# SEASONAL MIGRATION OF TERRESTRIAL BIRDS ALONG THE SOUTHERN AND EASTERN COASTS OF SOUTHERN AFRICA

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## SUMMARY

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Several species of terrestrial birds migrate in summer southwestwards along the coastal zone of southeastern Africa to breed, followed by a reverse migration to wintering grounds in Africa. These migrations were investigated using the Southern African Bird Atlas Project data base and the reporting rate as an index of relative abundance. Models of seasonality in the reporting rate for 18 bird species in each of six coastal areas from the southwestern Cape to northern Natal were fitted using Fourier series and generalized linear models. Altitudinal movements of each species were investigated in the two northernmost zones (Natal). New migration patterns are suggested for the Mangrove Kingfisher *Halcyon senegaloides* and the currently accepted migration movements of the Natal Robin *Cossypha natalensis*, Knysna Warbler *Bradyterus sylvaticus* and Dusky Flycatcher *Muscicapa adusta* are rejected. Known migrations are confirmed in greater detail for Pygmy Kingfisher *Ispidina picta*, Black Sawwing Swallow *Psalidoprocne holomelas*, Starred Robin *Pogoncichla stellata* and Paradise Flycatcher *Terpsiphone viridis*. Several factors other than migration may explain an increase in winter reporting rates for some resident forest species. The migration of the Spotted Thrush *Zoothera guttata* in southern Africa is apparently a truncated form of the migration existing in other forest bird species.

## INTRODUCTION

Bird migrations between Eurasia and Africa are well known (e.g. Morel & Morel 1992; Pearson & Lack 1992; Underhill *et al.* 1992), compared to the attention given to seasonal intra-African migrations. Oatley (1966) stated that altitudinal movements are widespread in bird species in the eastern half of southern Africa, yet few subsequent studies have investigated such movements (Oatley 1982; Cyrus 1989; Harrison & Navarro in press; Maclean & Johnson 1994).

This investigation of seasonal migrations of birds along the southern and eastern littoral of southern Africa was stimulated by the apparently unique migration of the South African population of the Spotted Thrush *Zoothera guttata*. At the outset of this investigation, it seemed to be the only southern African bird species in which the population breeds in the Transkei and winters in Natal (Clancey 1964; Maclean 1993). We used the data base of the Southern African Bird Atlas Project (SABAP) to investigate seasonal migrations of several terrestrial, forest or woodland bird species along the southern and southeastern coasts of Africa to gain insight into the apparently unique migration of the Spotted Thrush.

## METHODS

We used the SABAP data base to calculate the reporting rates of selected bird species in the coastal zone of southern and southeastern Africa. SABAP is described by Harrison (1987, 1992) and records are based on a monthly reporting of the presence of bird species in quarter degree grid squares (QGDS). The reporting rate is the fraction of checklists which include a given species and is expressed as a proportion or percentage of the total number of checklists for the given QDGS, or any combination of QDGSs. The reporting rate is used as a simple index of relative abundance (Harrison & Navarro in press). A high value represents relatively high abundance/density and a low value represents relatively low abundance/density. Variations in reporting rate are meaningful only for intraspecific comparisons, and not across species because of differences in conspicuousness and identifiability (Underhill *et al.* 1992). The modelling of the reporting rate parameter using generalized linear modelling and Fourier transformation is described by Underhill *et al.* (1992) and Harrison & Navarro (in press).

The study area is the eastern and southern coastal region of southern Africa from Cape Town in the southwest to the border of Natal and Mozambique in the northeast. This area was divided into six regions of approximately equal length of coastline (Fig. 1). Within the three Cape zones (southwestern Cape, southern Cape and eastern Cape), a QDGS was included if it was situated on the seaward side of the Cape Fold mountains which run more or less parallel to the coast as far as the Transkei. On the landward side of these mountains, arid conditions exist which exclude the species under investigation in this paper. For Transkei, southern Natal and northern Natal, a QDGS was included if the dominant altitude was less than 1500m, because most coastal species either do not occur, or are far less abundant, above this altitude.

To investigate whether the occurrence in winter of the selected species at the coast in Natal may be attributed to altitudinal rather than coastal migration, Natal was divided into altitudinal ranges of 0-300m, 300-900m and 900-1 500m a.s.l. A QDGS was classified according to one of these three dominant altitudinal classes using 1:250 000 topographical maps (Fig. 2).

The migration patterns suggested by the reporting rates were then compared with the literature, including published bird atlases for the southwestern Cape (Hockey *et al.* 1989) and Natal (Cyrus & Robson 1980).

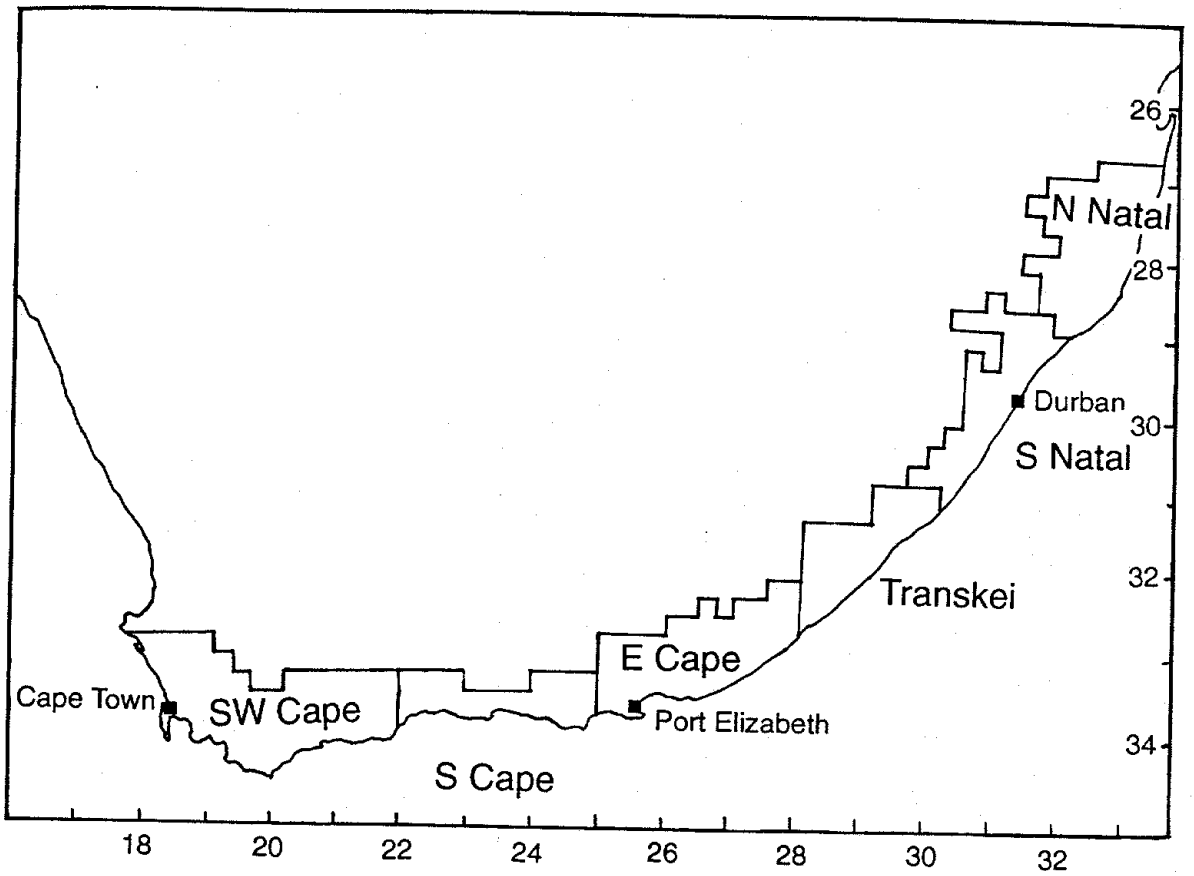


FIGURE 1

The six coastal zones designated for the investigation of coastal migration.

*Selection of bird species*

In southern Africa, many breeding bird species of the forests or dense woodlands have a narrow distributional range which begins on the coast somewhere along the western, southern or eastern Cape, and which then broadens inland along the Transkei and Natal coasts northwards into the eastern Transvaal and Mozambique (Maclean 1993). Seasonal coastal movements have been reported in several species that show this distribution (Maclean 1993). Where the range of the these species broadens inland from Natal northwards, seasonal altitudinal movements have also been reported (Clancey 1964, 1971). We restricted our analysis to forest species with the distribution described above, including migratory and non-migratory species. We also included three widely distributed, abundant and resident species of more open habitats to act as controls for the analysis.

## RESULTS

*The data base of the Southern African Bird Atlas*

A total of 34 577 cards formed the data base for the coastal analysis. The number of field cards in each month in each zone is given in Table 1. The Transkei zone had fewer cards than any other region. The number of cards per month was approximately the same within each zone. The number of cards used in the coastal migration analysis for each species is given in Table 2. The analyses of three species are based on less than 400 records (less than 1,2% of all cards) for three species (Mangrove Kingfisher *Halcyon senegaloides* (89 records), Spotted Thrush *Zoothera guttata* (208 records) and Knysna Warbler *Bradypterus sylvaticus* (200 records)).

A total of 12 058 cards were used for the altitudinal migration analysis (Table 3). The number of cards per month was approximately the same within each altitude class (Table 2). Two species (Knysna Warbler and Mangrove Kingfisher) were recorded only in the lowest altitude class whilst the three records of the Spotted Thrush above 900m were regarded as misidentifications of the Groundscraper Thrush *Turdus litsitsirupa*.

*Patterns and species accounts*

The patterns of seasonal variation in reporting rates are divided into five different types (Table 4).

Group 1. No changes in seasonality

The three widespread species (Cape Turtle Dove *Streptopelia capicola*, Fiscal Shrike *Lanius collaris* and House Sparrow *Passer domesticus*),

TABLE 1
NUMBERS OF RECORD CARDS PER MONTH FOR EACH COASTAL ZONE. COASTAL ZONE NUMBERS: 1 = SOUTHWESTERN CAPE, 2 = SOUTHERN CAPE, 3 = EASTERN CAPE, 4 = TRANSKEI, 5 = SOUTHERN NATAL AND 6 = NORTHERN NATAL

| Month | Coastal Zone No. | | | | | | Total |
|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | |
| January | 1071 | 375 | 551 | 118 | 465 | 231 | 2811 |
| February | 983 | 302 | 515 | 113 | 394 | 216 | 2523 |
| March | 1106 | 333 | 489 | 79 | 455 | 230 | 2692 |
| April | 1171 | 348 | 527 | 92 | 493 | 252 | 2883 |
| May | 1140 | 348 | 639 | 105 | 477 | 279 | 2988 |
| June | 1023 | 318 | 554 | 88 | 467 | 254 | 2704 |
| July | 1207 | 339 | 610 | 100 | 520 | 292 | 3068 |
| August | 1122 | 306 | 570 | 103 | 515 | 257 | 2873 |
| September | 1335 | 369 | 547 | 104 | 474 | 275 | 3104 |
| October | 1303 | 349 | 679 | 108 | 457 | 282 | 3178 |
| November | 1079 | 366 | 666 | 98 | 442 | 232 | 2883 |
| December | 1087 | 361 | 538 | 131 | 448 | 305 | 2870 |
| Total | 13627 | 4114 | 6885 | 1239 | 5607 | 3105 | 34577 |

which are regarded as sedentary, showed no marked variations in reporting rate (e.g. Fiscal Shrike, Fig. 3). However the small seasonal variations in reporting rates may represent real demographic changes (eg recruitment of juveniles) or changes in conspicuousness (eg winter flocking).

Migratory movements have not been described for these three species in South Africa (Clancey 1964, 1971; Hockey *et al.* 1989; Quickelberge 1989), although Irwin (1981) reported local movements in the Cape Turtle Dove in Zimbabwe related to water supply, and Maclean (1993) notes that there is an indication of some local movements in the Fiscal Shrike in the Transvaal.

Group 2. Coastal migration

The patterns of seasonality of five species (Pygmy Kingfisher *Ispidina picta*, Mangrove Kingfisher, Black Sawwing Swallow *Psalidoprocne holomelas*, Spotted Thrush and Paradise Flycatcher *Terpsiphone viridis*) are characterized by a summer or winter peak in reporting rate in one or more zones, for which the most parsimonious explanation is migration (e.g. Fig. 4).

The Pygmy Kingfisher is a summer migrant to South Africa, occurring as far south as the eastern Cape zone, arriving mainly in October and with most birds departing by April. There are records throughout the year, although some of these may be the result of confusion with the Malachite Kingfisher *Alcedo cristata*. The species was regarded as a coastal migrant in the Transkei (Quickelberge 1989) and Natal (Cyrus & Robson 1980). Clancey (1964) stated the species arrived in Natal to breed in early October and departed in March and April, with a few laggards, mainly young birds, still present in mid-May (Clancey 1964). In Mozambique, Clancey (1971) described the species as a summer breeding resident between the months of October and May. He also found birds present in the cool months, especially north of the Save River, and felt that these birds could have been wintering or resident birds. Clancey (1972) suggested that the northern limits of this southern population is at least as far as 1°N in western Uganda and adjacent Zaire. The present analysis shows a rapid, synchronous arrival in all

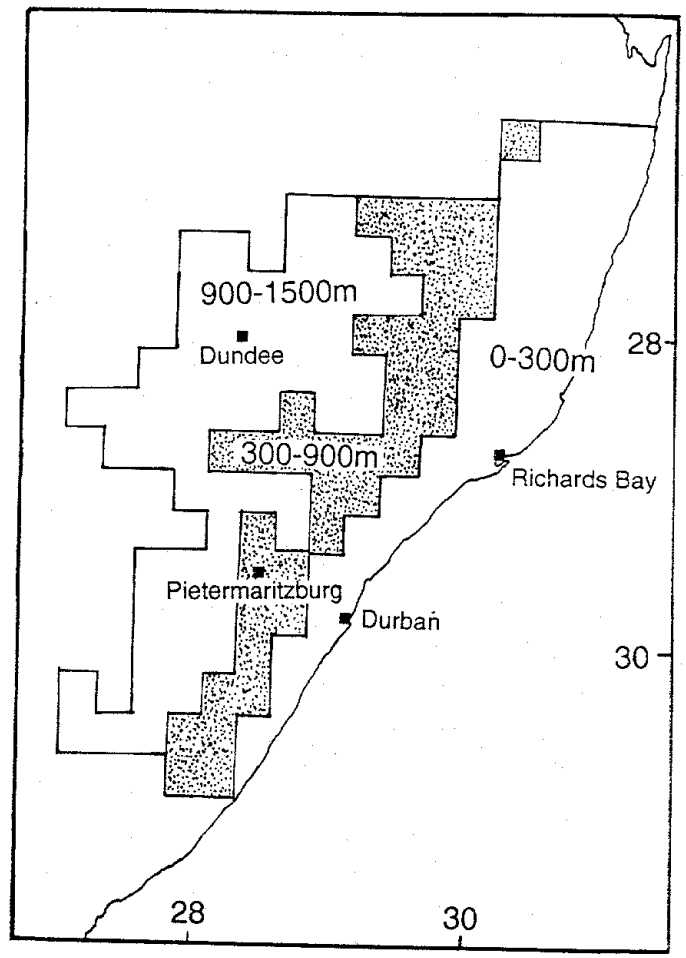


FIGURE 2

The three altitudinal classes in the southern and northern Natal zones used to investigate altitudinal migration.

TABLE 2
TOTAL NUMBERS OF RECORDS FOR EACH SPECIES GIVEN AS THE PERCENTAGE OF ALL CARDS USED IN THE COASTAL ANALYSIS AND AS THE PERCENTAGE OF THE CARDS IN THE ZONES IN WHICH THAT SPECIES OCCURS

| Species | Coastal | | Altitudinal | |
|---|---|---|---|---|
| | n | % Total | n | % Total |
| Buffspotted Flufftail | 476 | 1,4 | 466 | 3,9 |
| Cape Turtle Dove | 24 198 | 70,0 | 6 598 | 54,7 |
| Narina Trogon | 1 476 | 4,3 | 1 068 | 8,9 |
| Pygmy Kingfisher | 800 | 2,3 | 742 | 6,2 |
| Mangrove Kingfisher | 89 | 0,3 | — | — |
| Crowned Hornbill | 4 548 | 13,2 | 2 212 | 18,3 |
| Black Sawwing Swallow | 6 051 | 17,5 | 2 992 | 24,8 |
| Grey Cuckooshrike | 985 | 2,9 | 505 | 4,2 |
| Spotted Thrush | 204 | 0,6 | 191 | 1,6 |
| Natal Robin | 4 258 | 12,3 | 4 002 | 33,2 |
| Starred Robin | 418 | 1,2 | 317 | 2,6 |
| Knysna Warbler | 200 | 0,6 | — | — |
| Dusky Flycatcher | 7 369 | 21,3 | 2 897 | 24,0 |
| Bluegrey Flycatcher | 1 085 | 3,1 | 1 028 | 8,5 |
| Bluemantled Flycatcher | 1 360 | 3,9 | 638 | 5,3 |
| Paradise Flycatcher | 8 109 | 23,5 | 4 732 | 39,2 |
| Fiscal Shrike | 26 821 | 77,6 | 5 957 | 49,4 |
| House Sparrow | 15 928 | 46,1 | 8 701 | 72,2 |

parts of its South African range in October, and a slow unsynchronized departure between February to May. Small numbers of birds overwinter, mainly in Natal.

The Mangrove Kingfisher shows a summer peak in the Transkei zone and a winter peak in the northern Natal zone, with a slight winter increase in the southern Natal zone. This pattern would be consistent with migration from summer breeding grounds in the Transkei to coastal wintering grounds in northern Natal, and possibly further north. The breeding status and migratory pattern of this species in South Africa is poorly known. It is described as being present on the Natal and Mozambique coasts in winter, moving inland to breed (Clancey 1964, 1971; Cyrus & Robson 1980; Maclean 1993). However, there appear to be no confirmed breeding records for Natal (e.g. Dean 1971). Inland records need to be regarded with caution. Tarboton *et al.* (1987) question all six records of this species from the Kruger National Park because of the possibility of misidentification with immature Woodland Kingfishers *Halcyon senegalensis*. Quickelberge (1989) described the species as a sparse breeding resident in the Transkei (see Cooper & Swart 1992), breeding on the coast and inland, with summer and winter records. However, this analysis showed few winter records, despite the existence of similar numbers of field cards for the Transkei in winter. Thus this analysis, although based on only 89 positive records, suggests winter migration of Mangrove Kingfishers from their breeding area in the Transkei to northern Natal, moving through southern Natal, presumably because of the lack of mangroves which is their preferred winter habitat. This is the first time that this migration has been proposed for the South African population.

The Black Sawwing Swallow showed a clear pattern of migration, with birds arriving from the southwestern Cape zone to the Transkei zone in August, and with departures beginning in April. Both arrivals and departures are synchronized in the southern part of the range. However, the pattern differs in the southern and northern Natal zones, where birds winter in large numbers. In the two Natal zones, the species also shows an altitudinal shift in distribution, with few birds occurring above 900m between May and August. It is not known whether birds that occur at higher altitudes in Natal move eastwards to the coast or northwards to Mozambique. This species has pre-

TABLE 3
NUMBERS OF RECORD CARDS PER MONTH FOR THREE ALTITUDINAL CLASSES (0-300m, 300-900m and 900-1500m) IN SOUTHERN AND NORTHERN NATAL

| Month | Altitude class (m a.s.l.) | | | Total |
|---|---|---|---|---|
| | 0-300 | 300-900 | 900-1200 | |
| January | 513 | 177 | 289 | 979 |
| February | 459 | 150 | 255 | 864 |
| March | 508 | 177 | 279 | 964 |
| April | 555 | 188 | 283 | 1 026 |
| May | 575 | 180 | 276 | 1 031 |
| June | 567 | 153 | 283 | 1 003 |
| July | 620 | 191 | 276 | 1 087 |
| August | 583 | 189 | 260 | 1 032 |
| September | 579 | 170 | 266 | 1 015 |
| October | 556 | 183 | 304 | 1 043 |
| November | 491 | 182 | 262 | 935 |
| December | 548 | 205 | 326 | 1 079 |
| Total | 6 554 | 2 145 | 3 359 | 12 058 |

TABLE 4
THE FIVE PATTERNS OF SEASONALITY IN REPORTING RATES OF 18 BIRD SPECIES IN THIS ANALYSIS

| Group | Type of pattern | No. of species | Species names |
|---|---|---|---|
| 1 | None | 3 | Cape Turtle Dove<br>Fiscal Shrike<br>House Sparrow |
| 2 | Coastal migration | 5 | Pygmy Kingfisher<br>Mangrove Kingfisher<br>Black Sawwing Swallow<br>Spotted Thrush<br>Paradise Flycatcher |
| 3 | Peak summer abundance (possible coastal migration) | 3 | Buffspotted Flufftail<br>Narina Trogon<br>Knysna Warbler |
| 4 | Peak winter abundance | 5 | Crowned Hornbill<br>Grey Cuckooshrike<br>Natal Robin<br>Bluegrey Flycatcher<br>Bluemantled Flycatcher |
| 5 | Altitudinal migration | 2 | Dusky Flycatcher<br>Starred Robin |

viously been regarded as resident in Natal (Clancey 1964), largely resident in the Transkei (Quickelberge 1989), migratory in most of South Africa (Maclean 1993) and as both summer migrant and resident in the Southwestern Cape (Hockey *et al.* 1989). In southern Mozambique, Clancey (1971) described the species as apparently resident, but with an influx of birds from further south in winter, and also said that it occurred north of the Save River only as a non-breeding visitor. This analysis demonstrates the importance of Natal as a wintering ground, and that this coastal migrant (in the southern part of its range) has the most synchronized arrival and departure of the migrants in this analysis.

The Spotted Thrush did not show any marked

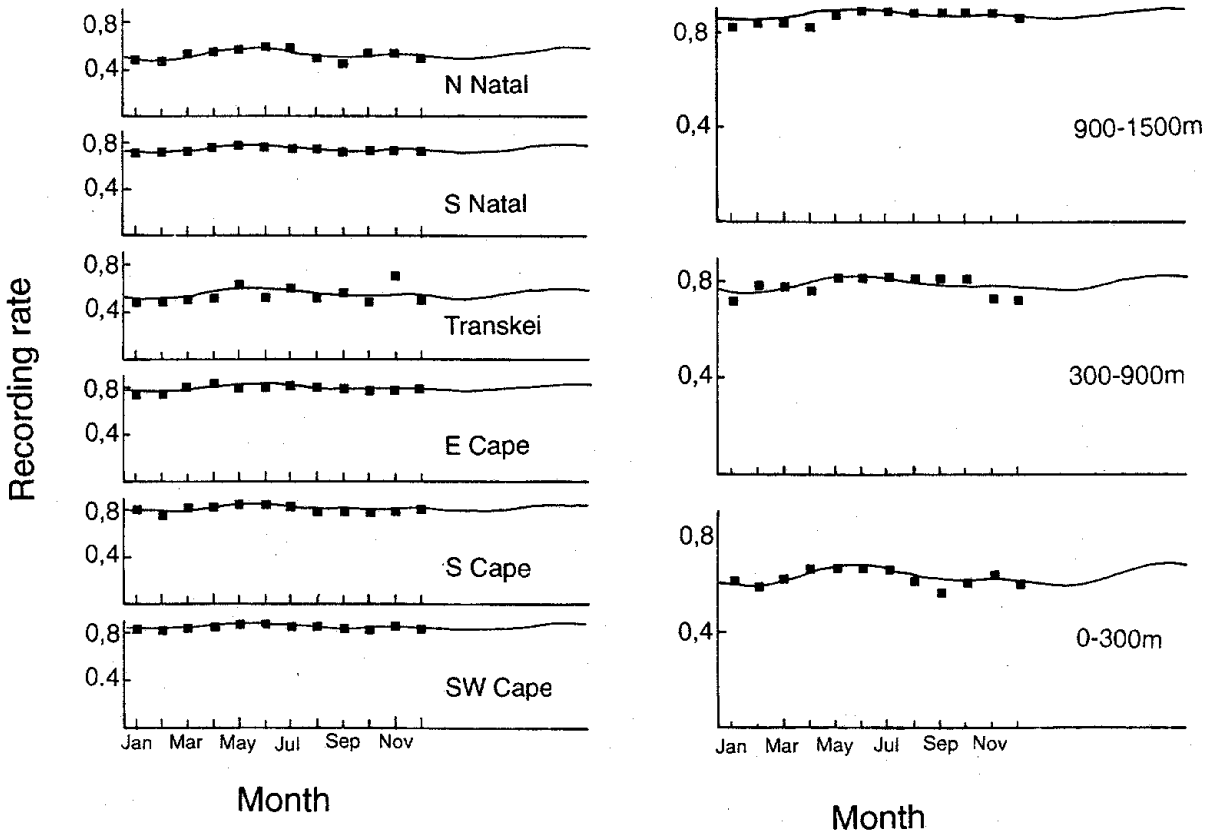


FIGURE 3

The reporting rates for the Fiscal Shrike *Lanius collaris* in coastal zones and altitudinal classes as an example of a resident species.

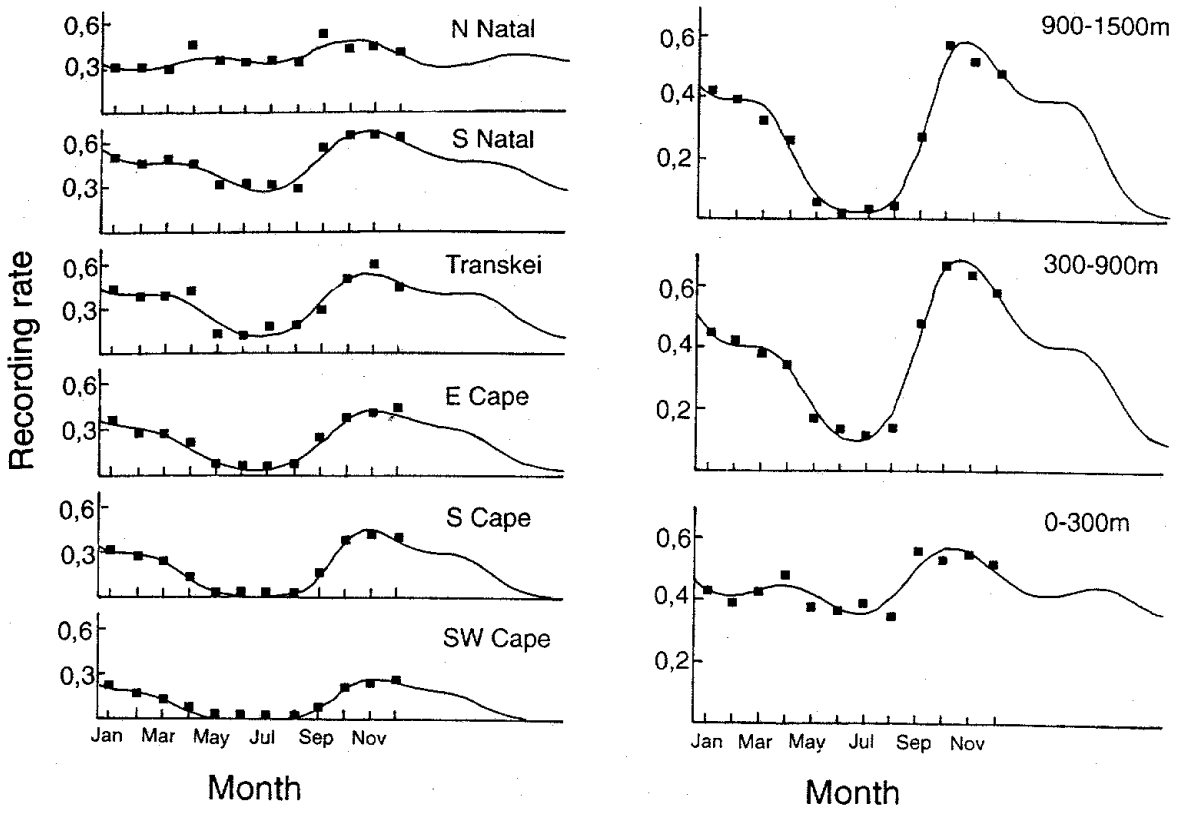


FIGURE 4

The reporting rates for the Paradise Flycatcher *Terpsiphone viridis* in coastal zones and altitudinal classes.

peaks in reporting rates throughout the year in the northern Natal and Transkei zones, but a very distinct winter peak in the southern Natal zone, strongly suggesting a winter migration into the southern Natal zone. However, there is no correspondingly clear pattern of movement away from the major breeding area in the Transkei, or the smaller breeding area in the northern Natal zone. This may be explained by the fact that this species is particularly elusive when breeding and may therefore be under-reported in summer. This species has been regarded as a winter migrant to Natal from the Transkei (Clancey 1964). Quickelberge (1989) regarded the species as a breeding summer visitor to the Transkei, although he reported several winter records. The movements of the birds breeding in Zululand are not known, and it has been suggested that these populations may migrate to the Zululand coast in winter (Ginn *et al.* 1989). This analysis is based on only 200 records. The migration of this species is discussed further later.

The Paradise Flycatcher showed a clear migratory pattern, with distinct seasonal changes in reporting rates from the southwestern Cape to southern Natal zones (Fig. 4). Arrivals were synchronized in September. Departures are less synchronized than arrivals, and occur earliest in the southwestern Cape zone, taking place later as one progresses towards the northeast. The proportion of wintering birds increases from the eastern Cape zone to the northern Natal zone. In the two Natal zones, reporting rates decrease dramatically between May and August above 300m a.s.l. In the northern Natal zone, reporting rates show little seasonal difference. The Paradise Flycatcher was previously regarded as migratory in the southwestern Cape (Hockey *et al.* 1989), Transkei (Quickelberge 1989), and was described as migratory with overwintering in Natal (Clancey 1964; Cyrus & Robson 1980). In southern Mozambique, Clancey (1971) regarded the species as migratory with the breeding race *plumbeiceps* migrating north in winter and being replaced by the southerly race *granti* between April and October. Maclean (1993) reported the recovery of a bird ringed in Pietermaritzburg in Mozambique. This analysis confirms the previously described migratory patterns and clearly demonstrates the importance of Natal as a wintering ground.

Group 3. Summer or spring peak in reporting rates (apparent coastal migration)

This group of three species (Buffspotted Flufftail *Sarothrura elegans* (Fig. 5), Narina Trogon *Apaloderma narina* and Knysna Warbler) show a summer or spring peak in reporting rate. They are separated from the previous group because all

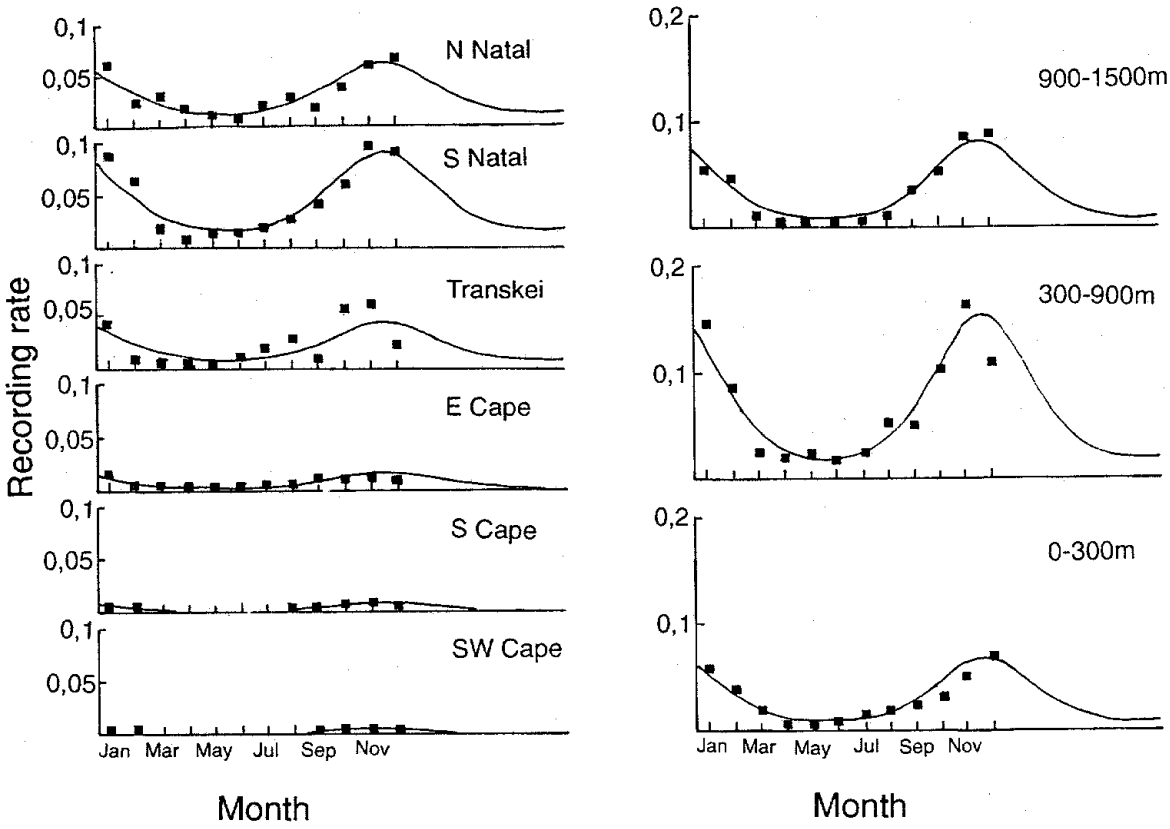


FIGURE 5

The reporting rates for the Buffspotted Flufftail *Sarothrura elegans* in coastal zones and altitudinal classes.

three species are usually detected by vocalisations, and it can be argued that the seasonality of reporting rate reflects nothing more than seasonal changes in vocalisations, because there are a few winter records for each species in most zones in which they occur. However, reporting rates cannot be used to distinguish between the alternatives that these species are either seasonally vocal or undergo seasonal migrations similar to those shown by the previous group.

Both the Buffspotted Flufftail and Narina Trogon show increasing reporting rates and proportions of wintering birds in the north (Transkei and Natal zones, similar to the patterns shown by three migrants Pygmy Kingfisher, Paradise Flycatcher and Black Sawwing Swallow. The Buffspotted Flufftail was not previously described as migratory (Clancey 1964; Maclean 1993), although unusual records have been recorded (Irwin 1981). Movements of this species, based on sight and specimen records, marked individuals, have been studied independently by Taylor (*in litt.*) in Natal. He established that the species is absent in winter from areas above 1 400m a.s.l., but is present in winter below 1 250m a.s.l., except in the winter of 1992 when severe drought conditions prevailed. He concluded that birds (usually adults) are normally present all year in lowland areas if food and cover were available. Taylor (1994) suggests that there may be a movement of birds, mainly immatures, along the coast in May, and another (presumably return movement) in September to October. It is concluded that there is altitudinal movement of this species, and possibly movement along the coast.

The Narina Trogon has previously been regarded as a partial migrant (Clancey 1964; Quickelberge 1989). Maclean (1993) described the species as largely resident. Clancey (1971) stated that resident populations of this species in southern Mozambique are augmented by the immigration of birds from further south. The pattern of seasonality shown by this analysis is consistent with coastal and altitudinal migration, but does not eliminate the possibility that seasonality in vocalisations is responsible for much of the seasonality in reporting rates.

The pattern for the Knysna Warbler is based on very few records, because the species is localized and difficult to identify, either visually or by call, except when in full song. Reporting rates are highest from the southern Cape to the Transkei. The patterns do not support migration. The reporting rates in the western and eastern Cape zones show little variation. Reporting rates are highest from June to January in the Transkei, and from June to February in the southern Cape. Nowhere does an increase coincide with a decrease, which would be

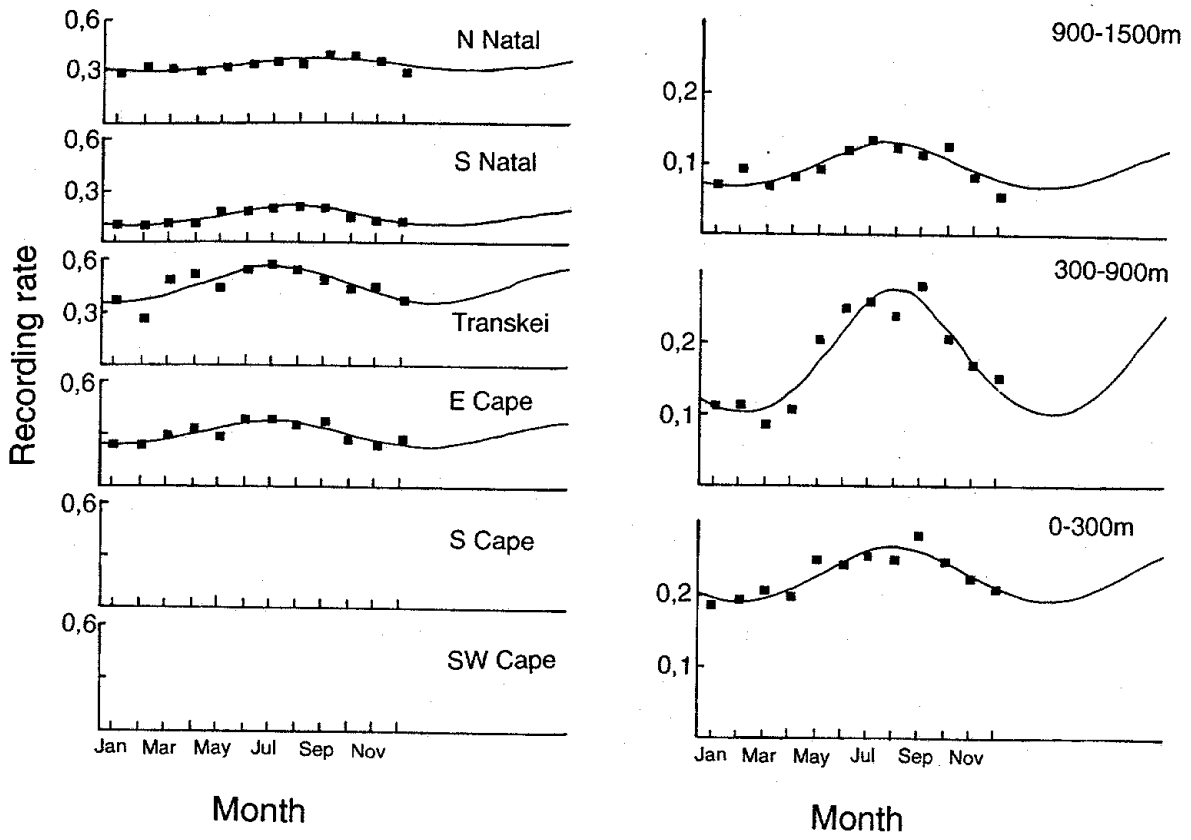


FIGURE 6

The reporting rates for the Crowned Hornbill *Tockus alboterminatus* in coastal zones and altitudinal classes showing winter peaks in reporting rates.

consistent with migration. The Knysna Warbler was previously regarded as a coastal migrant in the Transkei and southern Natal zones (Clancey 1964), and as a resident in the southwestern Cape zones (Hockey *et al.* 1989). The species has not been positively identified in Natal since 1966, and may now be extinct there, with no evidence of winter migration into that area (Berruti *et al.* 1993). All other species which show coastal migration, or partial migration, show increasing migratory tendencies (i.e. earliest departures and lowest proportions of overwintering bird) in the western populations of the Cape. This is not evident in this species, and further suggests that there is no coastal migration.

Group 4. Winter peak in reporting rate.

Five species (Crowned Hornbill *Tockus alboterminatus*, Grey Cuckooshrike *Coracina caesia*, Natal Robin *Cossypha natalensis*, Bluegrey Flycatcher *Muscicapa caerulescens*, Bluemantled Flycatcher *Trochocercus cyanomelas*) show a winter peak in reporting rates in coastal and altitudinal zones, which is not explained by migration. The possible causes of winter increases in reporting rates are discussed later.

The Crowned Hornbill is not regarded as a migrant (Clancey 1964; Tarboton *et al.* 1987; Quickelberge 1989), although Maclean (1993) reported "some local movements" and Clancey (1971) termed the species "somewhat nomadic". There were clear synchronized winter peaks in reporting rates in all zones (Fig. 6).

The Grey Cuckooshrike is usually vaguely described as showing some movement in winter. Clancey (1964) reported that this species was a seldom-recorded winter visitor to the coast of Natal. Maclean (1993) reported "some fairly extensive local movements after breeding". Quickelberge (1989) reported that it was subject to postbreeding dispersive movements. Tarboton *et al.* (1987) described the species as an altitudinal migrant down the eastern escarpment of the Transvaal in winter. This analysis shows a winter peak in reporting rates in three zones, but no evidence of altitudinal or coastal migration.

The pattern of reporting rates of the Natal Robin from the coastal zones are best described as showing a postbreeding (February-March) drop in records, rather than a winter peak in reporting rates. Altitudinal movements are difficult to interpret. The altitudinal reporting rates show a postbreeding drop in the 0-300m a.s.l. class, and a small increase in winter. The species is present throughout the year above 900m a.s.l., although as a comparatively rare resident, and seems to be

most often recorded during the early breeding season in the 300-900m a.s.l. class. If altitudinal migration occurs, it is confined to a smaller subset of the population. There is no evidence of coastal migration, even in the two southernmost zones of its occurrence. This pattern is in contradiction to that suggested by Clancey (1991), who suggested extensive migratory movements for all populations of the Natal Robin. He proposed the following movements for the two South African races: the southern race *egregior* breeds in the eastern Cape and Transkei and migrates to Natal and southern Mozambique between April and September, with some first-year birds spending their first full summer on the Natal coast; the nominate race breeds from Natal to eastern Transvaal and southern Mozambique, and migrates in winter to Mozambique. This model of migration was invoked by Clancey (1991) to account for the variation in plumage of specimens collected within the same geographic area. An opposing view was offered by Hall (1958), who argued for a conservative approach to the description of races of the Natal Robin, citing extensive intra-population variation. Ringing studies by Farkas (1969) in the eastern Transvaal and Boon (1993) in Pigeon Valley Park (Durban) have shown that all, or most, breeding adults remain on breeding grounds in winter, but that there is a dispersal of juveniles from breeding areas. In the Transkei, Quickelberge (1989) reported that there was no noticeable winter movement away from the breeding grounds. In the Transvaal, Tarboton *et al.* (1987) regarded the species as a seasonal migrant in some areas and resident in others. Irwin (1981) reported extensive winter movements of this species in the eastern highlands of Zimbabwe, which seemed to be altitudinal in nature. The present analysis suggests that the Natal Robin is essentially resident. The studies of Farkas (1969) and Boon (1993) suggest that adults are resident and that juveniles disperse, although adults of at least some high altitude populations (eastern Transvaal and Zimbabwe) may show winter migration.

The Bluegrey Flycatcher was been described as resident by Maclean (1993), but as being more mobile in winter in Natal (Clancey 1964) and the Transkei (Quickelberge 1989). Clancey (1971) suggested that the race *caerulescens* occurs in the Maputo district of southern Mozambique very largely as a non-breeding visitor from further south. Tarboton *et al.* (1987) reported that there is apparently altitudinal movement down the eastern Transvaal escarpment in winter. This analysis shows no signs of coastal or altitudinal migration of this species in South Africa, although there is a winter peak in reporting rates.

The pattern of reporting rates for the Bluemantled Flycatcher is best described as showing a postbreeding drop, rather than a winter increase. The Bluemantled Flycatcher was not described as migratory by Clancey (1964), although Maclean (1993) suggested that seasonal movements may occur. Quickelberge (1989) suggested that this species tended to move inland to breed in the Transkei. Interestingly, the winter increase in reporting rate is strongest in the Transkei, supporting the suggestion of altitudinal movement in this region. Tarboton *et al.* (1987) reported small scale winter movement down the escarpment of the eastern Transvaal and along the larger rivers in winter. In Natal, the reporting rate dropped slightly in winter above 900m a.s.l., whereas it increased markedly in winter at lower altitudes, suggesting limited altitudinal movement. There is therefore no evidence of coastal migration, but some evidence to suggest limited altitudinal migration.

Group 5. Altitudinal migration only.

The reporting rates of the two species (Starred Robin *Pogonocichla stellata* and Dusky Flycatcher *Muscicapa adusta*) indicated altitudinal movement.

The Starred Robin was recorded in small numbers, but shows small winter increases in reporting rates from the southern Cape zone through to northern Natal zone. This pattern is similar to that of the previous group of birds, which show a winter increase in abundance. Although reporting rates in the altitudinal classes are erratic, there is a restricted winter peak below 300m a.s.l., whereas the reporting rates of species in the previous group showed a longer winter duration or postbreeding drop in reporting rates. The Starred Robin is regarded as an altitudinal migrant in Transkei (Quickelberge 1989), Natal (Clancey 1964; Cyrus & Robson 1980) and southern Mozambique (Clancey 1971), being present on the coast in winter. Interestingly, it is regarded as a resident in the eastern Transvaal (Tarboton *et al.* 1987). Oatley (1982) described a clear but partial altitudinal movement in Natal. Breeding areas are always occupied and males never vacated their territories. This analysis confirmed the partial migration, as there are still many birds wintering at higher altitudes. Patterns of altitudinal movement in this and other forest species may be masked by the increase in winter conspicuousness of terrestrial forest birds.

The Dusky Flycatcher shows a relatively flat pattern in reporting rate from the southwestern Cape to the eastern Cape, and marked winter peaks from the Transkei to northern Natal (Fig. 17). There is distinct altitudinal seasonality in Natal, with numbers decreasing markedly above 900m in winter and a converse increase below 300m. This pattern of reporting rates is unexpected because the Dusky Flycatcher is regarded as a coastal migrant. For the southwestern Cape, Hockey *et al.* (1989) described the species as a common localized resident and partial migrant, breeding September to January. Lawson (1963) suggested that the race *adusta* (which breeds in the Cape and inland areas of the Transkei, Natal, eastern OFS and eastern Transvaal) wintered in Natal, southern Mozambique and Swaziland. Clancey (1964) regarded *adusta* as a winter migrant to southern Natal, and the race *fuscula* as a breeding resident on the coast. Clancey (1975) described the breeding range of *fuscula* as the Trans-

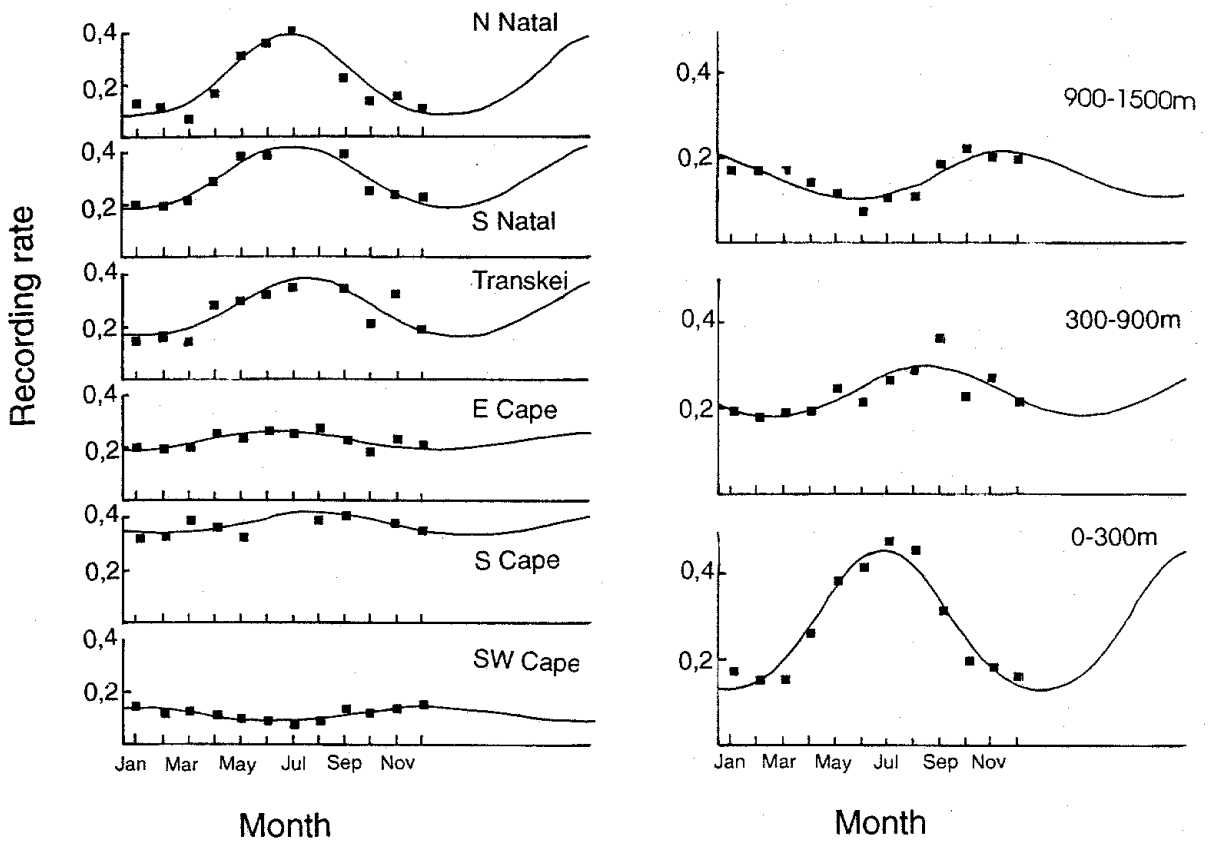


FIGURE 7

The reporting rates for the Dusky Flycatcher *Mucisicapa adusta* in coastal zones and altitudinal classes.

kei coast, and coastal and lower midlands of Natal, and regarded this race as a local and altitudinal migrant. In the Transkei, Quickelberge (1989) suggested that *adusta* of the high-level forests wintered on the coast, whilst *fuscula* is the endemic subspecies of littoral forests. On the coast to the south of the Transkei, it was present only in winter, presumably the temperate forest race *adusta* (Quickelberge 1989). In southern Mozambique, Clancey (1971) regarded this species as a nonbreeding visitor from further south, present between late April and September, although possibly breeding at higher levels in the Lebombo montains. Harrison & Navarro (in press) showed conclusively that the Dusky Flycatcher in Natal shows a strong altitudinal migration, with reporting rates dropping above 300m a.s.l. in winter but a dramatic increase below 300m. It is suggested that the reason that the reporting rates do not increase in winter in the three Cape zones is because there are no large inland populations which migrate to the coast as in Natal. The present analysis shows that coastal movement, if present at all, must be very limited, because the reporting rates vary little throughout the southwestern, southern and eastern Cape. The primary movement of this species appears to be altitudinal. In the Transvaal, Tarboton *et al.* (1987) report that there is altitudinal movement to lower altitudes in winter.

## DISCUSSION

### *Methodology*

Are patterns in reporting rates indicative of real demographic changes, or are they artefacts of either the statistical technique or observer bias? The use of the reporting rate has been discussed by Underhill *et al.* (1992), Navarro *et al.* 1993, Harrison & Navarro (in press). Reporting rates confound three variables: numerical abundance, conspicuousness and identifiability. Although the reporting rate is an index of abundance (Underhill *et al.* 1992; Harrison & Navarro in press), any analysis of the reporting rate of a species must take the biology of the species into account (Underhill *et al.* 1992). The conspicuous, abundant and widely-distributed species of open habitats, which were regarded as residents and hence as controls, showed no unexpected seasonality in reporting rates. We believe that the reporting rate is a robust quantification of species presence, although further work is required to investigate the phenomenon of the unexpected winter peak in reporting rates of several forest species (see following discussion).

### *Migrations*

This study provides evidence overturning the previously understood migration patterns in four

species: the Mangrove Kingfisher, Natal Robin, Knysna Warbler and Dusky Flycatcher. Currently understood coastal or altitudinal migration patterns are confirmed and quantified for four species: Pygmy Kingfisher, Black Sawwing Swallow, Paradise Flycatcher and Starred Robin and are weakly supported for the Spotted Thrush. Previously suggested migratory patterns in the Narina Trogon and Buffspotted Flufftail are consistent with the results of this study, but the evidence does not eliminate the competing hypothesis of seasonality in vocalisations. This analysis shows that five forest species (Crowned Hornbill, Grey Cuckooshrike, Natal Robin, Bluegrey and Bluemantled Flycatchers) show a winter peak in reporting rates. These species are usually regarded as resident. Reporting rates apparently vary with changes in vegetation density, bird behaviour or habitat selection, which in winter, make them more frequently reported by observers. In some species, the apparent winter increase is better regarded as a postbreeding decrease in reporting rates. Nevertheless, there are consistent suggestions of localized small-scale winter movements, primarily to lower altitudes (Tarboton *et al.* 1987). These patterns seem to be most marked at higher altitudes or periphery of ranges, e.g in the eastern Transvaal (Irwin 1981; Tarboton *et al.* 1987).

Oatley (1966) noted that many populations of the thrushes and robins showed winter altitudinal migrations. Importantly, he noted that the migration was partial, and that no population showed complete emigration from a particular forest. These results are confirmed in this analysis for the Spotted Thrush, Natal and Starred Robins. Subsequent studies of the Starred Robin (Oatley 1982) and Natal Robin (Farkas 1969; Boon 1993) have shown that territorial males or adults do not migrate.

*Non-migrational seasonality in reporting rate*

In this analysis, two types of seasonal pattern in reporting rates can be attributed to factors other than migration. The first of these is a summer peak in reporting rates for secretive species which are mainly recorded on the basis of vocalisations during the breeding season. In this analysis, the species involved were the Buffspotted Flufftail, Narina Trogon and Knysna Warbler. In all three cases, the existence of winter records demonstrates that migration is, at best, partial. In these circumstances, this type of analysis alone cannot reveal whether migration occurs, and supplementary evidence is required to detect migration.

The second type of pattern in reporting rate which is apparently under the influence of non-migratory seasonality is the winter peak in reporting rates of five forest species; a phenomenon which has apparently not previously been reported in South Africa. This was not noted in species showing coastal migration or in the conspicuous, widespread species of more open habitats. This pattern occurred in five species including two non-passerines. The decline in summer could be regarded as an increase in parental bird secretiveness, including reduced levels of vocalisations following egg laying. This explanation may account for the decline in reporting rates in summer, but does not account for the subsequent increase in reporting rates in winter. One or more of several factors may account for this phenomenon: the vegetation in the dense habitats occupied by these birds may become less dense in the dry winter; birds may be more active for a greater proportion of the observer's day finding sufficient food under conditions of reduced availability; birds may alter habitat usage on a local scale or behavioural patterns such as flocking. This aspect requires further investigation.

*Is the migration of the Spotted Thrush in southern Africa unique?*

We begin with the caveat that the extent and direction of winter migration in the small populations of Spotted Thrush breeding in Zululand are still poorly understood. These birds may move altitudinally to the coast (Ginn *et al.* 1989) or remain in the forests (Harebottle 1994). However, past and new evidence clearly shows a winter migration from the Transkei into Natal (Clancey 1964; Cyrus & Robson 1980; Harebottle 1994). The question is whether any population of other bird species breeding along the coast of Cape or Transkei winters in Natal. This analysis has revealed three other species which appear to show similar types of migration. The movement of the Mangrove Kingfisher from the Transkei, where it breeds in summer, to Natal where it overwinters, is very similar to that of the Spotted Thrush. Large numbers of the Black Sawwing Swallow and Paradise Flycatcher, which breed as far west as Cape Town, overwinter in Natal. However, for these species, precise definition of the breeding grounds of the birds which winter in Natal is not known.

The Spotted Thrush migration might still be regarded as unique because the wintering population is wholly contained within Natal. However, the migration of the southernmost (Transkei) population of the Mangrove Kingfisher appears to be very similar, although further confirmation is required. We argue that the migration of the Spotted Thrush should be seen as a truncated form of a migration shown by other species. The distribution of the Spotted Thrush is clearly relict, with four other races in Africa; two described on the basis of one specimen only, and the other two races numbering 40 pairs or less (Collar & Stuart 1985). The race *fischeri* of Kenya and Tanzania shows an altitudinal winter migration to the coast. It is argued that in the evolutionary past, the Spotted Thrush was more widely distributed under more favourable environmental conditions, and the species showed more extensive migrations. It has suffered evolutionary range contraction, and does not migrate further north than Natal because of its presently restricted population and range.

*Winter migrations to Natal*

Why do certain species breeding in the Trans-

kei, Cape and upland Natal overwinter on the Natal coast? Two potential interrelated factors are temperature and food supply. All these species are invertebrate feeders, and the availability of invertebrates (mediated by rainfall and temperature) in winter may be the proximate factor controlling coastal migration in Natal. Oatley (1966, 1982) has argued that food availability was not the cause of migration. However, data on the food availability given in Oatley (1982) suggest times of food shortage in winter, although these may be brief in duration. It is known that territorial Starred and Natal Robins do not migrate (Oatley 1982; Boon 1993). Non-migratory territorial adults may exclude inexperienced birds from prime habitat, forcing them to occupy sub-optimal habitats as floating individuals. In addition, at higher altitudes or more southerly coastal areas, the temperature stress at night for poorly provisioned birds would be greater. Altitudinal and coastal migration may relieve temperature stress.

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