Scans/Sec)
No. of Echos: 61

Left: 252
Right: 2514
Scans: 2263
Max level: -79.6
Level diff: 25.9
Seconds: 17.4
Echo ID: 2
Vg (m/s): 4.4
Altitude (m): 500
Distance (m): 1700
Points FFT: 2048
FNR:
PPV:
p Wader:
p Passerine:
p Swift:
p Unidentified:
Status: bird
Class: swift
Freq: 8.5 Hz
Frequency:

Figure 3. Display of Fixbeam software showing one measurement from 3 February 2014, 04:35, (time on the x-axis, 215 s), distance of the echoes on the y-axis, maximum 6 km. Each line (mostly coloured in red) shows an echo. The details of a marked echo (white frame) are shown in the frames below the blue frame. Within the dark grey frame the wingbeat pattern for the marked echo is shown. The wingbeat frequency (8.5 Hz) is shown in the frame to the right. This echo was detected at 1700 m distance at an altitude of 500 m above ground level and was defined as a swift species. Altogether 61 echoes were detected during this measurement.

Figures 4–6 below show typical examples for wingbeat patterns.

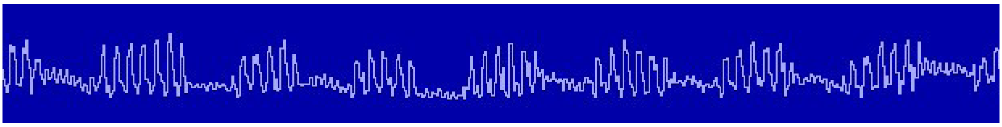


Figure 4. Typical pattern for passerine-like birds with regular beating phases and pauses, wingbeat frequency 12 Hz.

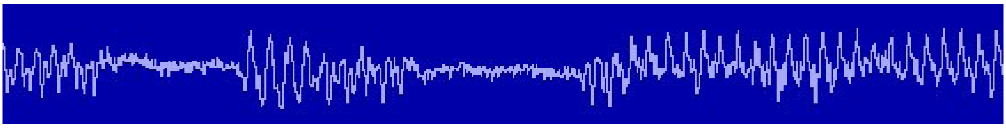


Figure 5. Typical pattern for swift-like birds with irregular wingbeat phases and pauses, wingbeat frequency 7.5 Hz.

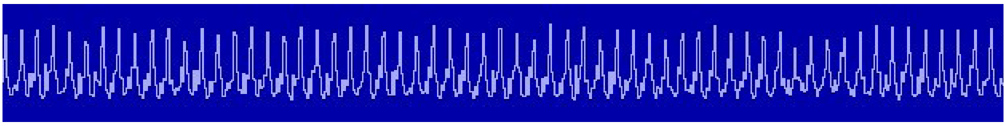


Figure 6. Typical wing beat pattern for wader-type birds with continuously-beating phases and a frequency of 8 Hz.

Twilight data set

For separating day and night, we used twilight data (civil sunset and civil sunrise, 6° below the horizon) derived from the R tool twilight (Lisovski & Hahn 2012). Because of the position of the radar station situated so close to the equator, there is no noticeable change in seasons throughout the six-month research period.

Results

Catching

In November and December 1969, when Ngulia Safari Lodge was opened, the area immediately in front (i.e., north) was illuminated during the night by several 1-kW and one 1.5-kW floodlights; the 1.5-kW light, sited high up on the building's wall, resulted in large numbers of birds and insects killing themselves (Pearson *et al.* 2014). This light was quickly removed in early December 1969 because of the carnage it caused (G.C. Backhurst, pers. comm.). From then onwards, for 50 years up until now, a ringing campaign has continued there, mainly during November and December. During some spring months, catching and ringing have been attempted. Since 1969, more than half a million Palaearctic birds have been ringed at Ngulia. Usually, the opening of the nets was decided by the weather conditions and by the number of ringing team members present. Misty weather conditions usually occur during the 20 or so days from the start of the ringing period, which are essential for catching. During the night, the nets were usually opened from 23:00 to 04:30 with three floodlights (3.5 kW in total) switched on; daytime nets were usually opened from 06:00 to 11:00. Nets were always under strict supervision and during nights when many birds were caught the ringers remained at the nets for as long as they were open. Often the nets had to be closed because of the large number of birds, and manpower constraints. During night time, the nets were open for a total of 2865 minutes or 47.75 hours (mean 3.2 h per night). For both day and night, 21 020 birds of 28 species were caught and ringed (Table. 1), of which 8564 individuals (41 %) were caught and ringed at night. The most-ringed species was the Marsh Warbler *Acrocephalus palustris* with 10 439 ringed, of which 4442 (43 %) were caught during the night and 5907 during the morning hours. During this ringing season, Thrush Nightingale *Luscinia luscinia* (5270 ringed), Common Whitethroat *Sylvia communis* (2330), and Barn Swallow *Hirundo rustica* (1541) followed the Marsh Warbler in numbers ringed.

Table 1. Numbers of birds ringed.

	Total night	Total day	Overall totals
Common Cuckoo *Cuculus canorus*	1		1
Eurasian Nightjar *Caprimulgus europaeus*	7		7
Eurasian Roller *Coracias garrulus*	3	1	4
Red-backed Shrike *Lanius collurio*	22	134	156
Isabelline Shrike *Lanius isabellinus*	10	23	33
Barn Swallow *Hirundo rustica*	1	1540	1541
House Martin *Delichron urbicum*		2	2
River Warbler *Locustella fluviatilis*	227	320	547
Basra Reed Warbler *Acrocephalus griseldis*	9	14	23
Great Reed Warbler *Acrocephalus arundinaceus*	3	2	5
Sedge Warbler *Acrocephalus schoenobaenus*	1	2	3
Eurasian Reed Warbler *Acrocephalus scirpaceus*		2	2
Marsh Warbler *Acrocephalus palustris*	4442	5907	10349
Olivaceous Warbler *Iduna pallida*	4	9	13
Upcher's Warbler *Hippolais languida*	9	24	33
Olive-tree Warbler *Hippolais olivetorum*	12	23	35
Willow Warbler *Phylloscopus trochilus*	103	89	192
Wood Warbler *Phylloscopus sibilatrix*		1	1
Blackcap *Syliva atricapilla*		3	3
Garden Warbler *Sylvia borin*	5	41	46
Barred Warbler *Sylvia nisoria*	7	37	44
Common Whitethroat *Sylvia communis*	812	1518	2330
Thrush Nightingale *Luscinia luscinia*	2719	2551	5270
Common Nightingale *Luscinia megarhynchos*	37	39	76
Irania *Irania gutturalis*	114	149	263
Rufous Bush Chat *Cercotrichas galactotes*	1	3	4
Common Rock Thrush *Monticola saxatilis*	2	6	8
Spotted Flycatcher *Muscicapa striata*	13	15	28
Red-backed x Isabelline Shrike *Lanius collurio* x *L. isabellinus*		1	1
Total	8564	12456	21020

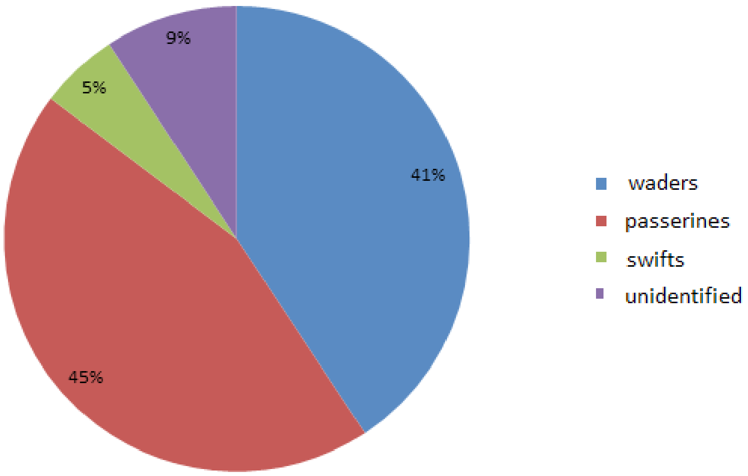


Figure 7. Distribution of all bird classes.

Composition of radar echoes

As shown in Fig. 7, the dominating classes of migrating birds over Tsavo West National Park were passerine (45%) and wader-like (41%) birds. Swift-like (5%), and unidentified birds (9%), played a minor role in the composition of migrating birds and are not presented in detail. In total, 3 million birds (extrapolated data) crossed a line of 1 km during the entire season (6 months, from November to April) over Ngulia Safari Lodge. Totals of 1.37 million passerine-like and 1.25 million wader-like birds were included in this passage.

General temporal distribution of bird migration

Figs. 8–13 show the general temporal distribution of bird migration intensities (MTRs) for all birds per month. Bird intensities increased in November from *c.* 500 to *c.* 2000 birds/km/h within the first ten days, after which there was a distinct decrease again (Fig. 7). After a technical failure of nine days, some nights towards the end of the month reached almost 3000 birds/km/h (Fig. 8).

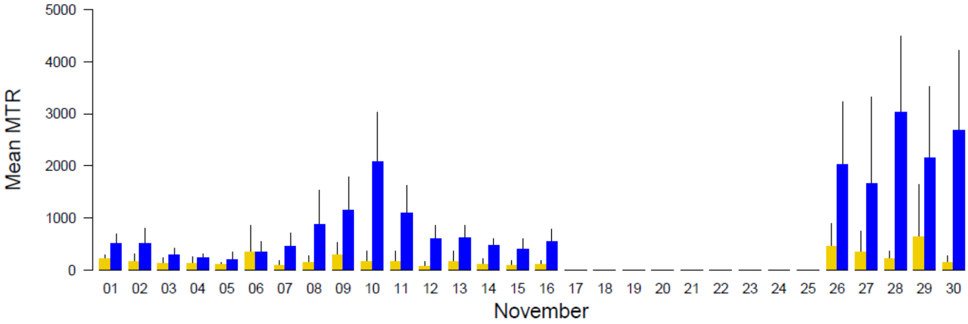


Figure 8. Seasonal phenology of MTR for all birds during November, separated by day and night (the missing data set from 17 November to 25 November was due to technical problems).

In December (Fig. 9), the MTRs rose steadily with the maximum peak on 5th (>3000 birds/km/h) and remaining at a high level (1500–2000 birds/km/h) throughout the month.

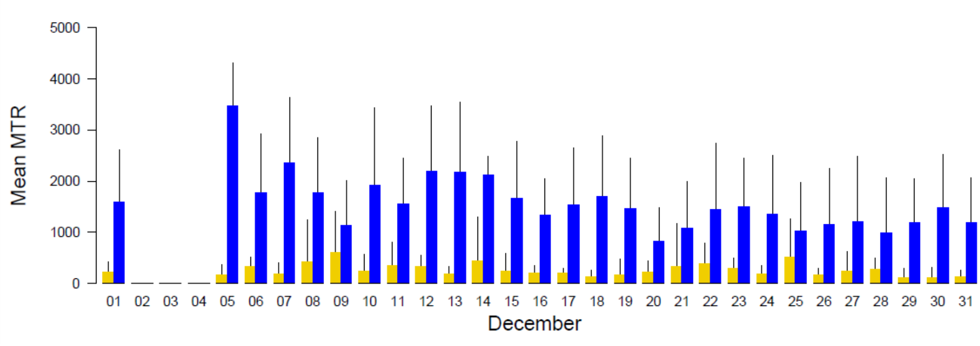


Figure 9. Seasonal phenology of MTR for all birds during December, separated by day and night (the missing data set from 2 December to 4 December was due to technical problems).

Migration in January (Fig. 10) was characterized by smooth fluctuations, often reaching over 1000 birds/km/h during the nights.

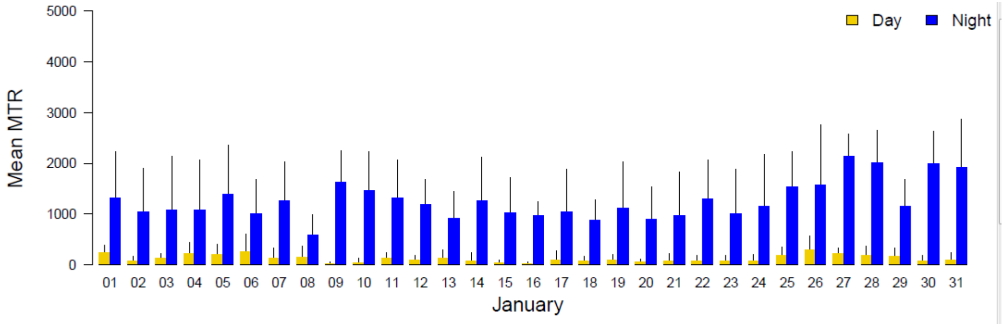


Figure 10. Seasonal phenology of MTR for all birds for January, separated by day and night.

In February (Fig. 11), the MTRs remained high up to 7th, after which they dropped rapidly to below 1000 birds/km/h, and they stayed at this lower level for the rest of the month (with the exception of 27 February 2014).

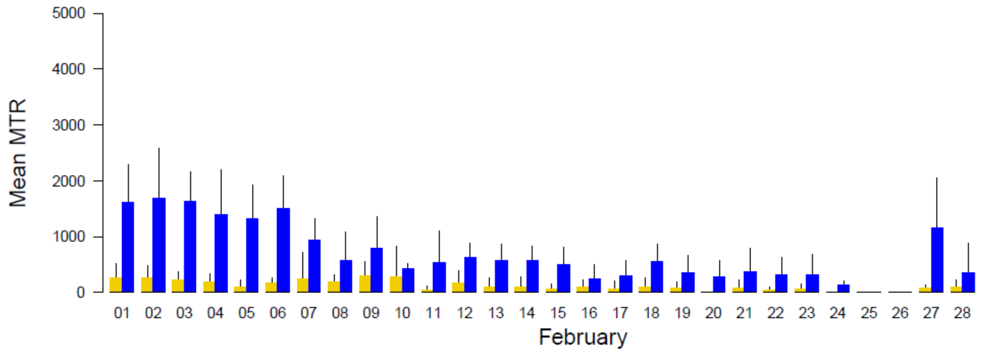


Figure 11. Seasonal phenology of MTR for all birds during February, separated by day and night (the missing data set from 2 February to 26 February is due to technical problems).

In March (Fig. 12), when northbound spring migration is expected, noticeable migration started after the first ten days with low MTRs throughout the month, reaching 1000 birds/km/h again in the last 10 days of March.

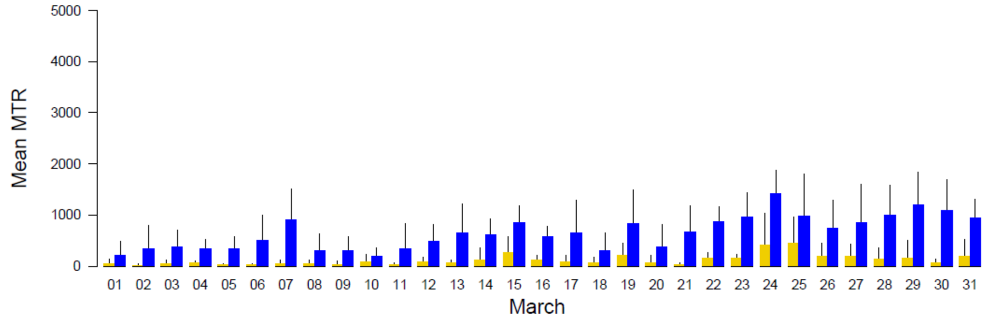


Figure 12. Seasonal phenology of MTR for all birds for March, separated by day and night.

In April (Fig. 13), the migration intensity (MTR) at Ngulia stayed continuously at a level above 1000 birds/km/h until the middle of the month. Afterwards, it dropped slightly to values of 500 birds/km/h.

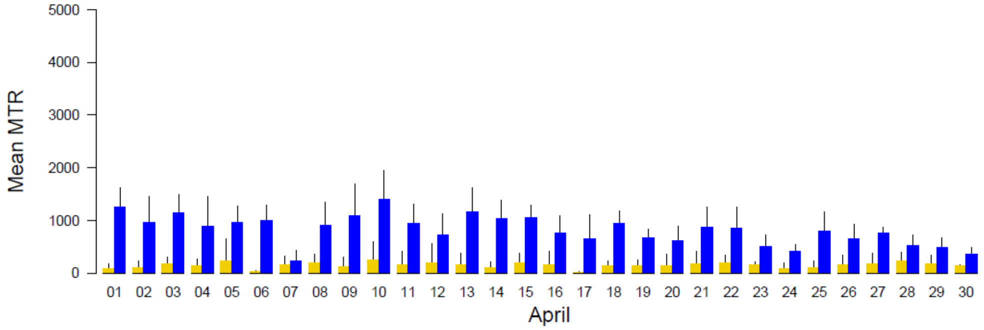


Figure 13. Seasonal phenology of MTR for all birds for April, separated by day and night.

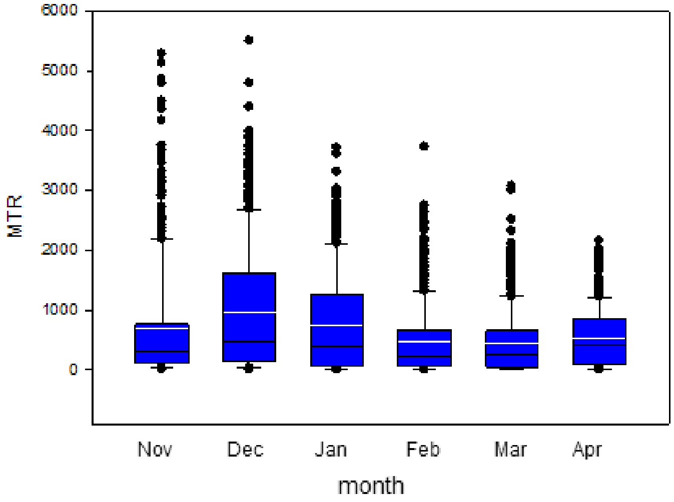


Figure 14. Mean MTRs per month for all birds, only nocturnal migration.

Monthly comparisons (Fig. 14) of MTR numbers for all birds appear to rise from November (mean = 702 birds/km/h) to December (mean = 974 birds/km/h), then decline in January (mean = 744 birds/km/h), but they still display high numbers. February and March show the lowest intensities with means of 482 birds/km/h and 441 birds/km/h respectively. In April, the values rise again (mean = 528 birds/km/h), but never reach the high numbers of November to January.

Migration in the course of the day

Throughout the season, passerine migration at Ngulia began two hours after sunset, at around 20:00 and continued at the same level until midnight whence it declined slightly into the morning hours, with a drop at sunrise around 06:00. This low rate remained until midday (Fig. 15).

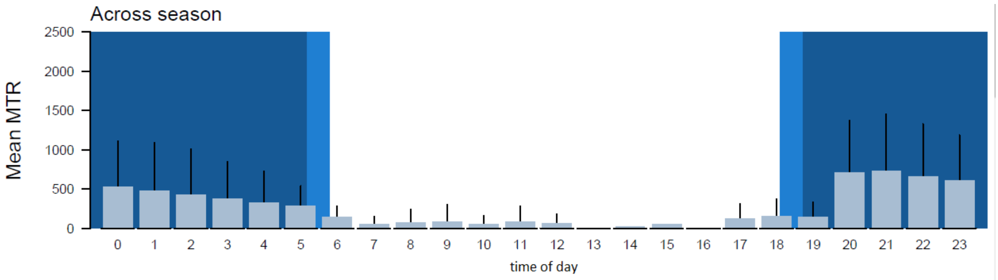


Figure 15. Mean MTRs per hour for passerines (light blue: sunset and sunrise, dark blue: night).

Catching and ringing numbers, and radar counts

Figure 16 shows the seasonal phenology of caught birds and bird intensities (MTRs, measured by radar) within the catching period. Unfortunately, there was a gap in radar data for five days because of technical problems. In general, the fluctuations in numbers of birds caught corresponded well with the radar counts, indicating that if many birds are in the air, many birds are caught. Finally, Fig. 17 shows the correlation of the numbers of birds caught with the MTRs for the opening hours (sum of MTRs from 23:00 to 08:00 next day). We found a strong correlation ($R^2 = 0.4094$, $p = 0.002$) with birds ringed and sums of MTRs.

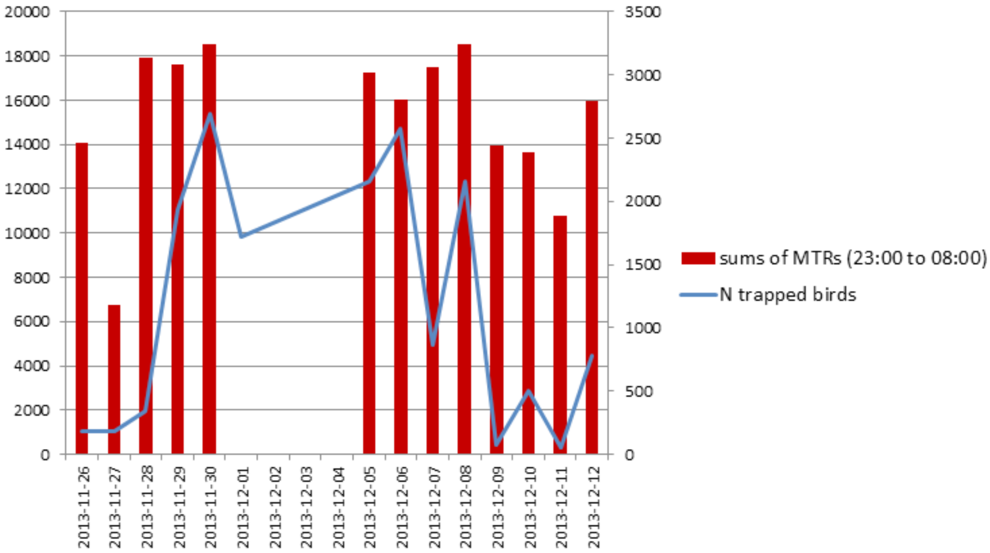


Figure 16. Comparison of MTRs (mean values from 23:00 to 08:00 next day) and catching, only for the period of catching (2 November–12 December).

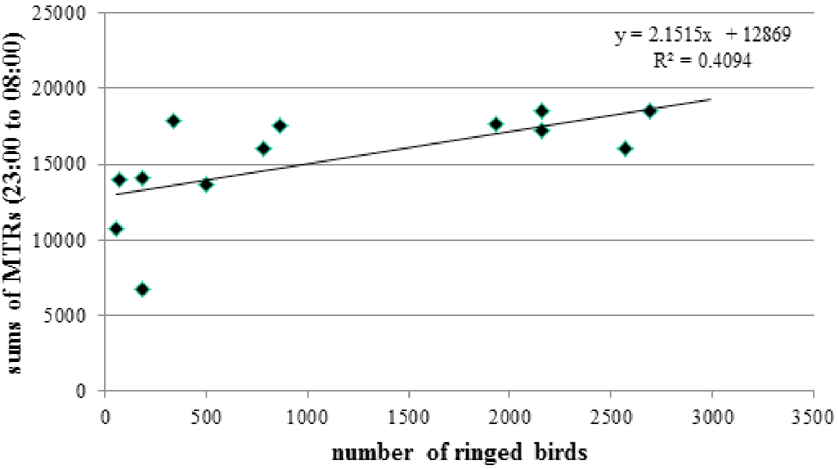


Figure 17. Correlation of caught birds and migration intensities (MTRs), sums per night (from 23:00 to 08:00 next day).

Spatial distribution

Bird migration below the horizontal view of the radar beam could not be measured with this radar system because technically, the radar beam can only be positioned to the horizontal view. Lower positions are not possible with this radar. This implies that a certain proportion of bird migration was missed, because birds flying below the escarpment were out of the detection range of the radar system.

As shown in Fig. 18, the majority (>50%) of the migrants used the lowest height ranges, up to 400 m a.g.l. (above ground level). The 5% margin was at around 1000 m a.g.l. Remembering that the radar station at Ngulia was positioned at 920 m above sea level, the majority of the radar-tracked birds were moving dominantly in height ranges of 950 m above sea level to 1300 m above sea level (a.s.l).

Comparing the spatial distribution by months (Fig. 18), in November, when migration intensity was increasing (Stark *et al.* in prep.), we found the highest proportion of migrating birds in the lowest height range (40%; 950–1150 m a.s.l). In December, with the highest MTRs, the passerine-like birds used a wider height range. Fifty percent used the height range from 950 m up to 1600 m a.s.l. In January and February, with a decreasing migration intensity, the height distribution was almost identical to that in December. In March, when northward migration is expected to start, the height distribution did not change, but in April, it showed a different pattern, with less migration in the lowest height range (0–200 m a.g.l) and a peak in the upper range from 200 to 400 m a.g.l (1100 m to 1300 m a.s.l).

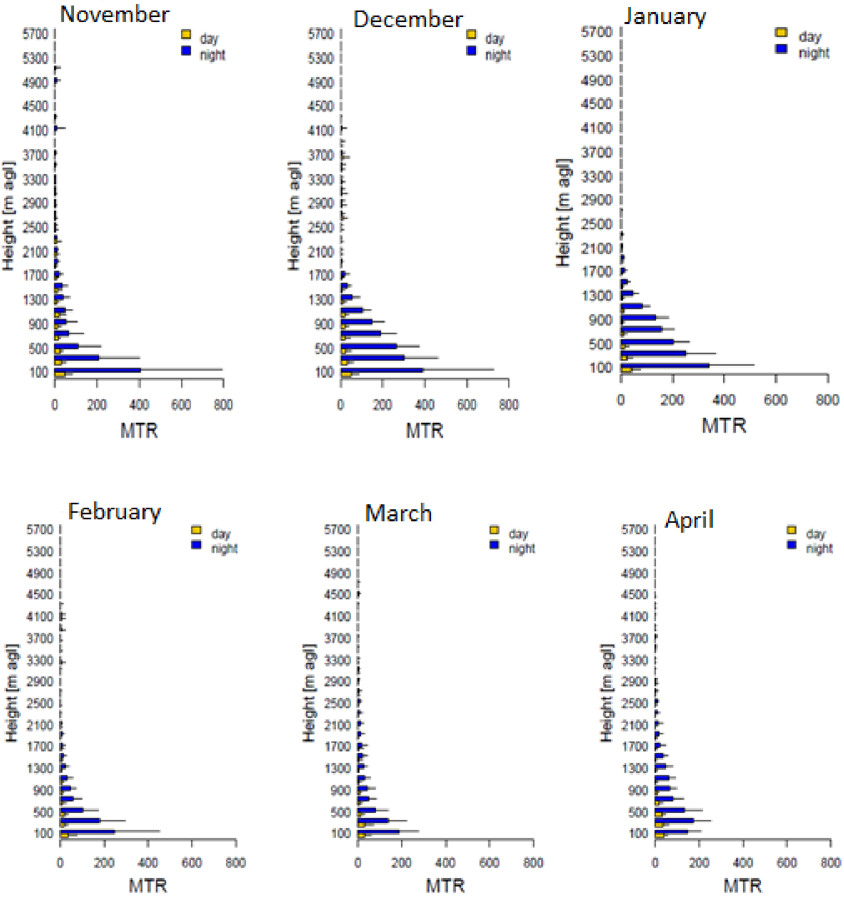


Figure 18. Monthly spatial distribution of MTRs for nocturnal passerine-like birds from November to April.

Flight directions

For the evaluation of flight directions, we used the data set when the beam was pointing to northeast (45°), expecting that changes in distances of a bird track passing the radar beam might provide an indication of flight direction. Assuming that the birds are flying southwards from November to January, and northwards from February to April, there should be noticeable changes in the course of the season. Figure 19 shows the principle of the evaluation of flight directions. In November/December, when a bird (coming from north) flies into the radar beam, the first distance when touching the beam should be higher than the second distance when the bird is leaving the beam. In this respect the subtraction of distance 1 from distance 2 should be positive, and the opposite when the birds are flying to the north. The subtraction of distance 1 from distance 2 should be negative. For this evaluation we only used longer tracks (staying in the beam for >2s). For passerine-like birds (Fig. 20), the higher proportion (71%) of negative values was seen in March and continued into April. The southbound migration was dominant during December with a proportion of 90%. Approximately 75% of these echoes showed a southbound direction, which was still visible in February, but with a lower proportion. In March and April, more than 70% of the echoes were oriented to the north.

The southbound migration of passerine-like birds was dominant during November (80%) and December (90%). Approximately 75% of echoes in January showed a southerly direction, which was still visible in February, but at a lower proportion (55%). In March and April, more than 70% of these echoes were oriented to the north, demonstrating the northbound migration back to the breeding grounds in Eurasia.

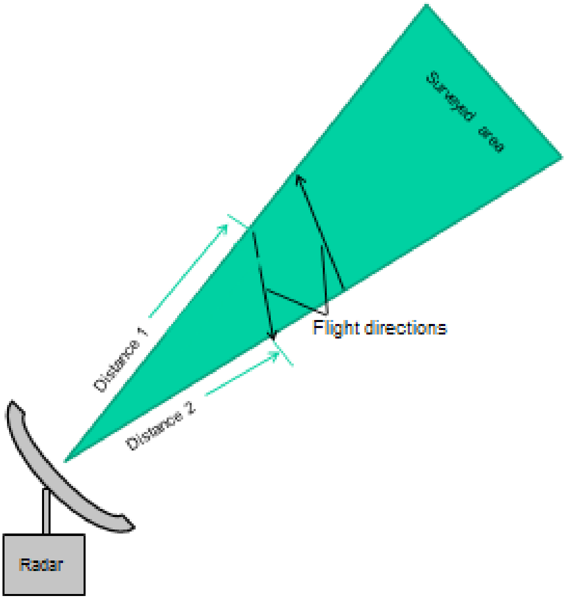


Figure 19. Principle of calculating flight directions with the radar beam pointed to the northeast (45°).

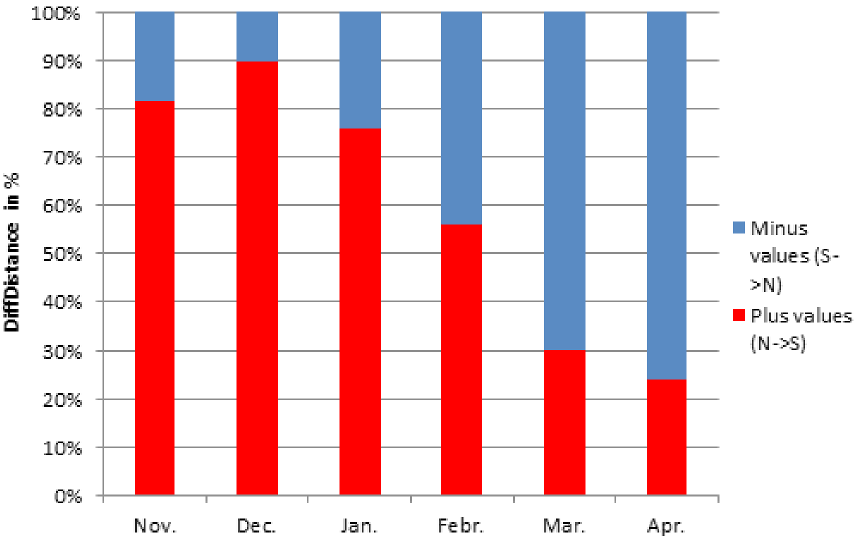


Figure 20. Distribution of negative and positive values for flight directions per month for passerine-like birds.

Wind and migration

The influence of wind speed and direction plays a major role in bird migration systems (Liechti *et al.* 1995). To understand the wind system close to the equator, we obtained a data set for wind direction and wind speed for different altitudes (from 850 mb = 1400 m a.s.l. up to 700 mb = 3000 m) with the RNCEP tool (Kemp *et al.* 2012). Direct meteorological measurements are not available in this region of Kenya. These data are extrapolated to show that, in the Tsavo highlands, mostly easterly winds dominate throughout the entire season. Figure 21 shows, for the lowest available altitude (850 mb corresponds to approximately 1400 m a.s.l) that wind directions during the night (midnight to 06:00) show a trend in the course of the season, from easterlies in November, and more northeasterly in December/January/February, shifting towards southeasterly from March to April. Wind speeds at the lowest altitude (850 mb) were moderate during the nights, ranging from 4.9 m/s (December and March) to 6.3 m/s (January), see Fig. 22.

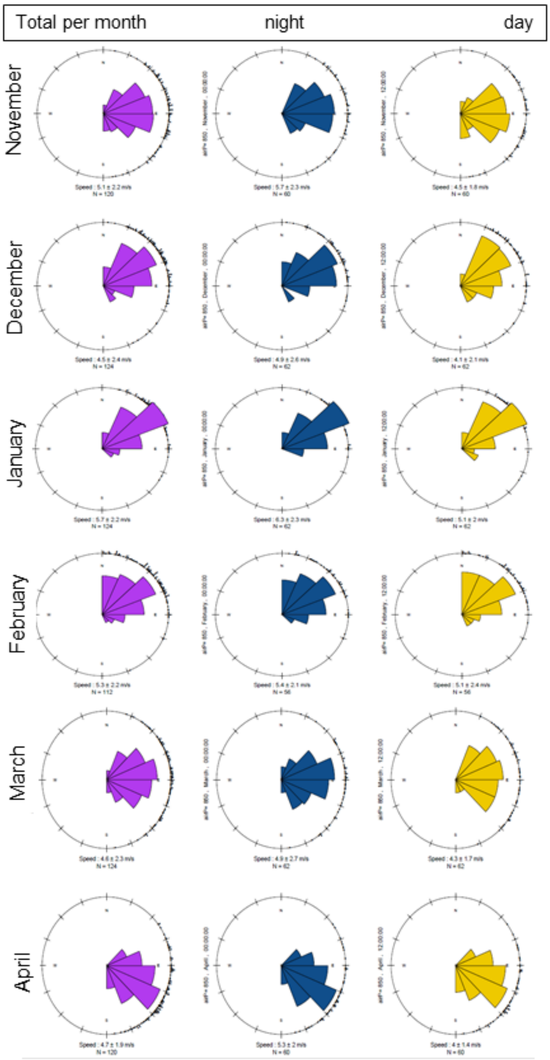


Figure 21. Wind directions and speeds per month for 850 mb (~1400 m a.s.l.) for the entire day (left column), for the night (column in the middle), and for daylight (right column).

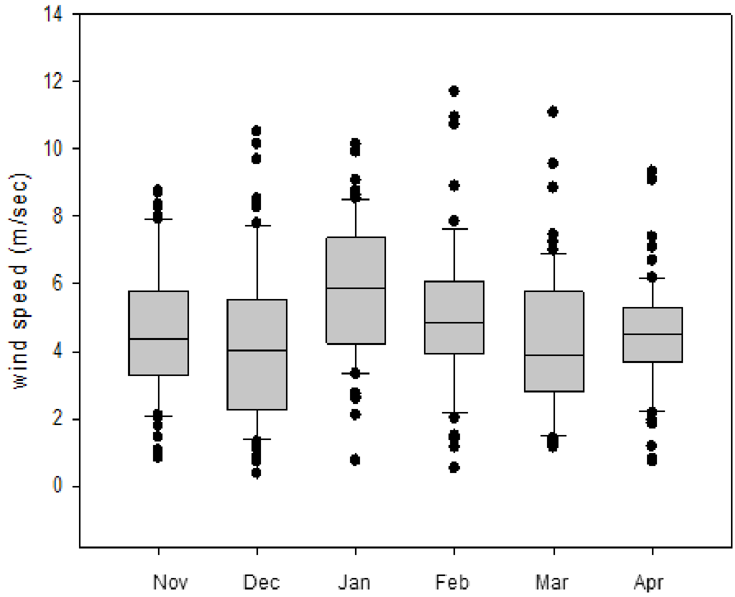


Figure 22. Nocturnal wind speeds per month at Ngulia Safari Lodge from November 2013 to April 2014.

Discussion

According to Pearson (1990), Palaearctic passerine species wintering in southern Africa originate from western Asian and Russian breeding areas, at 30° E to 80° E longitude, but a few European species, notably the Marsh Warbler and Thrush Nightingale, move southeast to join those from Asia in the Middle East. Eventually, all these birds then migrate together through eastern Africa, returning via a similar route in spring (Pearson 1990). Migrating birds reaching tropical Africa from the Palaearctic initially enter marginal savanna habitats that experience strong seasonal weather changes. These areas are relatively rich in resources during the June–September rainy season, but then become progressively desiccated (Moreau 1972). Thus, migrants tend to penetrate from the Sahel zone further south, where they find more suitable, humid conditions.

Migration intensity in the course of the season

Long-distance migrants from western Eurasia cross the Saharan or Arabian deserts to reach northern tropical areas. There they interrupt their migration for up to three months before resuming their flight to the south. During this stopover period, many birds undergo a partial or complete moult. It is known that these migrating birds, using the East African Flyway, stopover in Ethiopia for two to three months (Yohannes *et al.* 2007, 2009, 2013) to moult before continuing their southward migration in November when environmental conditions become unfavourable. This explains the peak of migration over eastern Kenya at the end of November and the beginning of December, when the migrants from northern parts of Africa also pass over, heading south. For the period from November to January, where we found pronounced southbound migration, in total 1.3 million birds crossed Ngulia Lodge over a line of 1 km, heading south. From February to April, around 50% of the autumn number headed north (730 000 birds/km/h). The figure of 50% heading back to the Palaearctic is due to many factors. Migrants leave their wintering areas in southern Africa only a few weeks before arriving back in the Palaearctic. The return passage through Kenya and Uganda between late March and early May is thus more rapid than the southward movement. Only a few ringing attempts have been possible in spring at Ngulia. Pearson (1990) reports that in several Rift Valley lakes in Kenya, and at two sites near Nairobi, some 4000 birds were caught and ringed in spring between 1971 and 1984. However, on the few occasions when suitable conditions have been encountered in April, birds at Ngulia were grounded in hundreds or thousands, much as in November–December (Pearson 1980). The species composition was different from that in November–December (Pearson 2014). In contrast to these findings, the radar data show that approximately 50% of the southbound migrants either did not return to the north, because of mortality in the wintering grounds, or because they used other flyways in spring, such as the Red-backed Shrike *Lanius collurio* (Tottrup *et al.* 2012). Also, it was found that migrating birds in spring are fatter than in winter, implying that these birds do not need to stop so often (Pearson 1990).

Migration intensity in the course of the day

The intensity of bird migration in the course of the day shows a typical pattern, known from many places in Europe and northern Africa. Passerine birds usually rest for foraging during the day then start the next stage, mostly shortly after sunset, and increase steadily, with a peak at midnight, then slowly decline into the morning hours with fewer migrating birds after sunrise. During the morning hours, and until midday, there is no noticeable migration over Ngulia Safari Lodge.

Comparison of migration intensity in East Africa and Europe

Overhead migration intensities over Kenya and Europe do not fluctuate very much during the course of the season (Nilsson *et al.* 2018). The comparison of maximum intensities shows clearly, as expected, that in Europe, higher intensities are reached. Comparing Ngulia radar results with radar data derived in autumn 2013 in Austria, we find that the maximum values at the Austrian station (Würzberg, 48°04′N, 14°30’E) were three times higher than at Ngulia. This is explained mainly by the different species composition of the migration in Europe and at the equator. At the equator, only long-distance migrants appear to migrate further down to South Africa. Bird migration south of the equator is dominated by a small number of Palaearctic species. Forty-four passerine species commonly reach the equator and 21 of these extend their migrations further, to winter mainly, or in part, between 5° S and 25° S (Pearson *et al.* 1988). These migrations between the Palaearctic and southern Africa, typically 6000–10 000 km, include some of the longest passerine journeys known.

Migration south of the equator is best known in Kenya in central Nyanza, around Nairobi, and in Tsavo (Pearson & Backhurst 1976), and in Uganda, around Kampala (Pearson 1972). In the Ngulia hills in Tsavo National Park (West), southward-bound night migrants are attracted and grounded in mist, often in thousands at the floodlights of a game viewing lodge during moonless periods in November and December. Over 566 000 Palaearctic (mainly) passerines have been caught and ringed since 1969 (Pearson & Backhurst 1976, Backhurst & Pearson 1977, 1984, 1988, Pearson 2013, 2014, 2015, 2016a, b). Appearances of grounded birds are not, however, always a good reflection of the strength of migration overhead (Pearson 1990).

The present study shows that for nocturnal bird migration, a good relationship exists between migration traffic rates (measured with radar) and numbers of birds caught simultaneously in mist nets. A comparison with daylight migration was not possible, because, due to technical reasons, daylight measurements could only be done up to 12:00. After 12:00, the electricity generator at the lodge was switched off every day until 17:00 to conserve diesel fuel.

The radar data clearly show that the period for catching and ringing migrating birds at Ngulia Safari Lodge was very well chosen during the time of the highest migration traffic rates, as determined by radar. Catching occurred during the strongest movements of migrating birds. The catching success under various conditions is quite diverse. The few trials under suboptimal conditions had absolutely no success. Clearly, the presence of mist and small moon conditions is essential for catching success. Under swirling mist conditions for example, a maximum of 471 birds have been caught per hour—on 30 November 2013.

'Logically', this implies that under clear, mist-free weather conditions, no birds are migrating, which is of course not the case! The migration intensities derived from radar show that under clear conditions with good visibility, migration is certainly ongoing, but there were no efforts undertaken to attract birds with floodlights and sound luring, because, from long experience of trying this over many years (G.C. Backhurst, pers. comm.), birds will never be attracted down during clear weather conditions.

This strong relationship, radar : catching, is due to the fact that nocturnal migrants were caught during active migratory flight, when weather conditions were changing over Ngulia Safari Lodge. There are other reports of the grounding of migrating birds in eastern Africa caused by lights (Boothroyd 1987, Nikolaus 1980, Pearson 1981). Additionally, in this case, the attraction of strong lights on the ground plays a major role. It is well known from coastal lighthouses, oil drilling platforms, and ships (Bourne 1979), that birds are attracted to light under bad weather conditions, such as mist or fog (Ballasus *et al.* 2009). In recent times, it was noted that at offshore wind energy facilities (FINO 1, North Sea) birds are attracted to the obligatory safety lights when visibility conditions are poor; birds then collide with vertical structures, resulting in casualties (Aumüller *et al.* 2011, Hüppop *et al.* 2006). On alpine passes such as the Col de Bretolet (1800 m a.s.l.) in Switzerland, with negligible resting habitat, during misty conditions birds are also attracted in large numbers to floodlights (Komenda-Zehnder *et al.* 2010). The reason for this attraction to lights under misty conditions is not really understood.

Spatial distribution and wind conditions

The spatial distribution of MTRs for passerine-like birds does not show any differences from month to month. Usually, birds on migration use altitudes with favourable tailwinds (Bruderer & Liechti 1995), as in Israel, where trade and anti-trade winds prevail. The trade wind conditions in Israel promote migration below wind shear level (1200–2000 m a.s.l.) in autumn, and flights above this limit in spring. In contrast to Israel, at the equator, we find a wind regime driven by the Intertropical Convergence Zone (ITCZ). The ITCZ, known to sailors as the doldrums, is the area encircling the Earth near the equator, where the northeast and southeast trade winds converge. In the Northern Hemisphere, the trade winds move in a southwesterly direction from the northeast, while in the Southern Hemisphere, they move northwestwards from the southeast. When the ITCZ is positioned north or south of the equator, these directions change, according to the Coriolis effect imparted by the Earth's rotation. For instance, when the ITCZ is situated north of the equator, the southeast trade wind changes to a southwest wind as it crosses the equator.

The stability in altitude distribution throughout the season is due to the wind regime, which at the altitude of Ngulia Safari Lodge (920 m a.s.l), changes from more northeasterly/easterly in November–January to more easterly/southeasterly winds in March and April. This change of wind direction from November to April supports migrating birds, so they are not forced to look for better wind conditions at higher altitudes. In line with many studies (Bruderer & Liechti 1995, Liechti 2006), we observed that migrants in Tsavo West National Park adjust their flight altitude to make optimal use of tailwinds along the predominant migratory direction.

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