Seasonal patterns of occurrence of Palaearctic migrants in southern Africa using atlas data

LESLIE G. UNDERHILL*, ROBERT P. PRÝS-JONES†, JAMES A. HARRISON* & PETER MARTINEZ‡

*Avian Demography Unit, Department of Statistical Sciences, University of Cape Town, Rondebosch 7700, South Africa
†British Trust for Ornithology, The National Centre for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU, UK
‡Department of Astronomy, University of Cape Town, Rondebosch 7700, South Africa

A statistical method, using presence/absence data from monthly fieldcards, to describe the phenology of migration is developed. The method uses the generalized linear model to fit a Fourier series to binomial-type data giving the proportion of fieldcards reporting a species. A method for estimating mid-arrival and mid-departure dates, and residency period is also developed. The methodology is applied to data collected during the 'Southern African Bird Atlas Project' for the following species: Willow Warbler Phylloscopus trochilus, Red-backed Shrike Lanius callurio, European Swallow Hirundo rustica, White Stork Ciconia ciconia, Steppe Buzzard Buteo buteo and European Bee-eater Merops apiaster.

The primary objective of the Southern African Bird Atlas Project (SABAP) (Harrison 1987, 1989, 1990, 1991) is to map the distribution of all bird species in Africa south of the Zambezi and Kunene Rivers. The collection of data relating to seasonality of distribution is a secondary objective, and it is this aspect of SABAP which is reported here. Detailed distribution maps will be presented in the final atlas publication.

The study area for the project (Fig. 1) covers a 20-degree latitudinal range (15°S-35°S). In broad terms, rainfall increases from west to east (11°E-33°E) across the subcontinent, resulting in a diversity of habitats from desert along the coast of Namibia to forest along the southeastern coast of South Africa. The focus of this paper is methodological. First, it describes a relatively cheap method of obtaining large volumes of quantitative data on the phenology of migration on a subcontinental scale. Second, a statistical method to describe phenology is also presented.

The previous major review of the phenology of migration in southern Africa was by Broekhuysen (1955/1956, 1971/1974). He summarized records of migrants submitted by observers because they were considered interesting (mainly first and last dates). These results were clearly open to the criticism that they were biased by the self-censoring of observations by recorders.

MATERIAL AND METHODS

SABAP was a mass-participation project with c. 7000 observers. Organizational aspects of SABAP were described in Harrison (1987). The project employed a quarter-degree grid scale (resulting in quarter degree grid 'squares' (QDGS) approximately 27 km north to south x 24 km east to west for its spatial resolution). The temporal resolution was the calendar month; data for the same month in successive years were cumulated.

The fieldwork protocol was for an observer to submit one atlas card for each QDGS visited per calendar month. Each species identified in the month was recorded on the atlas card, regardless of numerical abundance. Observer effort was not measured; some atlas cards were based on a few hours bird-watching, during which only the most conspicuous and abundant species were recorded, others provided comprehensive lists after exhaustive searches throughout all parts of a QDGS. All the records on each atlas card were incorporated into the SABAP database. The computerized database contains cumulative totals of the number of atlas cards for each QDGS per month, and the numbers of these cards that recorded each species.

The fieldwork for the project was scheduled to end in 1991. By the end of 1990, the project's database held five million records (Underhill et al. 1991), and it was this subset of the final database that was analysed for this paper. At that stage, atlas cards were available for 98% of the 2020 QDGS in South Africa, Lesotho and Swaziland, for 86% of the 1241 QDGS in Namibia, and 78% of the 602 QDGS in Zimbabwe. Computerization of atlas data for Botswana was in progress, but these were not available in
time for this paper. The political situation in Moçambique precluded effective atlas fieldwork there.

The fieldwork and data capture methodology enabled reporting rates to be computed. We define the reporting rate for a species as the percentage of field cards received for a region which record the species as present (Linsdale 1928). The reporting rate may loosely be interpreted as the likelihood of the species being recorded in a region in a calendar month (Temple & Temple 1986). For this paper, we use as regions 4°-wide latitudinal zones starting at 15°S and split the region into east and west, giving a total of ten regions labelled W15-19, ..., W31-35, E15-19, ..., E31-35 (Fig. 1).

The data for all QDCS within each region were combined, and overall reporting rates for each month were computed. A low reporting rate usually indicated that a species was rare, a high reporting rate that it was common.

We fitted Fourier models to the monthly reporting rates to provide a smoothed description of seasonality. These models are circular in the sense that the end of a year is joined continuously to its start (Zucchini & Adamson 1985, Zucchini et al. 1991). The exact form of the model was

\[
\text{logit } R = a_0 + b_1 \sin \theta + c_1 \cos \theta \\
+ b_2 \sin 2\theta + c_2 \cos 2\theta + b_3 \sin 3\theta + c_3 \cos 3\theta,
\]

where \( R \) was the reporting rate, \( \text{logit } R = \log \left( \frac{R}{1 - R} \right) \), the logistic transformation, and \( \theta \) is 1/24 of 360° for January, 3/24 of 360° for February, ..., and 23/24 of 360° for December, i.e., each month's data were considered to refer to the midpoint of the month. Because the data were essentially binomial in character, the seven parameters \( a_0 \), \( b_1 \), \( b_2 \), \( b_3 \), \( c_1 \), \( c_2 \), and \( c_3 \) were estimated using a generalized linear model with a binomial distribution, for which the logistic transformation is the appropriate link function (McCullagh & Nelder 1989, Genstat 5 Committee 1987). Thus we fitted a seven-parameter model to 12 data points; this means that there was a relatively small degree of smoothing and that the fitted model closely approximated the observed data (Fig. 2).

In order to compare the phenology of migration across latitudinal bands the following ad hoc procedure was adopted. Let the probability that a single bird in a region is detected be \( p \). Suppose there are \( n \) birds present in the region. Then the probability that at least one is detected is \( 1 - (1 - p)^n \). We set this equal to the reporting rate \( R \). It follows that \( n = - \log (1 - R) \). We define the mid-arrival date as the day \( t_a \) by which half the birds have arrived, the mid-departure date as the day \( t_d \) by which half the birds have departed, and the residency period as the period between these dates, \( t_a \), \( t_d \). Mathematically, if \( R \) is the reporting rate on day \( t \), and \( R_{\text{max}} \) is the maximum reporting rate, then the mid-arrival date is the day \( t_a \) on which \( \log (1 - R(t))/\log (1 - R_{\text{max}}) \) first exceeds one-half.

Note that our descriptions of the seasons are austral except where otherwise specified.

RESULTS

Overall migrant representation

Passerine and near-passerine Palaearctic migrants are remarkably poorly represented in the southern African
avifauna. Only 27 of the 91 such species treated by Moreau (1972) had been recorded during atlas fieldwork to the end of 1990, comprising between 5% and 6% of the total number of passerine and near-passerine species present in the subcontinent (c. 500). Consideration of other terrestrial non-passerines, i.e. excluding sea, intertidal and freshwater birds, does not alter this picture materially, with only raptors being at all well represented.

The entire subcontinent can thus be seen to lie to the south of that portion of the Afrotropical region in which the majority of Palaearctic terrestrial migrant species spend the boreal winter. Below, we provide examples of the information obtainable from the SABAP database regarding the patterns of occurrence of those migrants which do occur through reference to six of the more common and widespread species which between them encompass the spectrum of variation present.

**Willow Warbler Phylloscopus trochilus**

The distribution pattern of the Willow Warbler reveals a striking decrease in reporting rate from north to south and from east to west (Fig. 3). This exemplifies the most frequent overall pattern of distribution displayed by Palaearctic migrants, in particular the relatively well-represented warblers, although for most species the attenuation in reporting rate from the northeast is much more rapid, resulting in their being almost entirely absent from a greater or lesser part of the mostly arid areas to the south and west of the subcontinent.

On a finer scale, it is apparent that on the eastern side of the region where the species is most common, Willow Warblers arrive progressively later further south, with the mid-arrival date altering progressively from mid-October in E15–19 to December in E31–35 and W31–35. By contrast, departure from all parts of the subcontinent is almost simultaneous, with the mid-departure date near the beginning of April. In consequence, the residency period shortens from c. 5.5 months in the north to less than 4 months in the south.

**Red-backed Shrike Lanius collurio**

The reporting rate pattern of the Red-backed Shrike is similar to that of the Willow Warbler as regards an overall decline from north to south, but an east-west cline is less in evidence despite the clear peak in abundance in E19–23, i.e. southern Zimbabwe and northern Transvaal (Fig. 4). The Red-backed Shrike is one of the very few species for which there is evidence currently available which directly links atlas reporting rates to densities. B. Bruderer (pers. comm.) has shown that reporting rates show a positive
association with relative abundance within the higher density areas in which they were best able to do strip counts.

In contrast to the staggered arrival of Willow Warblers, mid-arrival dates of Red-backed Shrikes are strikingly synchronized across zones in southern Africa in mid to late November. This might be a result of territorial site fidelity, in contrast to the apparently continually shifting Willow Warblers. This compares with median passage dates from Ottenby, Sweden, of c. 14 August, from Khor Arbaat, Sudan, of c. 10 September, and from Ngulia, Kenya, of c. 15 November.

Departure is similarly synchronized across the subcontinent, with half the birds having left by early to mid-April.

**European Swallow Hirundo rustica**

The European Swallow has the highest overall reporting rate of any Palearctic migrant, although it is less common in the drier northwestern zones than elsewhere (Fig. 5). As for the Red-backed Shrikes, mid-arrival dates show no clear geographical trend; there is, at best, marginal evidence for a trend from late-October in the northeast to mid-November in the southwest. Departure appears synchronized across zones and occurs in early April.

On a finer analysis, a common factor in all the zones is that the build-up in reporting rate during arrival is slower than the decrease in reporting rate during departure. The converse pattern is observed in Britain, and presumably elsewhere on the breeding grounds; arrival during the boreal spring is rapid, and departure in autumn more gradual (Riddiford & Findlay 1981).

Overwintering has occurred in all zones, but the reporting rate is negligible.

**White Stork Ciconia ciconia**

White Storks are predominantly present in the east, with reporting rates peaking towards the south (Fig. 6). They are largely absent from the drier north-west. Birds reach southern Africa from the northeast; mid-arrival date there is mid-November, progressing to mid-arrival dates of around mid-December in the southeast and southwest. Withdrawal is similarly staggered, with mid-departure in early March in the south and early April in the northeast.

There is a minute breeding population in zone W31-35 (Roberts 1941, Brooke 1984). These birds make a negligible contribution to recorded reporting rates. However, significant numbers of White Storks overwinter, leading to substantial reporting rates, particularly in the northeast.
Steppe Buzzard *Buteo buteo*

The Steppe Buzzard has the most distinctive pattern of distribution in southern Africa of any terrestrial Palaearctic migrant. Steppe Buzzard reporting rates show almost the inverse pattern to the 'normal' pattern exemplified by Willow Warblers (Fig. 7)—they are most abundant in the southwestern Cape (zone W31-35), where the reporting rate reaches 45%, compared with only 11% in northern Zimbabwe (zone E15-19). Arrival in the subcontinent is almost simultaneous; similarly departure is well synchronized from all regions. First arrivals occur during September, with October an important arrival month. Departure starts in February, with March being the main departure month, and relatively few birds lingering till April.

The southwestern zone consists mainly of the Cape Floral Region, or Fynbos Biome, the smallest such region in the world (Fraser & McMahon 1988), and an area strongly avoided by most terrestrial Palaearctic migrants. However, it is not clear whether Steppe Buzzards are attracted to pristine fynbos, as their greatest densities in the southwestern Cape are in the wheatfields to the east and north of Cape Town (Hockey et al. 1989).

The unusual pattern of increase in abundance from north to south is also shown by extensive roadside transect data; one Steppe Buzzard per 33 km in the Transvaal compared to one per 2 km in the southwestern Cape (Tarboton & Allan 1984, D.G. Allan in litt.). However, it needs to be borne in mind that Steppe Buzzards are more conspicuous in the wheatlands of the southwestern Cape than in wooded habitats further north, especially in Zimbabwe.

European Bee-eater *Merops apiaster*

This species is particularly interesting. Like the White Stork, it has a migratory breeding population within Africa, breeding in the southern part of the study area (mainly in the four zones south of 27°S), and wintering in central Africa; unlike the White Stork, there is little overlap in distribution, except in the southwestern Transvaal, between the Palaearctic summer visitors and the breeding population (Brooke & Herroelen 1988).

The presence of the breeding population is revealed by those zones showing mid-arrival dates in mid-September (Fig. 8). By contrast, Palaearctic migrants concentrate in the northeast, and have mid-arrival dates c. 1 month later, in mid-October. The breeding populations withdraw northwards to a wintering area between 15°S and the equator (Brooke & Herroelen 1988), depa-
ture commencing during late January and February, having a mid-departure date c. 2 months in advance of the Palaearctic migrants (Fig. 7, see also Underhill 1990).

**DISCUSSION**

**Methodology**

We believe that the approach documented in this paper offers a powerful, cost-effective method for assessing year-round patterns of occurrence on a subcontinental scale without making impossible demands on a limited observer-force. The project has, in fact, provided a large stimulus to volunteer field ornithology in southern Africa. This is attributed to its straightforward methodology and the attention that has been paid to rapid feedback of information to participants, directing them to areas where little fieldwork has been done and providing field identification techniques. Effective computerization and data-processing systems have also enabled the project to cope with large volumes of data.

There are three important caveats to the interpretation of reporting rates, and to the modelled curves. First, reporting rates confound three variables: numerical abundance, conspicuousness and identifiability. Thus, comparisons of the relative abundance between species can only be valid if they are equally conspicuous and identifiable. Even within a species, conspicuousness can vary greatly between biomes; for example, a European Swallow is more conspicuous over desert than in forest, and more likely to be observed and reported. Conspicuousness and identifiability can also vary between seasons; many of the Palaearctic migrants are more vocal and active in the weeks preceding migration than they have been through the summer months, when many of them are moulting and tend to skulk. Bias in reporting rates may also be introduced if the identification skills of the observers vary between regions. We have no reason to suspect that this is a major problem with these data, each region having many observers with a broad mix of experience in identifying birds. In summary, any analysis of the reporting rates of a species must take account of the biology of that species.

Second, the relationship between reporting rate and numerical abundance is not linear, but has been shown by experience to be approximately monotonic; in general, if the reporting rate for a species is low, the species is relatively rare, and if it is high, the species is relatively abundant (e.g. Temple & Temple 1986, Hockey et al. 1989). At present few data relating bird densities to reporting rate are available. Further fieldwork aimed at calibrating this...
relationship would be invaluable. Reporting rate data can be gathered over large areas relatively inexpensively. These data could then be used to make estimates of the total population in a region.

Third, in fitting the model, the reporting rate for each observation period (here, the month) was considered to refer to the midpoint of the period. This is an approximation to the strictly correct interpretation that the reporting rate should be equal to the area under the modelled curve for the period. The approximation becomes closer to reality as the number of time periods increases. Periods of 1 month are the coarsest for which this approximation is acceptable.

The difficulties in determining arrival times for migrants were reviewed by von Haartman & Söderholm-Tana (1983), who considered only the first sighting of an individual of a species in an area. They pointed out various sources of bias in this method; in particular, they noted that the larger a population, the earlier the first individuals tend to arrive. The method described in this paper to highlight differences in arrival and departure between latitudinal zones was used to infer the date when approximately 50% of the birds had arrived or departed, a more useful measure of the phenology of migration than first arrivals (or last departures). Our method can, in theory, be used to determine mid-arrival and mid-departure rates to the day. However, the data were collected on a monthly time scale; a certain amount of interpolation is acceptable, but with the available data interpolation should not be to periods shorter than one week. However, our results for the relative timing of arrival and departure for a species between regions are likely to be correct.

The 1 month time scale used by SABAP has, with hindsight, proved too coarse to enable fine-scale resolution of differences in timing of arrival and departure of migrants between latitudinal zones to be made with confidence. Any project using the SABAP methodology with the primary objective of describing the phenology of migration should use a finer time scale. The extreme possibility is to produce field cards on a daily basis. The Fourier method of describing seasonality can equally well be applied to such data; this was done by Zucchini & Adamson (1984) in modelling daily probabilities of rainfall. However, a balance needs to be maintained between demands on amateur observers, volumes of data, and the possibility of statistical interpolation to a finer time-resolution than that of the adopted time scale. We recommend that a weekly time scale is the obvious alternative to the month.

Implicit in the fitting of a generalized linear model is the concept that the reporting rate represents the prob-
ability of a species being recorded in a month. Although we make this assumption in doing the modelling, we distance ourselves from this strict interpretation. The probability of a species being seen during a month clearly depends not only on numerical abundance, conspicuousness and identifiability, but also on the time spent observing and the skills of a particular observer.

The phenology provided by the methodology describes residency at the population level, and not at the individual level. Thus, we are unable to distinguish whether a staggered arrival pattern is due to leap-frog migration (with later arriving individuals being forced to occupy areas to the south of earlier arrivals) or blanket migration (where the entire population moves southwards). To distinguish between such patterns it is necessary to mark individual birds.

**Results**

There is considerable interspecific variation in spatial patterns of occurrence among Palaearctic migrants. However, the most predominant overall pattern is of a decline in representation towards the south and/or towards the drier west.

Certain species, notably the Steppe Buzzard, are exceptions to this pattern of decline for reasons which have not yet been adequately documented. In this context, it needs to be noted that discussion of patterns in a clinal context is complicated by the presence in the southwestern Cape of a region which is unique within the subcontinent both climatically (winter rainfall) and in its vegetation (high species diversity and endemism) (Fraser & McMahon 1988). Both the Fynbos and the Karoo biomes lack grass and trees, which are important bird habitats, especially for passerines.

Despite restrictions on the temporal resolution of the methodology, as discussed above, considerable variation is apparent between species in the way they structure their arrival and departure strategies and their range occupancy. An emerging pattern for many species is that they display staggered arrival and synchronized departure.

**Future directions**

Within southern Africa, the project should be followed up by detailed studies relating reporting rate to relative (or even absolute) densities, as pioneered by B. Bruderer (pers. comm.) for the Red-backed Shrike. This calibration will enable the concepts of mid-arrival and mid-departure dates, and residency period, to be better defined. Within the context of global warming, and intensifying habitat...
destruction in Europe and Africa, an ongoing atlas project could provide valuable information on range contraction or expansion of migrants (Underhill et al. 1991). Reporting rates also have the potential to monitor changes in relative abundance (Underhill & Hockey 1988, Harrison 1989).

Detailed comparisons of the phenology of Palearctic migrants in southern Africa with that in Europe are surprisingly difficult. Europe tends to lack equivalent standardized studies on the appropriate temporal and spatial scales. Most European atlas projects have suffered two major constraints: the year is perceived as consisting of two discrete periods, the breeding season in spring and summer, and winter, with little of interest in between; the projects are defined on a country-by-country basis, and have boundaries which have little relevance to bird populations. A Europe-wide, amateur-based, study of migration phenology would seem a project which has scientific merit and is attainable.

Major sponsors of SABAP are the De Beers Chairman’s Fund, Distillers’ Corporation, Endangered Wildlife Trust, Gold Fields Foundation, Mazda Wildlife Fund, South African Department of Environment Affairs, Southern African Nature Foundation, Southern African Ornithological Society, University of Cape Town, and the Wildlife Society of Southern Africa. We are grateful to the Namibian, Zimbabwean and Swazi atlas projects for giving permission for data to be used in this publication. LCU acknowledges support from the Foundation for Research Development and the University of Cape Town. D.G. Allan, C.J. Brown, K. Hustler, T.B. Oatley, R.W. Summers, and W. Zucchini commented on earlier drafts and we thank S.P. Carter and R. Navarro for help in preparing the figures. We especially acknowledge the contributions of the thousands of atlas observers throughout southern Africa to the SABAP database.

REFERENCES


