

SPATIO-TEMPORAL PATTERNS OF ABUNDANCE OF *Hirundinidae* IN THE PROVINCE OF KWAZULU-NATAL, SOUTH AFRICA

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ABSTRACT

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The Province of KwaZulu-Natal lies on the south eastern seaboard of South Africa. The province has a very rich avifauna. We have investigated the spatial and temporal patterns of 14 species of *Hirundinidae* which inhabit the province, *i.e.* about 20% of this world-wide family of beautiful and diminutive birds. We found that some species are rare (occurring in less than 10% of the 170 15' by 15' grid-cells which cover the province, *e.g.* *Hirundo atrocaerulea*) while others are ubiquitous (found in 100% of grid-cells, *e.g.* *H. rustica*). Some species are predominantly winter visitors (*e.g.* *H. smithii*), certain others are breeding summer migrants (*e.g.* *H. semirufa*), some are non-breeding summer migrants (*e.g.* *Riparia riparia*) and others are present all year at a constant density (*e.g.* *H. fuligula*). However, the patterns of seasonal abundance are often more subtle. Some species are both passage migrants, passing through the province in spring and autumn, while also breeding in the province in large numbers during the summer (*e.g.* *H. albigularis*, *H. spilodera* and *H. cucullata*). At first glance, *H. rustica* gives the appearance of a „classic“ summer migrant but we suspect that its numbers build up slowly during the summer in inverse proportion to those of *H. abyssinica* who arrive in vast numbers in the early spring, breed and then slowly decline. The seasonal abundance of *Delichon urbica* is even more asymmetrical than that of *H. rustica* as it peaks very late in the summer.

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INTRODUCTION

Swallows and martins form the family *Hirundinidae* within the order *Passeriformes* (Cramp 1988). A more detailed account of their morphology and classification can be found in Turner and Rose (1989). They are familiar birds throughout the

world, often existing in close association with people, in some cases even nesting inside their homes. They are known as harbingers of spring and symbols of good luck (Turner and Rose 1989). Despite this association with man, we understand little about the dynamics of the spatial and temporal patterns of abundance of these diminutive insectivores.

The sixteen hirundine species occurring in KwaZulu-Natal (Table 1) constitute more than 20% of the total number of species occurring worldwide and this province thus plays as a host to a considerable proportion of the world's hirundines. This number is sure to change in the future, if man continues to have such a profound impact on the natural environment. Anthropogenic influences have considerably altered the spatio-temporal patterns of abundance of hirundines in KwaZulu-Natal (Harrison *et al.* 1997a). The numbers of certain species have crashed to critically low levels as they have been becoming increasingly constrained in distribution and abundance by the progressive destruction and degradation of their habitats. For instance, Allan (1988) found that the Blue Swallow (*Hirundo atrocaerulea*) has disappeared from 21 of 29 known localities in South Africa and it currently heads the list of endangered South African Birds (Brooke 1984). However, not all species have been negatively affected by anthropogenic influences. Many have increased in their numbers and ranges, probably as a result of the increased availability of artificial nesting sites, *e.g.* the Lesser Striped Swallow (*H. abyssinica*) (Earlé and Herremans 1997).

In addition to the changing spatial patterns of abundance of hirundines in KwaZulu-Natal, they exhibit complex temporal patterns of abundance, which are little understood and poorly documented. Hirundines are very mobile birds, with most species in KwaZulu-Natal being either Palearctic (three of sixteen) or intra-African migrants (eight of sixteen). Even resident birds may undergo local movements in response to changing environmental conditions, *e.g.* Rock Martin (*H. fuligula*) moving to lower altitudes after the breeding season (Hockey *et al.* 1989). One of the objectives of this study is to gain an insight into the effect that migratory species, such as the European Swallow (*H. rustica*), have on the species present all year in KwaZulu-Natal. Besides, it is aimed to get the information about where and when they enter the province and about the details of their subsequent dispersal.

According to Moreau (1972), Africa plays as a host to nearly 1000 million migrant hirundines each year. South Africa, as one of the prime destinations for these birds would accommodate a large proportion of these migratory species. It is likely that KwaZulu-Natal alone, with its favourable conditions, receives many millions of hirundines each summer. It has been suggested by Jones (1996) that these migrants may place substantial strain on resident species and their ever decreasing resources. The breeding activities of a considerable number of southern African birds occur at the time when the Eurasian migrants share their habitats, what may also be an important factor in competition for food (Curry-Lindahl 1981). With nestlings to raise and thus a greater dependence on an abundant food supply, local hirundines may

be forced to seek less densely populated areas, after the arrival of Palearctic and intra-African migrants.

Table 1
Species list of studied hirundines. Temporal status: IA – intra-African migrant,
P – Palearctic migrant, all year – present all year

Latin name	Code	Common name	Temporal status	Spatial status
<i>Hirundo rustica</i>	HIR.RUS	European Swallow	P	Ubiquitous
<i>Hirundo albigularis</i>	HIR.ALB	White-throated Swallow	IA	Upland
<i>Hirundo atrocaerulea</i>	HIR.ATR	Blue Swallow	IA	Upland
<i>Hirundo smithii</i>	HIR.SMI	Wire-tailed Swallow	all year	Lowland
<i>Hirundo dimidiata</i>	HIR.DIM	Pearl-breasted Swallow	IA	?
<i>Hirundo semirufa</i>	HIR.SEM	Red-breasted Swallow	IA	Lowland
<i>Hirundo cucullata</i>	HIR.CUC	Greater Striped Swallow	IA	Upland
<i>Hirundo abyssinica</i>	HIR.ABY	Lesser Striped Swallow	IA	Lowland
<i>Hirundo spilodera</i>	HIR.SPI	South African Cliff Swallow	IA	Upland
<i>Hirundo fuligula</i>	HIR.FUL	Rock Martin	all year	Upland
<i>Delichon urbica</i>	DEL.URB	House Martin	P	Ubiquitous
<i>Pseudhirundo griseopyga</i>	PSE.GRI	Grey-rumped Swallow	all year	Lowland
<i>Riparia riparia</i>	RIP.RIP	Sand Martin	P	Ubiquitous
<i>Riparia paludicola</i>	RIP.PAL	Brown-throated Martin	all year	Ubiquitous
<i>Riparia cincta</i>	RIP.CIN	Banded Martin	IA	Upland
<i>Psolidoprocne holomelas</i>	PSA.HOL	Black Saw-wing Swallow	all year	Lowland

This paper identifies and describes the spatio-temporal patterns of abundance of *Hirundinidae* within KwaZulu-Natal, drawing extensively on the distribution data of individual species provided by the South African Bird Atlassing Project (SABAP) (Harrison *et al.* 1997a).

STUDY AREA

This study was conducted within the Province of KwaZulu-Natal, situated on the south eastern seaboard of South Africa. It also includes the Eastern Cape Island which is situated within the boundary of KwaZulu-Natal. The low altitude (< 1000 m a.s.l.), high rainfall (> 800 mm/year) and sub-tropical climate characteristic of a large proportion of KwaZulu-Natal (Schulze 1997) provides an ideal locality for the survival of hirundines. The province covers 92 285 km² (Schulze 1997) and encompasses a large diversity of habitats from the high Drakensberg peaks in the west and lowland coastal forests to the hot arid woodlands in the north and cool mistbelt forests in the interior.

The region was divided into 170 (15' longitude × 15' latitude) grid-cells, to correspond with the scale of the distribution data (Harrison *et al.* 1997a), with each

grid-cell roughly representing 23 km by 27 km on the ground (approximately 670 km² in extent).

METHODS

Species data

This study is based on the bird distribution data provided by the South African Bird Atlassing Project (SABAP) (Harrison *et al.* 1997a). These data were collected on a monthly basis in each of the 170 grid cells covering KwaZulu-Natal, recording the number of sightings of each species in each grid-cell (between 1987 and 1991 for KwaZulu-Natal). The number of sightings of each species in each grid-cell was converted to a percentage reporting rate by dividing the number of sightings by the number of reporting cards completed for that grid-cell. This raw reporting rate is a measure of sightability. The data available for the Pearl-breasted Swallow (*H. dimidiata*) exists as a single record for this species in KwaZulu-Natal. Its vagrant status thus prompted us to discard it from the analysis.

The fact that the coverage of KwaZulu-Natal by SABAP (Harrison *et al.* 1997a) was both comprehensive and far more even than that for previous atlas schemes in the region (*e.g.* Cyrus and Robson 1980) removes some of the possible problems related to considering the reporting rates as an index of relative densities (Underhill *et al.* 1992). A remaining problem was that of observer bias. Inconspicuous and more difficult to identify species are recorded less often or incorrectly by inexperienced observers (Underhill *et al.* 1992). According to Harrison *et al.* (1997a), the range limits of the Greater Striped Swallow (*H. cucullata*) and the Lesser Striped Swallow (*H. abyssinica*) are difficult to assess due to misidentification and the fact that they are both migrants and therefore may be seen outside of their normal ranges. Two other particular identification problems are confusions between the Grey-rumped Swallow (*Pseudhirundo griseopyga*) and the House Martin (*Delichon urbica*), and between the White-throated Swallow (*H. albigularis*) and the Wire-tailed Swallow (*H. smithii*) (Harrison *et al.* 1997a).

These data were imported into a computer based Geographic Information System (GIS) („Idrisi” for Windows, v. 2.01), to generate spatial distribution images for each species. Following data manipulation (the details of which can be found in Piper *et al.* 1998), a single database was extracted from these images. This database contained the monthly reporting rate data per 15' × 15' grid-cell for all the hirundine species considered in this study.

As an aid to answering the spatio-temporal questions posed by this study, the database was further modified to obtain three separate matrices. These included a species by month matrix (15 × 12), a species by grid-cell matrix (15 × 170) and a species by month by grid-cell matrix (15 × 12 × 170). These data were then imported into the computer programme CANOCO (ter Braak 1987) for multivariate analysis in the form of Correspondence Analysis (CA) (ter Braak 1986).

Environmental data

Topographic data for KwaZulu-Natal, in the form of altitude, were obtained from the Computing Centre for Water Research at the University of Natal, Pietermaritzburg (Dent *et al.* 1989, Schulze 1997). As with the bird data, the environmental data were imported into a GIS computer programme („Idrisi” for Windows, version 2.01) and converted to a 15'×15' grids, as used for bird data, and modified further, in accordance with the GIS requirements. The details of how these environmental data were obtained, converted and compiled are described in a separate report (Piper *et al.* 1998).

Analysis

A time series graph was plotted for each species (Fig. 2), showing how the species reporting rate for the province varies seasonally. These were based on the most recent atlassing data (1987-1991) supplied by SABAP (Harrison *et al.* 1997a).

For preliminary investigations and descriptions of the general spatial and temporal patterns of abundance of hirundines within KwaZulu-Natal, a Correspondence Analysis (CA) (ter Braak 1986, 1987) was used on the „species by sites” (Fig. 1) and „species by months” (Fig. 3) matrices. CA is a popular ordination method among community ecologists and has been fully described and widely applied (Boshoff and Piper 1993). The benefit of such a multivariate procedure is that

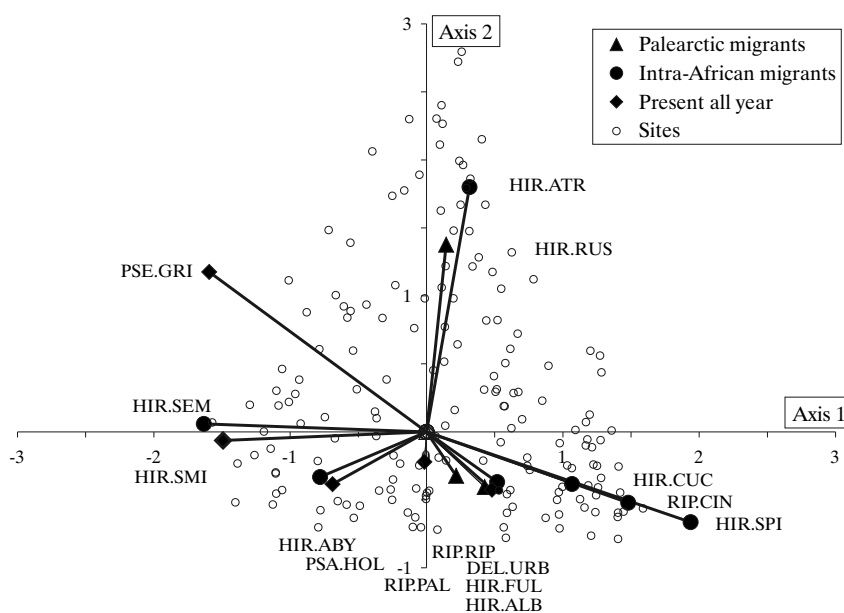


Fig. 1. Spatial separation of species according to a Correspondence Analysis. Species codes – as in Table 1.

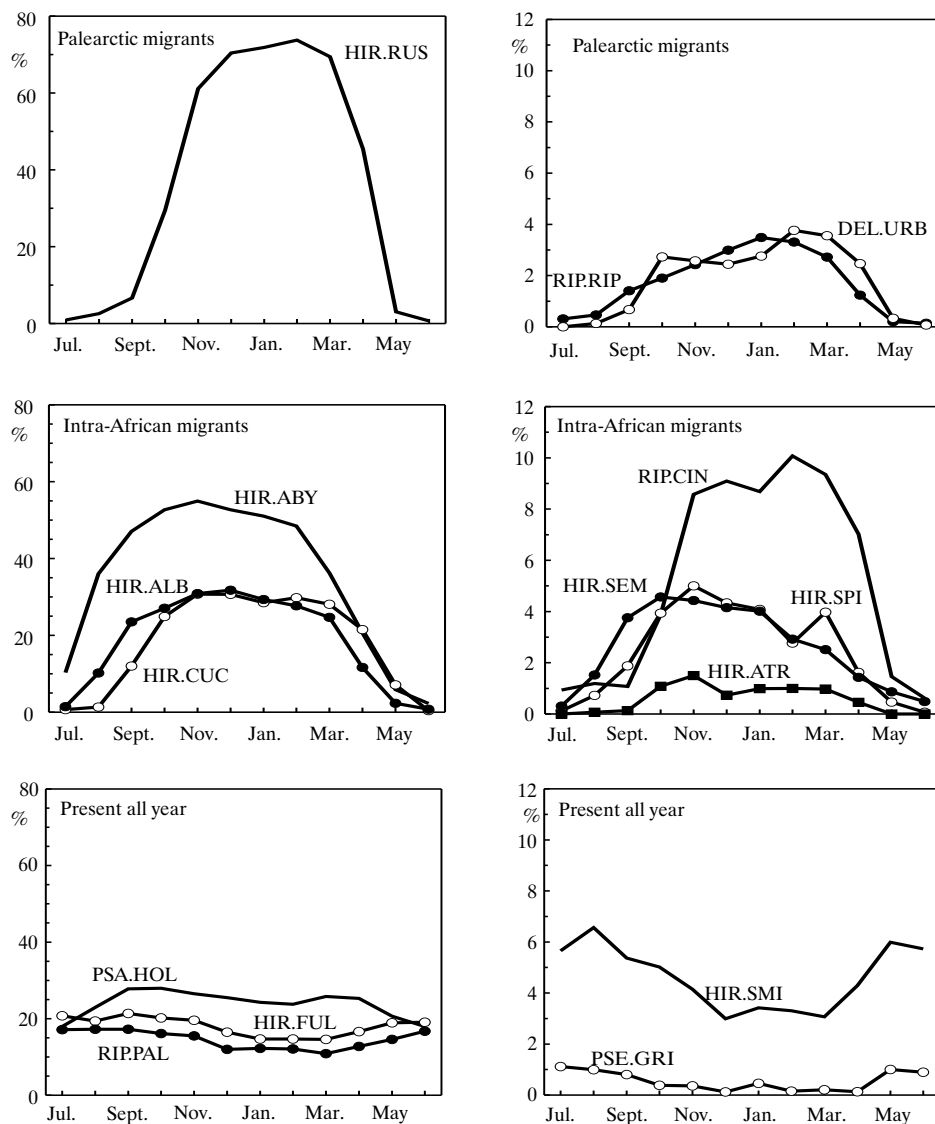


Fig. 2. Seasonal variation of different species reporting rate (occurrence). Species codes – as in Table 1.

it allows species and sampling units to be positioned in relation to one another on one or more co-ordinate axes, providing maximum information about their ecological similarities (Ludwig and Reynolds 1988). Some of the main advantages of CA can be summarized as follows: (1) it can cope with a large data-set; (2) „corresponding” sampling unit and species ordinations are simultaneously obtained, allowing an evaluation of their ecological inter-relationship in a single analysis; (3) species, samples and variables are simultaneously handled; (4) it is less scale dependent than

other ordination techniques; and (5) interpretation, by way of graphical displays, is relatively simple (Boshoff and Piper 1993).

Thereafter, a CA of the „species by months by grid cells” matrix was performed to gain an insight into the interaction between the spatial and temporal patterns of abundance of hirundines in KwaZulu-Natal (see Fig. 4). In order to visually assess whether the spatial and temporal patterns had been clearly captured by this ordination procedure, the sample points were re-plotted. This was performed after first di-

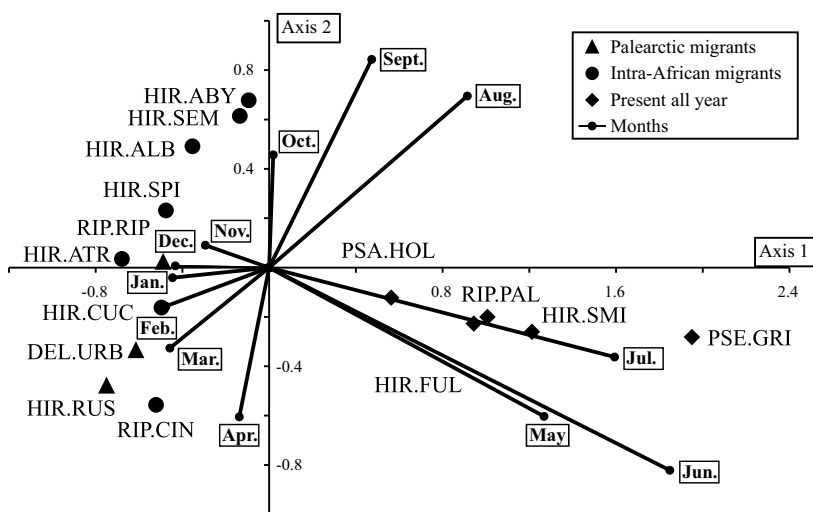


Fig. 3. Temporal separation of species according to a Correspondence Analysis. Species codes – as in Table 1.

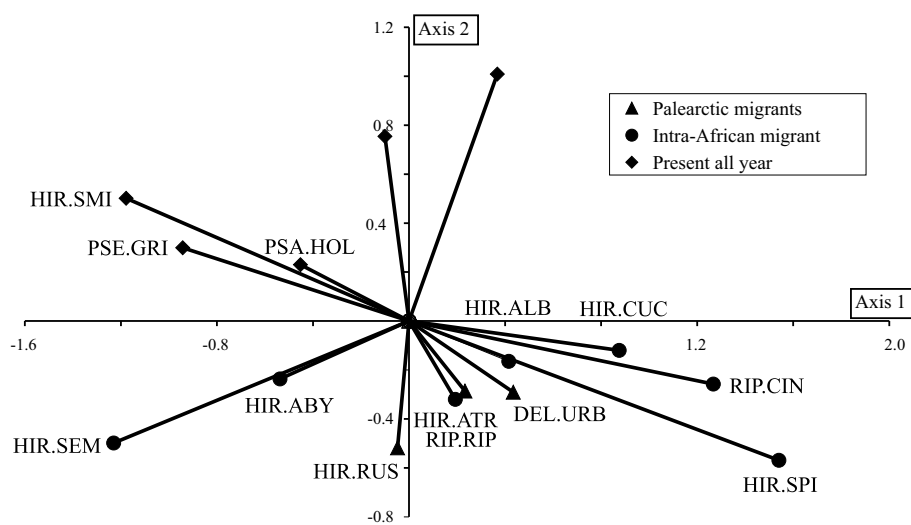


Fig. 4. Spatio-temporal separation of species according to a Correspondence Analysis. Species codes – as in Table 1.

viding the sample points into categories according to month (temporal) – see Figure 5, and altitude (spatial) – see Figure 6. These modified sample categories were presented as convex polygons incorporating at least 50% of the sample points for each category (month or altitude). These convex polygons were obtained through the process of convex peeling which was carried out on the computer programme GENSTAT (v. 3.22 for Windows).

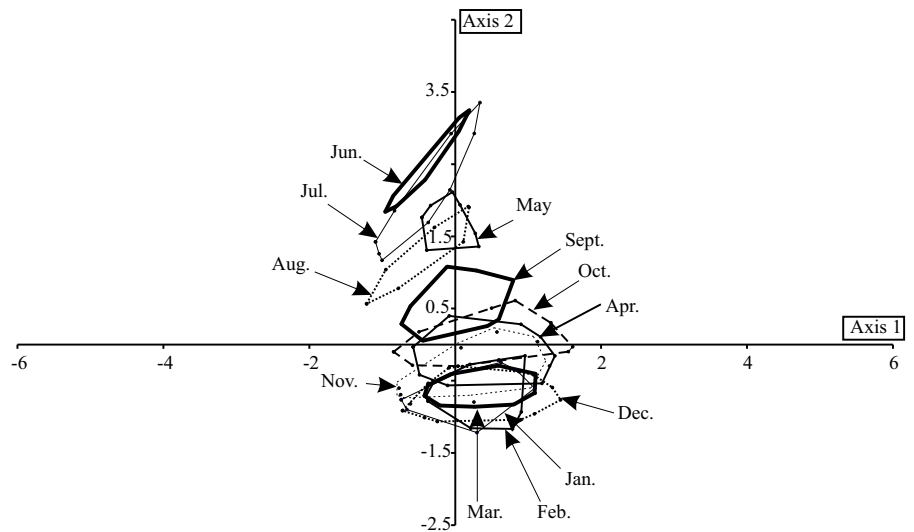


Fig. 5. Convex peeling – monthly data.

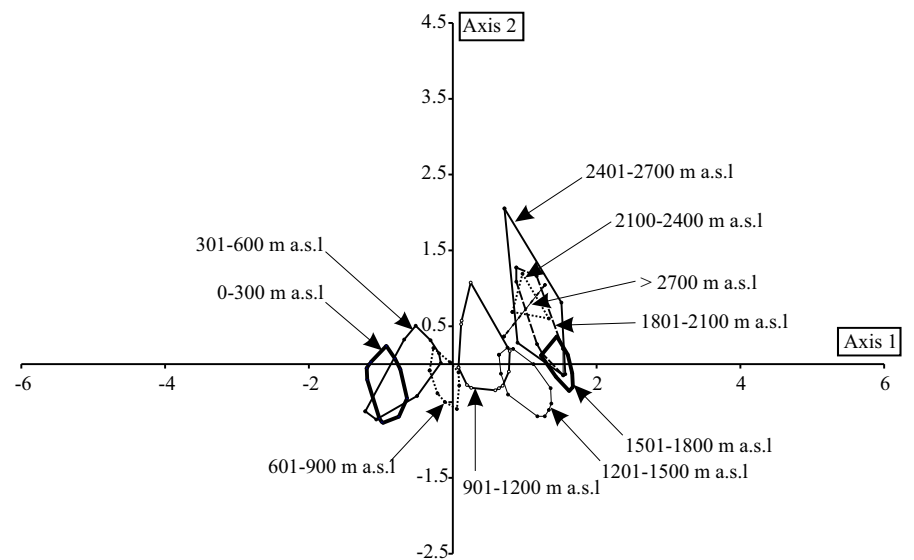


Fig. 6. Convex peeling – altitude (spatial) data.

RESULTS

Spatial distribution

The first two axes of the CA (Fig. 1) of the 15 hirundine species considered in this study (averaged over all grid cells) and each of the 170 (15'×15') grid-cells constituting the province (15×170 matrix) account for 48.2% of the species variation (Table 2). As an aid to interpretation, only the first two axes of the ordination diagram have been used. With the most substantial difference in eigenvalues occurring between axis two and axis three, it was felt that further axes would not yield additional explanations regarding the species data.

Table 2
Eigenvalues and cumulative percentage variance for spatial
and temporal patterns of abundance

Spatial

Axes	1	2	3	4	Total inertia
Eigenvalues	0.312	0.242	0.132	0.102	1.149
Cumulative percentage variance of species data	27.2	48.2	59.7	68.6	
Sum of all unconstrained eigenvalues					1.149

Temporal

Axes	1	2	3	4	Total inertia
Eigenvalues	0.182	0.035	0.005	0.001	0.225
Cumulative percentage variance of species data	80.8	96.4	98.5	99.1	
Sum of all unconstrained eigenvalues					0.225

Spatio-temporal

Axes	1	2	3	4	Total inertia
Eigenvalues	0.325	0.239	0.165	0.129	1.542
Cumulative percentage variance of species data	21.1	36.6	47.2	55.6	
Sum of all unconstrained eigenvalues					1.542

The first axis shows a marked spread of species across all sites. This suggests that most sites within KwaZulu-Natal are inhabited by at least one species during part of the year. The patterns evident in the CA ordination bi-plot correspond with published results (Cyrus and Robson 1980, Maclean 1985, Turner and Rose 1989, Harrison *et al.* 1997b), with species situated close together on the ordination bi-plot

having similar distribution patterns within the province. Species such as *P. griseopyga* and the Red-breasted Swallow (*H. semirufa*) exhibit a close spatial association (in the northern lowland regions), as do the Banded Martin (*Riparia cincta*) and South African Cliff Swallow (*H. spilodera*) at higher altitudes. *Hirundo rustica*, *H. albicularis* and *H. fuligula* appear to be closely spatially associated in that they are all widespread throughout KwaZulu-Natal. Similarly, *H. abyssinica* and the Black Saw-wing Swallow (*Psolidoprocne holomelas*) show very similar spatial habits (both occurring most frequently below the escarpment).

Temporal distribution

The first migrant species reaching KwaZulu-Natal in substantial numbers are the intra-African migrants such as *H. abyssinica* and *H. cucullata* (Fig. 2). They appear to arrive suddenly, as a massive wave, during the spring months (August-September). In contrast, their numbers slowly decline towards the end of summer (February-April) as they gradually leave the province to begin their vernal migrations.

The Palearctic migrants (e.g. *H. rustica*) arrive in KwaZulu-Natal up to a month later than the intra-African migrants (Fig. 2). The majority of these Palearctic migrants arrive in early summer (October-November), with their numbers gradually building up until the end of summer (January-February). The Palearctic migrants tend to remain in the province after the intra-African migrants have begun their northward migration. In contrast to their gradual arrival, they depart very abruptly with most of these Eurasian migrants leaving KwaZulu within two months (April-May).

Those hirundine species that are present year round, e.g. *P. griseopyga* and the Brown-throated Martin (*R. paludicola*), show a marked difference in temporal abundance to the migratory species (Fig. 2). Where the migrant species have their highest reporting rates during the summer months (November-February), the reporting rates of the resident species decline to a minimum during this period. They exhibit their highest reporting rate during the winter months (May-August).

These findings are confirmed by CA of the „species by months” matrix (15×12). The first two axes of CA of the temporal distribution of hirundines (Fig. 3) account for 96.4% of the species variation (Table 3), hence the ordination effectively describes the major temporal patterns in the distribution of the 15 hirundine species (averaged over all grid-cells). Axis one has a considerably higher eigenvalue (0.182) than axis two (0.035) (Table 2) and is thus responsible for capturing most of the species variation. The gradient is primarily one of seasonality, producing a clear separation of species along axis one. It is evident from the ordination graph that the hirundines of KwaZulu-Natal can be classed as either present all year round or migratory. The species that are present throughout the year, e.g. *P. griseopyga* and *H. smithii*, are most closely associated with the winter months (May to August) while the migrants, e.g. the Sand Martin (*R. riparia*) and *H. cucullata*, are associated with the summer months (November to March). The migrant species are considera-

bly separated along axis two which helps in explaining additional species variance. The migratory species are separated according to their peak time of arrival in KwaZulu-Natal. Species such as *H. abyssinica* and *H. semirufa* are strongly associated with the late spring months (September and October) and are the first migrants to arrive in KwaZulu-Natal. *H. atrocaerulea* and *H. spilodera* are more closely correlated with the early summer months (November), showing a peak in reporting rate soon after the arrival of the first migrants. Species such as *H. rustica* and *R. cincta*, which are some of the last migrant species reaching their peak reporting rate in KwaZulu-Natal, are more closely associated with the mid-summer months (December and January). These observations are confirmed by the individual time-series graphs presented in Figure 2.

The most rapid rates of species turnover occur between seasons, either when the migrants are arriving at or departing from KwaZulu-Natal. Within seasons, there is very little species turnover as the large scale spatio-temporal population changes brought on by migrations have generally ceased.

Spatio-temporal distribution

The CA of the „species by month by grid-cell matrix” ($15 \times 12 \times 170$) (Fig. 4) further corroborates the findings of the spatial (Fig. 1) and temporal CAs (Fig. 3). The initial CA ordination graph showed *P. griseopyga* to be an extreme outlier, resulting in clumping of the other species around the centroid. This made interpretation of the ordination output difficult. As an aid to interpretation, *P. griseopyga* was made passive in the ordination with the result that the total inertia dropped from 1.780 to 1.542. The species did, however, become separated along both axes, assisting in further analysis. Although the first two axes account for only 36.6% of the cumulative percentage species variance (Table 2), the substantial drop in eigenvalues between axis two and three (Table 2) suggests that the first two axes are adequate in explaining a large proportion of the species variance and that analysis of additional axes are unlikely to yield further information.

Axis one clearly depicts the spatial separation between species (Fig. 4), from lowland species on the left of the centroid (e.g. *H. semirufa* and *P. griseopyga*) to upland species on the right (*R. cincta* and *H. spilodera*). This gradient has been highlighted in Figure 6 which shows a clear separation of sample points along axis one according to altitudinal categories. Low altitude sample points (0-600 m a.s.l.) occur to the left of the centroid, the mid-altitude sample points (600-1200 m a.s.l.) are located around the centroid and the higher altitude (> 1200 m a.s.l.) sample points are found to the right of the centroid. Hirundine species left of the centroid are largely confined to the lowland regions of the province. Within the lowland species, there is further subdivision into two sub-groups. Species such as *H. semirufa* and *P. griseopyga* (extreme left of the centroid) are encountered most frequently in the northern lowland regions while *H. abyssinica* and *P. holomelas* (slightly left of centroid) inhabit the coastal lowland regions. Those species situated towards the centroid of the ordination graph are characteristically ubiquitous within KwaZulu-

Natal with species such as *H. rustica*, *R. paludicola*, *R. riparia* and *H. albigularis* occurring throughout the province. Those species encountered towards the right hand side of the ordination graph possess similar spatial habits in that they occupy the upland regions of the province. *H. cucullata*, *H. spilodera* and *R. cincta* are all species characteristic of high altitude and hilly terrain encountered towards the central and western regions of KwaZulu-Natal. These results are in accordance with the results of previous ordination findings (see Fig. 1) and current literature (Harrison *et al.* 1997b).

Axis two is almost as important as axis one in capturing species variation (see Table 2) and is effective in explaining the temporal separation of species (Fig. 4). Species are effectively separated along axis two according to their temporal patterns of abundance (*i.e.* migratory status). The convex polygons presented in Figure 5 support this finding, showing a marked separation between sample points according to months. Points below the centroid are dominated by the summer months and those above the centroid are largely defined by the winter months. All the species located above the centroid (*e.g.* *H. smithii*, *R. paludicola* and *H. fuligula*) are found in KwaZulu-Natal throughout the year. Those species situated below the centroid are migratory in nature. These migratory species are separated into either intra-African migrants (*e.g.* *H. semirufa*, *H. atrocaerulea* and *R. cincta*) or Palearctic migrants (*e.g.* *H. rustica*, *R. riparia* and *D. urbica*). These results confirm the findings of previous ordinations (see Fig. 3) and are in accordance with current literature (Harrison *et al.* 1997b).

DISCUSSION

According to Turner and Rose (1989), hirundines are very specific in their habitat requirements and one would thus expect them to show distinct patterns of spatial abundance within KwaZulu-Natal. This assumption is confirmed by the ordination graph of the „species by sites” matrix (Fig. 1) and the „species by sites by months” matrix (Fig. 4). All 15 hirundines considered in this study are clearly separated along axis one in each of the ordination graphs, indicating that each species possesses a unique spatial pattern of abundance, occurring only in those regions that cater for its specific feeding, nesting and habitat requirements.

It appears that hirundines in the province can be grouped into one of three distinct spatial categories, separated on the basis of altitude. There are the five lowland species (*H. semirufa*, *P. griseopyga*, *H. smithii*, *H. abyssinica* and *P. holomelas*), three upland species (*H. cucullata*, *R. cincta* and *H. spilodera*) with the rest of the hirundines being classed as ubiquitous (*R. paludicola*, *H. rustica*, *H. atrocaerulea*, *R. riparia*, *D. urbica*, *H. fuligula* and *H. albigularis*). Although *H. atrocaerulea* is classed as ubiquitous according to the ordination graphs, it is in fact a bird of higher altitudes. It appears to be ubiquitous on the ordination graph, because its limited range occurs towards the centre of the distributional ranges of the more widespread species.

„Altitude” is a useful separation factor (indirect variable), because it has a large influence on other variables such as rainfall and temperature, to which hirundines are particularly sensitive (Turner and Rose 1989), and thus the vegetation of an area. For example, the five „lowland” species are all associated with woodlands (e.g. *H. semirufa*) or forest edges (e.g. *P. holomelas*) of some kind, vegetation types which are most common in the lowland regions of KwaZulu-Natal. The woodlands are characteristic of the more mesic northern regions of the province and the forests are to be found in the valley and coastal regions, where the mean annual precipitation is higher. The three „upland” species are associated with more open vegetation in the form of grasslands (e.g. *H. spilodera*) or cultivated areas (e.g. *R. cincta*). These vegetation types and land-use policies are characteristic of the higher altitude regions extending from the Natal Midlands to the Drakensberg. These patterns of spatial distribution are supported by the distribution maps presented in Harrison *et al.* (1997b). The altitudinal gradient is further emphasised by the spatio-temporal ordination graph depicting the sample points as polygons, arranged according to altitudinal categories (Fig. 6). There is a clear separation of altitudinal categories along axis one, from low altitude sample points (left of the centroid) to high altitude sample points (right of the centroid), much the same pattern depicted by the ordination of the species data (Fig. 4).

In addition to this clear separation of species along axis one for both the „spatial” (Fig. 2) and „spatio-temporal” ordination graphs (Fig. 4), there appears to be further species separation along axis two of the spatial ordination graph (Fig. 2). In this ordination diagram, the species are further divided into two distinct groups along axis two. The first group is constituted by *H. rustica*, *H. atrocaerulea* and *P. griseopyga* (above the centroid) with the remaining species making up the second group (on or below the centroid). On a spatial scale, these three species appear to show no distinct association with *P. griseopyga* occupying the northern lowland regions of the province, *H. rustica* being entirely ubiquitous and *H. atrocaerulea* being extremely localised in distribution around its breeding sites (in the mountainous interior regions of KwaZulu-Natal). It was thus uncertain why this separation of species should occur. According to the eigenvalues presented in Table 2, axis two is relatively important in explaining additional species variation (*i.e.* not captured by axis one), unfortunately no discernible gradients could be identified.

It is interesting to note, however, that of the three species forming a distinct „spatial” group above the centroid (Fig. 1), *P. griseopyga* (Earlé 1997d) and *H. atrocaerulea* (Allan and Earlé 1997) are both highly dependent on the availability of natural nesting sites for successful breeding and have not benefited from the construction of artificial impoundments. Of all the other breeding hirundine species found in KwaZulu-Natal (intra-African migrants and species present all year round), only *R. cincta* has not benefited (in terms of range expansion and breeding success as a result of the increased availability of artificial nesting sites) from the erection of artificial impoundments and the construction of man-made structures (Earlé 1997d, Allan and Earlé 1997, Earlé and Herremans 1997).

According to Earlé (1997a), *H. albigularis* and *H. smithii* occupy similar niches but due to interspecific competition are not often found in close proximity to one another. This observation is supported by the ordination graphs (Fig. 1 and 4), where the two species show a marked separation in spatial distribution (*H. smithii* favouring the lowlands and *H. albigularis* frequenting the higher altitude regions of KwaZulu-Natal). Similarly, *H. abyssinica* and *H. cucullata*, although alike in nature and survival requirements (Earlé 1997c), show a distinct altitudinal separation (Fig. 1 and 4) as a consequence of interspecific competition.

There also appears to be a relatively close spatial association of hirundines according to migratory status (Fig. 1). The Palearctic migrants (e.g. *R. riparia*) are predominantly ubiquitous in distribution. An explanation for this pattern could lie with Moreau's (1972) predictions of the number of Eurasian migrants reaching sub-Saharan Africa. KwaZulu-Natal provides an ideal locality for the survival of overwintering hirundines (high rainfall, low altitude, warm conditions) and with many millions of Palearctic migrants flocking to South Africa's eastern seaboard between November and February, the most favourable habitats will quickly become occupied, forcing the later arrivals to inhabit other, less favourable, regions. Thus, within a month or two after the onset of summer, these Palearctic migrants can be found almost anywhere in the province, making use of the favourable conditions. The intra-African migrants (e.g. *H. cucullata* and *H. spilodera*) are predominantly upland birds in nature. Only two of the intra-African migrants (*H. semirufa* and *H. abyssinica*) are associated with the lowland regions of the province (Fig. 1). This could be attributed to intra-specific competition with *H. cucullata* (Earlé 1997b), which occupies the upland regions of KwaZulu-Natal and forces the other two species to inhabit the lowland regions, where competition for nest sites is less intense. The hirundines that are present in the province all year round are predominantly lowland species (e.g. *H. smithii* and *P. holomelas*).

In addition to their marked spatial patterns of abundance, hirundines show definite patterns of temporal separation. The annual migration of many millions of Palearctic migrants (e.g. *H. rustica*) and intra-African migrants (e.g. *H. semirufa*) in addition to the local movement of resident species (e.g. *H. fuligula* moving to lower altitudes –Macleane 1985) has ensured that many unique temporal patterns of abundance have come to exist among the *Hirundinidae*. The ordination of the „species by months” matrix showed this relationship clearly (Fig. 3). There is a distinct separation of species along axis one according to their migratory status, with the Palearctic and intra-African migrants strongly correlated with the summer months (November-February) to the left of the centroid and the species that are present all year round being closely correlated with the winter months (May-August). This axis captures over 80% of the species variance and thus effectively describes the temporal patterns of abundance that exist between them.

The migrant species are further separated along axis two (Fig. 3) according to their time and nature of arrival in KwaZulu-Natal. The intra-African migrants are the first birds to arrive in relatively substantial numbers with species such as

H. abyssinica and *H. albigularis* arriving as a massive „wave” during late Spring (September-October) (see Figure 2 for the time series graphs). With the onset of summer just a few weeks later, the next intra-African migrants (e.g. *H. spilodera* and *H. atrocaerulea*) begin to arrive (November-December) and reach their migratory peaks (in terms of reporting rates) in KwaZulu-Natal. With the arrival of these later intra-African migrants at the beginning of summer, there come the first Palearctic migrants in the form of *R. riparia*. This period marks the beginning of the gradual occurring of other migrants such as *H. cucullata* and *R. cincta* (intra-African) or *D. urbica* and *H. rustica* (Palearctic), which reach their peak reporting rates during late summer (January-February) (see Fig. 2).

The nature of arrival appears to be markedly different between the two migrant types. The intra-African migrants tend to arrive earlier than the Palearctic migrants as a sudden, massive wave of birds that swamp the province. They breed quickly during summer and their number slowly dissipate with the arrival of autumn (Fig. 2). This may be an advantage to these migrants because they are able to breed quickly and make use of the available resources before competition is escalated dramatically by the arrival of Palearctic migrants. The Palearctic migrants, on the other hand, tend to arrive later and much more gradually than the intra-African migrants and depart later but much more suddenly (Fig. 2). Bykhovski (1973) noted that this pattern is not restricted to hirundines only and that in general, southerly birds (e.g. intra-African migrants already present in Africa) arrive at their African migratory destinations far sooner than birds from more northerly regions (e.g. Palearctic migrants from Europe and Asia).

The resident species (e.g. *H. smithii* and *P. griseopyga*) all exhibit very similar patterns of temporal abundance with their numbers becoming noticeably depressed during the summer months. Although there is little intrinsic evidence to support theories describing such patterns, Jones (1996) suggested that the huge numbers of Palearctic visitors arriving south of the Sahara might be expected to have a significant effect on the food resources and habitat distributions of local species. Curry-Lindahl (1981) speculated that the very similar feeding habits of swallows may lead to species, such as *H. rustica*, (which are present in vastly superior numbers to local species and far more wide-spread) outcompeting afrotropical swallows during periods of food shortage (e.g. in cold spells). As many of the local hirundine species are trying to breed during the summer months this may hold the key to their depressed reporting rates with the arrival of the migrants. O'Connor (1990) suggested that birds nesting in crowded habitats may do better to move into intrinsically poorer but less crowded alternatives. With the pronounced competition for food brought on by the influx of migrants (Curry-Lindahl 1981), this may very well apply to the KwaZulu-Natal scenario, accounting for the depressed reporting rate of the local species during the highly competitive summer months.

For more detailed information, on where the hirundines enter the province, KwaZulu-Natal was divided according to altitude (low vs high), degrees latitude (north, central and south) and finally altitude and latitude combined (giving a high

and low altitude zone for the north, central and south regions) and the reporting rate for each region plotted. These time series graphs did not yield any consistent patterns with regards to the source of entry of hirundines into KwaZulu-Natal. This could be attributed to the large time intervals, over which the data was presented (*i.e.* months). If the data could be presented on a weekly or daily basis, noticeable temporal trends may have been uncovered.

These patterns of temporal abundance are further emphasised by the spatio-temporal ordination graph (Fig. 4), with temporal separation of species occurring along axis two of the ordination diagram. Here, the migrant species are situated below the centroid and the species that are present all year – above it. Similarly to the temporal ordination graph presented in Figure 3, species exhibiting similar times of arrival in KwaZulu-Natal are situated close together on the spatio-temporal ordination graph (Fig. 4). This temporal gradient is highlighted by Figure 5, where the sample points have been plotted as monthly polygons. There is a clear separation along axis two between winter months (above the centroid) and summer months (below the centroid), corresponding with the species ordination graph (Fig. 4).

CONCLUSIONS

It is evident that the hirundines of KwaZulu-Natal exhibit an array of spatial and temporal habits. It is apparent from the spatio-temporal ordination graph (Fig. 4) that spatial separation is the most important aspect in separating the different hirundine species from one another. This gradient is represented by axis one which captures most of the species variation (Table 2). The 15 hirundine species considered in this study can be divided into three main groups according to their altitudinal patterns of abundance, namely lowland species (*e.g.* *H. semirufa* and *P. griseopyga*), upland species (*e.g.* *H. cucullata* and *R. cincta*) and ubiquitous species (*e.g.* *H. rustica* and *R. riparia*).

However, the high eigenvalue of axis two suggests that temporal separation of species is almost as important as spatial separation in identifying unique patterns of abundance amongst the 15 hirundine species considered in this study (Fig. 4). In addition to their spatial separation, the hirundines of KwaZulu-Natal can further be classified according to their migratory status, namely Palearctic migrants (*e.g.* *H. rustica* and *D. urbica*), intra-African migrants (*e.g.* *H. abyssinica* and *H. atrocaerulea*) and those species that are present all year round (*e.g.* *P. holomelas* and *R. paludicola*).

The different patterns of abundance of the hirundines of KwaZulu-Natal can thus be classed according to nine different spatio-temporal combinations. Of these possible combinations, six are exhibited by the species analysed in this study, indicating that there are unique patterns of spatial and temporal abundance adopted by the hirundines of KwaZulu-Natal. The reasons for such marked spatio-temporal separation between species will be addressed in a future study.

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