

## Do ringing numbers reflect true migratory activity of nocturnal migrants?

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### Summary

In autumn 1998, nocturnal bird migration at Falsterbo was recorded over a period of three months by means of a passive infrared device. At the same place a standardised trapping scheme is in operation. This study reveals for the first time a positive correlation between the migratory intensity of birds aloft and the numbers of trapped birds. By relating the migratory patterns of single species with the nocturnal migratory intensities, we show that the species composition aloft can at least partly be deduced from the number of grounded birds. The numbers of trapped pre-Saharan migrants were related more strongly to the migratory intensity of the preceding night than were the numbers of trans-Saharan migrants. Assuming that the number of trapped birds varies according to the weather to the same extent as the migratory intensity of birds aloft, we conclude that in shorter range migrants the decision to engage in a migratory flight is influenced more strongly by weather conditions, and that the migratory activity of trans-Saharan migrants is possibly more intensely controlled by their endogenous migratory urge.

**Keywords:** migratory intensity, ringing numbers, infrared observations, nocturnal bird migration, trans-Saharan migrants.

### Zusammenfassung

#### Widerspiegeln Fangzahlen die tatsächlichen nächtlichen Zugdichten?

Fangzahlen aus der Vogelberingung werden Studien verschiedenster Gebiete der Ornithologie zu Grunde gelegt. Insbesondere in der Vogelzugforschung und in Populationsanalysen wurden dadurch grosse Fortschritte erzielt. In dieser Arbeit wird erstmals untersucht, inwiefern die Fangzahlen mit dem nächtlichen Zuggeschehen in Verbindung stehen. In Falsterbo, Südwest-Schweden, werden seit 20 Jahren Vögel in einem standardisierten Verfahren mit Japannetzen gefangen. Im Herbst 1998 beobachteten wir am gleichen Ort während drei Monaten den nächtlichen Vogelzug mittels einer Wärmebildkamera, wobei Singvögel bis maximal 3000 m über Boden erfasst werden. In 63 Fällen konnten wir die täglichen Fangzahlen mit den Zugintensitäten der vorangegangenen Nacht vergleichen, wobei wir eine signifikante positive Korrelation feststellten. Dabei mag die Lage der Fangstation an der Küste eine Rolle spielen, indem hier täglich ein bestimmter Anteil der Zugvögel eine Rast einlegt, bevor der Überflug der Ostsee bewältigt wird, während gleichzeitig kaum nicht-ziehende Vögel vorhanden sind. Der Vergleich der Zugmuster der 12 am häufigsten gefangenen Arten zeigt, dass die Anzahlen der Kurzstreckenzieher

besser mit den nächtlichen Zugintensitäten übereinstimmen. Unter der Annahme, dass die Fangzahlen in gleichem Masse vom Wetter abhängen, wie dies für die Intensität des nächtlichen Zuges gezeigt werden konnte, schliessen wir auf eine deutliche Reaktion der Kurzstreckenzieher gegenüber dem Wetter. Im Gegensatz dazu scheint der Zug der Langstreckenzieher stärker von weiteren Faktoren beeinflusst, beispielsweise von der inneren Uhr. Möglicherweise bedeutet die Ostsee hinsichtlich ihrer weiten Reise ein unbedeutenderes Hindernis als für Arten, welche nur bis Mittel- oder Südeuropa ziehen. In der Folge neigen Kurzstreckenzieher wohl eher dazu an der Küste zu landen als Langstreckenzieher.

## Introduction

Scientifically controlled bird-trapping is an indispensable source of data for large-scale migration studies and the monitoring of bird populations (Berthold & Schlenker 1975, Dunn & Hessel 1995, Jenni 1999). Bird-trapping data is, however, often biased towards certain species and/or age classes, and numbers depend on the location of the capture site with regard to topography and habitat, trap types (e.g. mesh size of mist nets), the position of the traps in the vegetation, and weather (Degen & Jenni 1990, Jenni et al. 1996). Moreover, studies of bird migration are faced with the problem that non-migrating birds, such as individuals on post-breeding or post-fledging dispersal, can hardly be differentiated from migrating individuals (Jenni 1984).

This has frequently cast doubt on the relationship between numbers of captured birds and true migratory activity (Alerstam et al. 1973, Richardson 1978). Overall migratory intensities in time and space can be studied more accurately by the use of other methods, such as radar, thermal imaging, or moonwatching (Liechti et al. 1995, Gauthreaux 1996, Bruderer 1997). These techniques are used particularly for the investigation of night migration. In general, they do not allow species identification, but only a differentiation between broad groups of species (Bloch et al. 1981). Hence, to get a desired insight into the species composition of nocturnal migration, it would be useful to analyse trapping data from a place close to the observation site.

At Falsterbo, in south-western Sweden, a standardised trapping scheme was established in 1980 (Roos & Karlsson 1981). Since then, on average 18,000 birds have been ringed annually in autumn. During the autumn ringing season of 1998 the intensity of nocturnal bird migration was recorded by means of a passive infrared device (Zehnder et al. in press). Thus, these observations gave the opportunity to compare the numbers of birds captured at the coastal ringing site with those observed migrating aloft at the same site. This was the first time that such simultaneous observations had been performed in a systematic way for migrating birds.

## Study site and methods

The study was conducted out at the Falsterbo Peninsula, the south-westernmost point of Sweden (55° 23' N, 12° 50' E). Mist-netting was carried out at two trapping sites: from 21 July until 10 November at the Lighthouse garden which is a small stand of bushes and trees in an open field, and from 21 July until 30 September at Flommen, a reed bed area about 1 km north of the Lighthouse garden (Karlsson 1993). The number of nets (9 m in length and with 16 mm mesh) varied according to weather conditions, with a maximum of 20 nets at each site. The nets were installed before dawn and controlled every half hour. The daily trapping routine lasted at least six hours at each location and continued thereafter as long as the number of captured birds exceeded ten individuals per hour.

The present study is based on the number of ringed birds per species and day. Recaptures are not included. Only species migrating mainly at night

were included in the analyses (cf. Glutz von Blotzheim & Bauer 1988, 1991, 1993, 1997). The species were grouped according to their main wintering grounds as pre-Saharan (shorter range) or trans-Saharan migrants and as SW or SE migrants (Table 1). Unlike central European populations, northern populations of Chiffchaffs (ssp. *abietinus*) and Blackcaps are considered to be mainly trans-Saharan migrants (cf. Glutz von Blotzheim & Bauer 1991). SE migrants are species which fly to the Middle East, East Africa or southern Asia. Those migrating to East Africa and Southern Asia were considered as long distance migrants and were included in the trans-Saharan group.

Observations by means of a passive infrared device (IR) were performed from 07 August until 30 October. The camera (Long-Range-Infrared-System LORIS, IRTV-445L, Inframetrics, Massachusetts, USA) was placed on the ground inside the Lighthouse garden and directed vertically upward. Birds of the size of an average passerine are detectable by the camera up to 3000 m above ground level against the clear sky (Liechti et al. 1995). The thermal radiation emitted by their bodies is represented on a monitor as dark dots. If birds pass close by bird-shaped silhouettes can occasionally be observed, but species can never be identified. The flight altitude of the bird is estimated according to its silhouette size on the screen; the silhouette size is assigned to one of seven height classes. The calibration of the height classes was achieved by measuring the distances to the targets with the pencil-beam of a tracking radar (Bruderer & Liechti 1994, Liechti et al. 1995). The flight directions are assessed according to the clock face method used in moonwatching (Lowery & Newman 1955). Since the opening angle of the camera of 1.4° leads to an altitude dependent probability of detecting birds aloft, number of birds is translated into migration traffic rate (MTR). MTR is calculated as the number of birds crossing perpendicularly a line of one kilometre length in one hour. A detailed description of the method is given in Zehnder et al. (in press). Birds migrating in the time interval between the end of civil twilight at dusk and the beginning of civil twilight at dawn were considered as night migrants (see Zehnder et al. in press).

In linear regression analyses the daily ringing totals of the autumn of 1998 were related with the migratory traffic rates registered by IR. Migratory intensities were expressed as means of the whole night (mean MTR) and as means of the time interval

before midnight (mean MTR PM) and after midnight (mean MTR AM), respectively.

We investigated the relation between mean MTR and the numbers of captured birds per species by using long term ringing data gathered at Falsterbo Bird Observatory to establish the species' specific migratory patterns (L. Karlsson, unpublished data). We calculated for each species the averages of the pentads 44 to 60 based on the daily counts between 1980 and 1998. The pentads were selected according to Berthold (1973). The absolute numbers per day of the long term averages (expected numbers) and the number of birds ringed each morning in the autumn of 1998 (observed numbers) were transformed to percentages per species of the observation period. The difference of these relative numbers was related in a linear regression to the mean MTR (log transformed) of the preceding night. This analysis was restricted to bird species with ringing totals in 1998 of  $n > 100$  (Table 1) and to time periods when more than 1 bird could be expected according to the long term ringing data (Table 2). The four mornings with the largest ringing totals of the 1998 season (Fig. 1; 24 Aug, 12 Sept, 17 Sept and 24 Oct) were not included in this analysis since migration increased only in the second half of the night and was most intense after the beginning of civil twilight at dawn, when IR observations had already ceased (see below). No other nights were characterised by this particular pattern.

For comparison of expected and observed flight directions, we defined a SE-sector (90°–179°) and a SW-sector (180°–269°). The expected flight directions are those corresponding to the migratory routes of each species derived from ringing recoveries (Zink 1973, 1975) (Table 1); the observed directions correspond to the tracks recorded by IR.

MTR and ringing totals were log transformed in order to satisfy the requirement of normal distribution of residuals (Stahel 1995). Linear regression analyses were performed with the aid of STATISTICA 5.0 software. Circular statistics are according to Batschelet (1981).

## Results

During the study period of 83 days, IR observations were possible on 68 nights and ringing activity in 76 mornings. In 63 cases successful ringing coincides with IR observations (mean

**Table 1.** Species captured at Falsterbo during the period of infrared observations. SE migrants are marked with an asterisk.

**Tab. 1.** Vogelarten welche während der Wärmebild-Beobachtungsperiode gefangen wurden. Südost-Zieher sind mit einem Stern gekennzeichnet.

Species	Scientific name	Total ringed birds
<b>Trans-Saharan migrants</b>		<b>5448</b>
Reed Warbler	<i>Acrocephalus scirpaceus</i>	2107
Willow Warbler	<i>Phylloscopus trochilus</i>	1636
Sedge Warbler	<i>Acrocephalus schoenobaenus</i>	565
Chiffchaff	<i>Phylloscopus collybita</i> <sup>1</sup>	221
Redstart	<i>Phoenicurus phoenicurus</i>	219
* Blackcap	<i>Sylvia atricapilla</i>	121
Pied Flycatcher	<i>Ficedula hypoleuca</i>	120
Garden Warbler	<i>Sylvia borin</i>	107
* Marsh Warbler	<i>Acrocephalus palustris</i>	78
Whitethroat	<i>Sylvia communis</i>	60
* Lesser Whitethroat	<i>Sylvia curruca</i>	57
Spotted Flycatcher	<i>Muscicapa striata</i>	48
Whinchat	<i>Saxicola rubetra</i>	42
Icterine Warbler	<i>Hippolais icterina</i>	20
* Red-Backed Shrike	<i>Lanius collurio</i>	12
Wood Warbler	<i>Phylloscopus sibilatrix</i>	8
Wheatear	<i>Oenanthe oenanthe</i>	7
Grasshopper Warbler	<i>Locustella naevia</i>	6
* Red-breasted Flycatcher	<i>Ficedula parva</i>	6
* Bluethroat	<i>Luscinia svecica</i>	2
Great Reed Warbler	<i>Acrocephalus arundinaceus</i>	2
* Greenish Warbler	<i>Phylloscopus trochiloides</i>	2
* Wryneck	<i>Jynx torquilla</i>	1
* Yellow-Browed Warbler	<i>Phylloscopus inornatus</i>	1
<b>Pre-Saharan migrants</b>		<b>5469</b>
Robin	<i>Erithacus rubecula</i>	3023
Goldcrest	<i>Regulus regulus</i>	1570
Wren	<i>Troglodytes troglodytes</i>	676
Song Thrush	<i>Turdus philomelos</i>	184
Blackbird	<i>Turdus merula</i>	9
Firecrest	<i>Regulus ignicapillus</i>	3
Redwing	<i>Turdus iliacus</i>	2
Water Rail	<i>Rallus aquaticus</i>	1

<sup>1</sup> 41 % ssp. *collybita*, 55 % ssp. *abietinus*, 2 % ssp. *tristis*, 2 % not identified

**Tab. 2.** Result of linear regression analysis relating differences of long term ringing data and ringing data of 1998 (daily percentages) with the migratory intensities of the preceding nights (log [mean MTR]). N indicates the number of ringing mornings that coincided with IR observation of the preceding night within the analysed time period.

**Tab. 2.** Resultate der linearen Regressionsanalysen, in welchen die Differenzen zwischen langjährigen Erfahrungswerten (Pentadenmittelwerte) und den Fangzahlen von 1998 (in Prozenten ausgedrückt) mit der nächtlichen Zugintensität der vorangegangenen Nacht (log[mean MTR]) verglichen werden. N sind die Anzahl Fangtage, welche mit Wärmebild-Resultaten verglichen werden konnten.

Species	Analysed time period	N	r	p
Reed Warbler	07 Aug–01 Oct	41	0.30	0.057
Willow Warbler	07 Aug–01 Oct	42	0.30	0.054
Sedge Warbler	07 Aug–26 Sept	36	0.09	0.608
Chiffchaff	22 Sept–16 Oct	23	0.55	0.006
Redstart	23 Aug–26 Sept	25	0.21	0.260
Blackcap	02 Sept–26 Sept	17	0.42	0.089
Pied Flycatcher	07 Aug–06 Sept	23	0.42	0.049
Garden Warbler	07 Aug–21 Sept	32	0.34	0.057
Robin	23 Aug–28 Oct	49	0.45	0.001
Goldcrest	02 Sept–28 Oct	41	0.62	< 0.001
Wren	07 Sept–28 Oct	36	0.64	< 0.001
Song Thrush	17 Sept–21 Oct	32	0.44	0.011

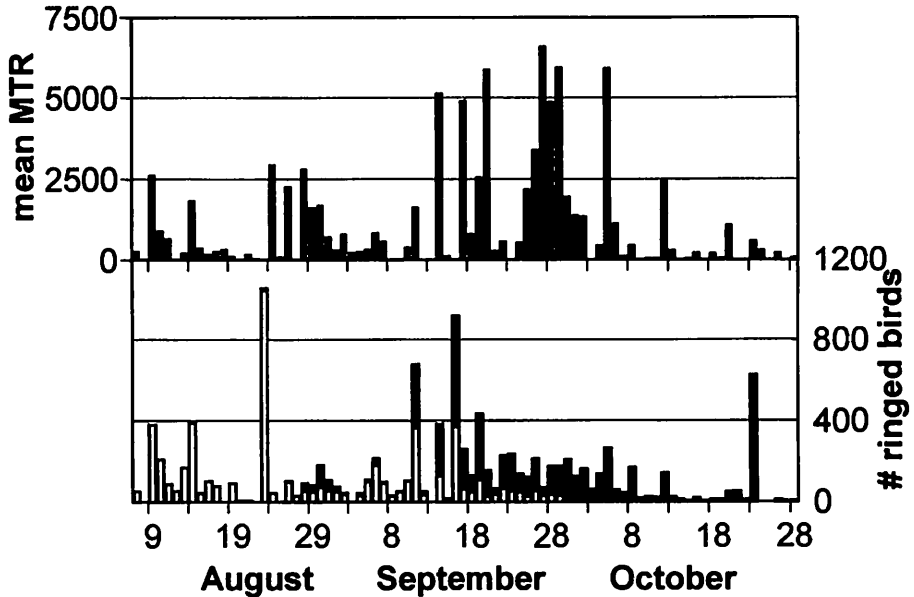
MTR) of the preceding night. By splitting the IR observation periods at midnight, 62 ringing mornings coincide with IR observations PM (mean MTR PM), and in 59 cases with IR observations AM (mean MTR AM). The average MTR over the whole season recorded by IR was 1319 birds  $\text{km}^{-1} \text{h}^{-1}$  (s.d.  $\pm 1701$  birds  $\text{km}^{-1} \text{h}^{-1}$ ) and the migration was most intense in the second half of September (Fig. 1).

A total of 10,917 ringed nocturnal migrants were included in this study. These included 24 species of trans-Saharan migrant (50 % of ringed nocturnal migrants) and 8 of pre-Saharan migrant (50 %; Table 1). In August, trans-Saharan migrants predominated (Fig. 1). In September, both trans- and pre-Saharan migrants were caught. In October there were almost exclusively pre-Saharan migrants.

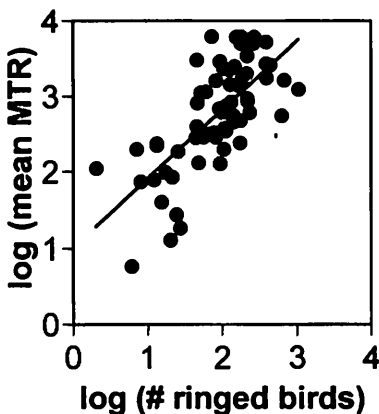
Ringing totals of night migrants correlated positively with mean MTR recorded in the preceding night ( $n = 63$ ,  $R^2 = 0.49$ ,  $p < 0.001$ ; Fig. 2). The correlation between ringing and mean MTR AM totals of the preceding night was stronger than that between ringing and

mean MTR PM ( $n = 59$ ,  $R^2 = 0.62$ ,  $p < 0.001$ ;  $n = 61$ ,  $R^2 = 0.35$ ,  $p < 0.001$ , respectively), but not due to different sample sizes.

Extraordinarily high numbers of trapped birds in autumn 1998 were achieved on 24 Aug ( $n = 1057$ ), 12 Sept ( $n = 675$ ), 17 Sept ( $n = 918$ ) and 24 Oct ( $n = 626$ ). The sum of these mornings corresponds to 20 % of caught nocturnal migrants during the observation period. However, the mean MTR recorded in the preceding nights corresponds to average intensities (23 Aug: 1207 birds  $\text{km}^{-1} \text{h}^{-1}$ ; 11 Sept: 1646 birds  $\text{km}^{-1} \text{h}^{-1}$ ; 16 Sept: no IR observations owing to rain; 23 Oct: 616 birds  $\text{km}^{-1} \text{h}^{-1}$ ). The nocturnal pattern of migratory intensity recorded with IR during these nights was first moderate and increased towards morning (Fig. 3). This is very different from the average nightly pattern observed for the rest of the season, which showed peak intensity approximately two to three hours after the end of civil twilight at dusk (third tenth of the night) and declining intensity towards dawn.



**Fig. 1.** Seasonal course of migratory intensities registered by IR (above) and ringing totals of trans- and pre-Saharan migrants (below). Trans-Saharan migrants are marked with white bars, pre-Saharan with black.  
**Abb. 1.** Saisonaler Ablauf der mittels Wärmebildkamera ermittelten nächtlichen Zugdichten (oben) und der Anzahl beringter Vögel (unten). Trans-Sahara Zieher sind weiss markiert, Pre-Sahara Zieher in schwarz.

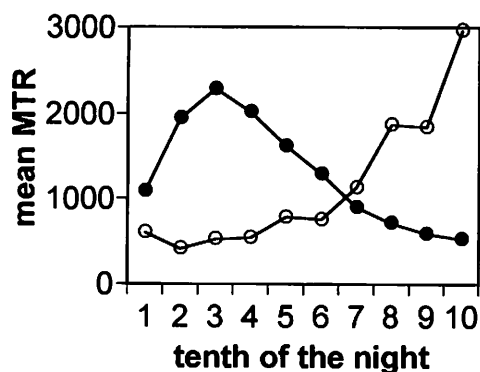


**Fig. 2.** Mean MTR as recorded by infrared device against ringing totals of the following morning ( $n = 63$ ,  $r = 0.70$ ,  $p < 0.001$ ). Mean MTR and ringing totals were log transformed.

**Abb. 2.** Korrelation zwischen der mittleren nächtlichen Zugdichte und der Anzahl Vögel, die am nächsten Morgen gefangen wurden ( $n = 63$ ,  $r = 0.70$ ,  $p < 0.001$ ). Mittlere MTR und Fangzahlen wurden log transformiert.

The differences of expected and observed ringing numbers per species correlated significantly with the migratory intensity ( $\log[\text{mean MTR}]$ ) in all pre-Saharan migrants considered, i. e. Robin, Goldcrest, Wren and Song Thrush (Table 2). Figure 4 illustrates the results for the Robin. For the trans-Saharan migrants the result was only significant for the Chiffchaff and the Pied Flycatcher. In the cases of the Reed Warbler, Willow Warbler, Blackcap, and the Garden Warbler the results indicate a positive relationship although the p-values are slightly larger than 0.05. No correlation was found for the Redstart and the Sedge Warbler.

The distribution of flight directions as registered by IR showed a predominant SW direction (mean track direction =  $219^\circ$ ,  $n = 17,411$ , mean vector length = 0.62,  $p < 0.001$ ; Rayleigh test; cf. Zehnder et al. in press). Whereas 11 % of the birds observed by IR flew towards the SE sector, the SE migrants represented 2.6 % of ringed birds (Table 1).



**Fig. 3.** Nocturnal pattern of migratory intensities as recorded by IR. The black dots represent the mean MTR per tenth of the night throughout the observation period, the open circles represent the nights preceding the mornings with the highest trapping counts (23/24 Aug., 11/12 Sept., 23/24 Oct.; no IR observations due to rain on 16/17 Sept.).

**Abb. 3.** Nächtliche Zugmuster, die mit der Wärmebildkamera ermittelt wurden. Die schwarzen Punkte stellen die über die ganze Beobachtungsperiode gemittelten Zugintensitäten pro Nachtzehntel dar. Die Kreise entsprechen der mittleren Zugintensitäten jener Nächte, denen die höchsten Fangzahlen folgten (23/24 Aug., 11/12 Sept., 23/24 Sept.; keine Wärmebildbeobachtungen von 16/17 Sept. wegen Regens).

## Discussion

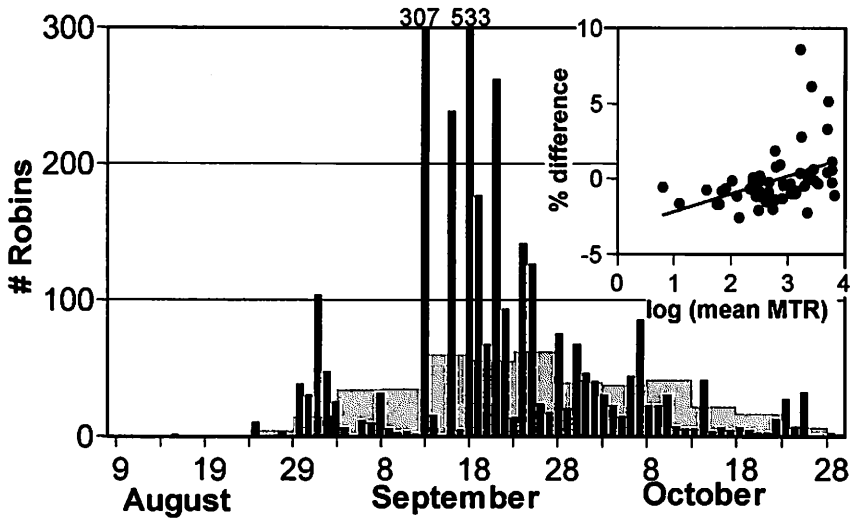
This study reveals a positive correlation between numbers of birds observed aloft during the night and numbers of nocturnal migrants ringed the following morning. This seems to suggest that a certain proportion of nocturnal migrants comes to ground at Falsterbo peninsula before tackling the open seas to the south. These findings are at variance with those of a radar study by Alerstam (1972, see also Alerstam et al. 1973). His results indicated no relation between ringing totals and migratory volume at Falsterbo. His conclusion was, however, based on data stemming (a) from surveillance radar incapable of detecting low-flying birds and (b) from a Falsterbo trapping system which at that time had not yet been standar-

dised. The present study has the advantage of more reliable data emanating from the IR and from a standardised trapping system, both of which were applied in close proximity to one another and over a large part of the migration season, a time when at Falsterbo the numbers of resident and resting birds are negligible.

The numbers of trapped birds are more representative of the numbers of migrants flying in the second half of the night than of those in the first half. This indicates that birds caught at Falsterbo are migrants that interrupt their flight during the second half of the night. At this time, the birds already have been flying for several hours since the majority initiate their migratory flight shortly after sunset (for reviews see Moore 1987, Åkesson et al. 1996a). We believe that birds trapped at Falsterbo are a representative sample of migrants en route, except for birds that were forced to ground by adverse weather conditions such as fog.

Surprisingly, the four mornings with the largest trapping counts in the observation period were not preceded by heavy migratory traffic during the night. Unlike on an average night, the migratory intensities began low, increasing only towards the morning. In the particular case of the morning of 24 August, fog had built up over the Baltic sea provoking a high incidence of landfall of birds aloft. The weather situation on the other three mornings was very similar, partly associated in one instance with light rain. Thus, such "big landfall events" must be interpreted circumspectly when ringing data are analysed in relation to migratory intensity (cf. Richardson 1978).

According to Bairlein (1981) the trapping results gathered by capture are an index of actual bird densities on the ground. However, the proportion of a particular species caught at a specific site greatly depends on the conditions at the trapping site (Degen & Jenni 1990, Jenni et al. 1996). As suggested by the findings of Jenni et al. (1996), larger birds, for instance, might have avoided capture to a larger extent than smaller species owing to the small mesh size of 16 mm used at Falsterbo. Birds with a



**Fig. 4.** Comparison of expected and observed number of ringed Robins. The grey bars represent the long term pentad averages (expected numbers), the black bars the number of Robins ringed in 1998 (observed numbers). The inset graph illustrates the regression between the differences of the percentages of expected and observed numbers with the mean MTR (log transformed) of the preceding nights. Statistics are given in Table 2.

**Abb. 4.** Vergleich zwischen erwarteten und beobachteten Anzahlen beringter Rotkehlchen. Die grauen Säulen stellen die langjährigen Pentadendurchschnitte (Erwartungswert) dar und die schwarzen Säulen die Anzahl 1998 beringter Rotkehlchen (Beobachtungswert). Das eingeschobene Diagramm illustriert die Regression zwischen der Differenz der Erwartungs- und Beobachtungswerte (in Prozenten) und der mittleren Zugintensität der vorangegangenen Nacht ( $\log[\text{mean MTR}]$ ). Die statistischen Werte sind in Tabelle 2 gegeben.

habitat preference for the top part of the vegetation (as for instance flycatchers) might be underrepresented (L. Karlsson pers. obs.; Degen & Jenni 1990). Hence, to reach a conclusion about the actual composition of birds aloft based on trapping data is difficult. Nevertheless, our study gives at least some evidence for a direct correlation between the species composition of free-flying birds and that of birds landing in the nets.

Zehnder et al. (in press) showed that the intensity of nocturnal bird migration at Falsterbo is higher with light tailwinds, and high and rising air pressure. Assuming that the same weather conditions influenced the trapping numbers, we can conclude that the decision of pre-Saharan migrants to engage in a migratory flight is influenced more strongly by the prevailing weather than is that of trans-Saharan

species. In general, pre-Saharan migrants initiate their migratory journey later in the season when good migratory conditions are less frequent than in the time period at which trans-Saharan migrants leave. Therefore, in the latter group, the selection of favourable weather conditions and hence risk minimisation may have a stronger bearing on the process of natural selection. For trans-Saharan migrants, our results suggest that additional factors influence the decision of the birds to engage in a migratory flight. Possibly, the migratory urge is regulated more directly by endogenous factors which might be related to the much longer distance to their wintering grounds (cf. Berthold & Dorka 1969).

Facing the open sea – an ecological barrier – south of Falsterbo, birds might land in order to refuel before engaging on the sea crossing



(Alerstam 1978, Lindström & Alerstam 1986, Sandberg et al. 1988, Åkesson et al. 1996b). Our disparate findings for pre- and trans-Saharan migrants might indicate that the pre-Saharan migrants are more apt to interrupt their flight. Whereas for species wintering in central or southern Europe the Baltic sea is a major ecological barrier which they face on their journey, species migrating to tropical Africa are confronted with much larger obstacles, such as the Mediterranean Sea or the Sahara.

The results for the Chiffchaff represent an exception to these general findings. The migratory peak of different subspecies lies within the same period. While the northern spp. *abietinus* is classified as trans-Saharan migrant, the southern spp. *collybita* is known to winter around the Mediterranean Sea. The genetic separation of populations into the two groups might be inadequate or, alternatively, evolutionary constraints might be responsible for the weather response of this species.

Such relationships are more difficult to demonstrate for species captured in low numbers or, as for instance in the Redstart, in widely fluctuating numbers. In the case of the Sedge Warbler, however, reasons other than statistical shortcomings must be responsible for the missing relationship. In 1998 considerably fewer Sedge Warblers (29 % of the total) were caught in the period (21 Aug–10 Sept) when the migratory peak (44 % of the total) was expected according to long term ringing data. Possibly, this is a result of the very special wind conditions when many of them were under way. From 21–31 August there were continuous strong westerly winds at the time of the passage of mainly south-west Scandinavian Sedge Warblers (as indicated by retrapped birds ringed elsewhere, unpublished data, L. Karlsson) causing them to drift away from Falsterbo or not to migrate at all. This was followed by a period of strong easterly winds during the first ten days of September. According to retraps of birds ringed elsewhere Sedge Warblers from northern Sweden and Finland pass Falsterbo

during September (unpublished data, L. Karlsson). Therefore these populations may have occurred in higher numbers than normal, drifted westwards by the winds. Food availability is another possible explanation of the Sedge Warbler's migratory pattern in 1998. Sedge Warblers feed mainly on aphids, a superabundant but patchily distributed prey (Bibby & Green 1981). Consequently, Sedge Warblers present higher fat deposition rates and engage in long-distance flights once they achieve a sufficient fat load (Schaub & Jenni 2000). If places situated north of Falsterbo offered good stopover conditions during their main migratory period, the Sedge Warblers simply passed Falsterbo without stopping over to a greater extent than normal.

The distribution of migratory directions reported for central and southern Europe consistently present a single preferred direction towards the SW (e. g. Bruderer & Liechti 1990). Nevertheless, some bird species follow exclusively south-eastern routes. The migratory directions of other species are split into south-west and south-east cohorts, which complicates the classification of some Scandinavian populations as SW or SE migrants (e. g. Blackcaps). However, the predominance of SW migrants is reflected in the main migratory flight direction towards the SSW as registered by IR. South-easterly flight directions observed by IR were more frequent than expected from the proportion of SE migrants captured at Falsterbo. Alerstam (1975) observed by radar an intense SE migration of Redwings, a diurnal migrant wintering in south-west Europe, over southern Sweden. Westerly winds prevailed during ours and Alerstam's study. Flight directions are determined endogenously and are modified, among other things, by wind. Zehnder et al. (in press) showed that high flying birds do not compensate for wind drift. Therefore, we conclude that south-westerly winds caused a shift of flight directions towards the E for which the birds presumably compensate later. As a consequence, it is not possible to deduce from the actual flight direc-

tion of birds en route in what direction the target area of the migrants lies.

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