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ALTITUDINAL MIGRATION IN SOUTH-EASTERN AFRICA

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MIGRATION

ALTITUDINAL MIGRATION IN SOUTH-EASTERN AFRICA

Terrence B Oatley

Deceased

Editorial introduction

This manuscript was written by Terry Oatley, and was never published. A copy was found in the Animal Demography Unit, in the files of papers assembled by James Harrison, coordinator of the First Southern African Bird Atlas Project, but it was not cited in the published atlas (Harrison et al. 1997). The paper has been scanned and is presented as found. It is in portrait format, in contrast to the landscape format used in every other paper published in *Biodiversity Observations*.

Terry Oatley must have written this paper in the mid-1970s, towards the end of the period during which he was a member of the staff of the then Natal Parks Board (1957–1979), where he held the position of ornithologist. The last-published paper in the references is dated 1972.

It seems that this paper was never published, and it is not known what occasion prompted it to be written, or why it never saw the light of day. It was written as an essay; it has no tables and no figures. It contains insights and ideas which were not published in any of his later writings; for example, they are not the *Robins of Africa* (Oatley & Arnott 1998) and this manuscript was not cited in that book.

Terry Oatley passed away in July 2016; one of his great passions in life was sharing an understanding of biodiversity with a broad public, and not only scientists, as pointed by his daughter in her obituary to her father (Freeman 2017). It therefore seems appropriate that this paper should give him another opportunity to enrich our understanding of altitudinal migration, a topic which has been largely neglected by ornithologist globally (Boyle 2017). Four decades after it was written, this paper still makes an interesting and valuable contribution to this topic.

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Les G Underhill

ALTITUDINAL MIGRATION IN SOUTH-EASTERN AFRICA

T.B. Oatley

A B S T R A C T

Altitudinal migration is defined as the seasonal movement of birds from high level breeding haunts to lower levels during the winter. The phenomenon occurs in the southern and eastern parts of Africa where there are abrupt transitions from sea level to interior plateaux, rift valley systems and isolated massifs.

The climatic regimes involve wet summer breeding seasons and dry winters. Examples are given of non-forest and forest bird movements : the former are seldom as extended as those undertaken by forest species, which include members of five families. Data is given on the movements of selected species and it is shown in some cases that the migrants maintain a territory in their winter quarters. Evidence from ringed birds shows that species undertaking altitudinal migration do so year after year proving that the phenomenon is not merely a dispersal by young birds. There are no known forests where the whole population moves to lower levels.

The significance of the migration is discussed and it is concluded that its evolution was related to vicissitudes of the Pleistocene climate. At the present time it is probably important in maintaining gene flow between populations in montane forest, a highly fragmented and, in many areas, a vanishing habitat.

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ALTITUDINAL MIGRATION IN SOUTH-EASTERN AFRICA

T.B. Oatley

ALTITUDINAL MIGRATION IN SOUTH-EASTERN AFRICA

T. B. Oatley

INTRODUCTION

Within sub-saharan Africa there is a great deal of movement by bird populations. A lot of movements are of a nomadic nature, but many are genuine seasonal migrations. Following Moreau (1966) whose chapter on migrants within the African continent underlines the complexity of the subject, the seasonal regularity rather than the extent of a movement qualifies it for the term of migration. Altitudinal migration can thus be defined as the seasonal movement of birds from high level breeding haunts to lower levels during the non-breeding season which, for the regions and species here concerned, is during the winter months.

Chapin (1932) writing on the ecology of Congo (now Zaire) birds was the first ornithologist to comprehensively document examples of intra-African migration. Referring specifically to altitudinal migration, which is a well known phenomenon in northern continents, he stated that such migrations were virtually unknown in equatorial Africa but mentioned a pigeon Columba arquatrix and a turaco Ruwenzorornis johnstoni (significantly both montane forest species) for which there was evidence of altitudinal movement.

Subsequent documentation has been scanty, probably because the majority of authors have been primarily concerned with taxonomy. Records of montane birds in lowland localities are well scattered through the literature on African birds, particularly in some Check Lists, but are in most cases attributed to wanderers or vagrants. However, Irwin (1957) realised the significance of such records and established definite altitudinal movement by six montane forest birds in the eastern highlands of Rhodesia.

Finally, in the course of studies of small African Turdidae (Oatley, 1959; 1966) it became apparent that altitudinal migration was far more widespread than was earlier believed.

Because most of the interior of the southern African sub-continent is elevated, any latitudinal migration of sufficient distance involves a change of altitude. However, the bulk of the data here presented are from the south-eastern part of the continent and in particular from the Province of Natal and the neighbouring country of Lesotho where seasonal movements are characterised by large altitudinal changes over relatively short distances.

TOPOGRAPHY AND CLIMATE

The Province of Natal, although small (approximately 90,000 km^2) is very rugged with a relief from the coast to the summit of the Drakensberg Mountains in excess of 3,385 m. The ruggedness is due to the fact that the entire Province has been tilted seawards by a geomorphological feature known as the Natal monocline. This tilting increased in geologically recent time, steepening all the major rivers and causing them to incise deep valleys across the full width of the Province (King, 1972). Just south of Durban, at 30°S, the distance from the shoreline to the 3,048 m (10,000 ft.) contour is only 160 km. This gradient is modified by a series of steps or scarps, each of which is a manifestation of a different erosional cycle, and they tend to provide suitable conditions for forest growth. Moist evergreen forests of afromontane affinity thrive in the altitudinal range of 900 - 1,500 m above sea level. In this region the Tugela valley is some 900 m deep, and like other large river valleys to the south and north permits the extension of warm, dry woodland far into the cool grasslands of the interior of the Province. These valleys are generally aligned from north-west to south-east, and their northern slopes frequently support evergreen forest, the character of which changes with increasing altitude. The north-eastern portion of the Province is characterised by a broadening coastal plain (the southern extremity of the Mozambique coastal plain) bounded on the west by the 600 m high north-south range of the Lebombo Mountains.

Climatically, south-eastern Africa is subject to summer rains, with the bulk of the annual precipitation falling in the six months centered on the summer solstice. This broad pattern is subject to local modification by topographic features and proximity to the coast. In Natal, climatic data summarised for the Tugela basin by Edwards (1967) show that the coastal zone receives from 29 to 33% of the mean annual rainfall of 1,250 mm during the winter months of April to September. By comparison the highlands receive only 15-21% of a mean annual precipitation of up to 1,500 mm during the same period.

The lower extremes of temperature are important in a consideration of bird migration. In this regard frost, which does not occur on the Natal coast, may be expected in at least six months of the year in the highland regions with the frequency of severe frosts (below -3°C) increasing markedly above 1,800 m. There are no data available on temperature minima in the high mountains of Lesotho, but Edwards (op.cit) recorded a July minimum of below -18°C on the top of the Drakensberg escarpment.

From the foregoing it may be appreciated that Natal is a particularly suitable place in which to observe altitudinal migration, embracing as it does extremes of topography in combination with alpine and (on the north-eastern coastal plain) tropical temperature regimes.

To the north, important topographic features are the re-appearance of the Drakensberg escarpment (in lower, less grandiose form) in the north-eastern Transvaal Province; the broad, hot, dry Limpopo River valley; the eastern highlands of Rhodesia and, to the east of these, the isolated, forest-covered massif of Gorongosa Mountain in Mocambique. Useful topographic notes on Rhodesia and southern Mocambique can be found in respective checklists of their birds by Smithers et al.(1957) and Clancey (1971), and quite adequate coverage of the rest of the continent is provided in one invaluable volume by R.E.Moreau (1966).

ALTITUDINAL MIGRATION BY NON-FOREST BIRDS

Following Moreau (op.cit.) it is convenient to group the birds into non-forest and forest-dwelling categories. However, whereas

Moreau was able to subdivide both categories into montane and lowland groupings on a pan-african basis, this is not possible in the context of the non-forest avifauna here considered, since not all of the birds which frequent the high Drakensberg in summer are montane species.

The evidence for altitudinal migration is best reviewed by listing in systematic order those species (excluding known African and Palearctic migrants) which are only seasonally present in the Natal highlands or in the alpine region above the escarpment edge in Lesotho at altitudes of 2,743 - 3,353 m (9,000 - 11,000 ft.). The nomenclature used is that of the S.A.O.S.List Committee (1969).

PICIDAE

Geocolaptes olivaceous Ground Woodpecker

Found throughout the Drakensberg foothills and above the escarpment in the summer months, where it may be found nesting in December and January. The bird is absent from the higher altitudes in winter but at that time may be encountered on rocky hilltops in the Natal midlands from which it is normally absent in summer.

TURDIDAE

Monticola explorator Sentinel Rock Thrush

A regular non-forest altitudinal migrant which can be found breeding in summer across the Drakensberg foothills and over the whole of the high mountain ranges in Lesotho. In the winter months it may be encountered at much lower altitudes. A pair of birds appeared in the Queen Elizabeth Park at an altitude of 900 m near Pietermaritzburg for two successive winters, frequenting the office parking lot. Individuals have also been recorded in Durban and at Cowies Hill near Pinetown, only some 14 km inland. However, on a brief visit to Lesotho in July 1971, I found these Rock Thrushes to be fairly common on rocky ridges at an altitude of about 2,900 m. The noon temperature here was relatively mild compared with that on a nearby mountain range where at 3,300 m there were widespread areas of snow and ice. It is

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possible that these birds had only moved a short distance down from higher levels; certainly their presence seemed to indicate that they do not totally evacuate the alpine zone in winter.

Cercomela sinuata — Sickle-winged Chat

A species of the mountains of Lesotho where, in December and January it may be found breeding at the highest levels (Jacot-Guillarmod, 1963). On rare occasions it is recorded in the Drakensberg foothills in Natal in winter months, but the altitudinal migration which takes place seems to be largely westwards towards the 'lowlands' of Lesotho and the O.F.S.

Saxicola torquata — Stonechat

In discussing altitudinal migration in Africa, Moreau (op.cit.) states "Stonechats .....move downhill in Malawi and from the interior plateaux of south-eastern Africa to winter." In support of the movement by Malawi populations Benson (1953) states that the species is common above 3,000 ft.but is only recorded below 2,000 ft.in the period April to September. Populations of this widespread species which spend the summer months and breed at high altitudes in Natal and Lesotho, swell the numbers of resident populations at lower levels in the winter months.

SYLVIIDAE

Chloropeta natalensis — Yellow Warbler

According to the Check List of birds of S.Africa (S.A.O.S. List Committee,1969) this species is "resident though subject to altitudinal movement." It is certainly not resident in the Drakensberg foothills, but arrives in October to nest in Leucosidea trees along the rivers. In the period April to September it is absent, but little is known about its movements. It is possible that the species moves to lower levels in and via river valleys. One was recorded on the move in the Umkomaas Valley at ca. 450 m in the month of May, and a record of this species in the lower middle Zambesi River Valley in July (Cooper, 1972) is probably significant in this context.

MUSCICAPIDAE

Stenostira scita — Fairy Flycatcher

Breeds on the high plateaux of Lesotho which it vacates in the winter. Some individuals move down into Natal, but the majority of birds appear to move to lower levels in the west of the country.

MOTACILLIDAE

Anthus chloris — Yellow Pipit

A bird which in the Drakensberg Mountains breeds in the summer months up to about the 2,133 m (7,000 ft.) contour). It vacates the mountainous areas in winter and has been recorded at various lower altitudes, including the Natal coast. However, little is really known about its movements.

LANIIDAE

Malaconotus zeylonus — Bokmakierie Shrike

A very widespread bird in South Africa and one which is found (and presumably breeds) in the highest peaks of Lesotho in summer. It is not clear where these birds go in winter, but it can only be downwards, and they presumably join populations resident at lower levels.

NECTARINIIDAE

Nectarinia famosa — Malachite Sunbird

Skead (1967) has dealt comprehensively with the movements of this species and shown that in eastern Cape Province its movements are unpredictable, but populations which spend the summer months in the highlands of Lesotho at altitudes of up to 3,000 m or more are forced by the severity of the climate in winter to evacuate these haunts and move to lower levels in the Orange Free State and Natal. Similar but less severe conditions pertain in the eastern highlands of Rhodesia and an altitudinal migration is documented on the Inyangani Mountain.

This is a very widespread species and is in some places resident, in others subject to seasonal or irregular movement.

ALTITUDINAL MIGRATION BY FOREST BIRDS

Forest birds in Africa are usually termed montane or lowland according to their habitat affinity. In southern Africa such

terminology becomes misleading because the afromontane forest occurs at sea level in the southern Cape Province, as do elements of the avifauna normally associated with it at lower latitudes. Consequently the forest bird fauna can be grouped into three categories: those characteristic of afromontane forest only; those restricted to the warmer coastal forests and those which occur in any evergreen forest, irrespective of altitude. The last two subdivisions really comprise the lowland forest element, as at lower latitudes they tend to be thus confined.

With one exception, the species involved in altitudinal migration all belong specifically to the montane forest avifauna and in systematic order are as follows:

PICIDAE

Mesopicos griseocephalus — Olive Woodpecker

A characteristic species of the highland forests of Natal, this species is not infrequently found in the coastal belt in the winter months, and there is some evidence that it attempts breeding. Further north on the boundary between Swaziland and north-eastern Zululand it visits the forests of the Lebombo Mountains (600 m) but is not recorded there in the summer months. In Malawi, where its normal forest habitat lies at altitudes above 1,500 m it is occasionally encountered at levels down to 1,000 m in the winter months (Benson, 1953).

CAMPEPHAGIDAE

Coracina caesia — Grey Cuckoo-Shrike

Regularly encountered in the midlands forests of Natal, where it breeds. It visits the Lebombo Mountains in the winter months and at these times has been recorded in riverine forest on the Tongaland plain in north-eastern Zululand. Further north in Mocambique Clancey (1971) quotes lowland localities where it has been collected and states that one was obviously a wintering bird. In the eastern border of Rhodesia, a record of one in the Chipinga district at 910 m seems likely to be that of an altitudinal migrant (Scott, 1972).

This is not a vociferous species, and with its silent flight and habit of frequenting the canopy it is probably overlooked by many observers.

TIMALIIDAE

Lioptilus nigricapillus — Bush Blackcap

A species endemic to South Africa. In Natal in summer it is to be found in high forest in the Drakensberg foothills and fringing Leucosidea thickets up to altitudes of 1,800 m. It visits forests at lower levels down to about 1,000 m in Natal midlands and 600 m on the Lebombo Mountains in winter and may linger in these haunts well into October, later than most other altitudinal migrants. It seems never to reach the coast, and some birds may be found in the highest forests even in midwinter.

TURDIDAE

Turdus olivaceus — Olive Thrush

This species is so widespread in such a range of habitats in South Africa that many would not consider it a forest bird. However it is typically an evergreen forest bird in Natal and an afromontane species in forests northwards. There is some evidence of altitudinal movement in Natal but it is only partial and tends to be masked by the presence of resident populations at many levels throughout the year. It is one of the species found by Irwin (1957) to be involved in seasonal altitudinal movement on the eastern slopes of the Inyangani Mountain on the Rhodesian border.

Cossypha dichroa — Chorister Robin

Another South African endemic, characteristic of the temperate evergreen forests from Knysna in the Cape Province to the Zoutpansberg in the Transvaal, on the southern edge of the Limpopo Valley. In Natal it is a notable altitudinal migrant, though like other robins, not all the members of its populations indulge in movement so the species can be found in its breeding haunts throughout the year. Breeding occurs in forests near sea level in southern Natal, but seldom below 450 m further north (from about latitude 30°S) where this robin is a regular visitor to what is left of the coastal forests as far north as Richards Bay during the months April to September. It is likewise a winter visitor only to the Gwaliweni Forest on the Lebombo Mountains. Unlike some other robins, it is not encountered in habitats other than well-developed evergreen forest, and birds en route from summer to winter

quarters or vice versa have not been observed, which may indicate that they move by night.

In general these migrations probably don't involve great distances; possibly none of those evident in Natal involve distances in excess of 80 km. The breeding haunts of birds wintering in forests near Durban are not known, but it is reasonable to believe that those recorded at Mtunzini and Richards Bay have come down from the nearby 600 m high Ngoye range, where a large forest supports a particularly dense population of Chorister Robins. Birds wintering on the Lebombo Mountains may come from the Ngome forest about 70 km distant and some 500 m higher.

Of considerable interest is the evidence for what might be termed 'leapfrog' migration. A bird ringed in its first winter in the author's garden at Winterskloof (altitude 1050 m) near Pietermaritzburg, returned each winter for five successive years. His arrival in April was always marked by loud singing, displaying and chasing by himself and the two resident Choristers who in summer occupied adjoining territory in the same forested gully. The visitor always managed to wedge in a territory between the two. It was not at first evident that he was an altitudinal migrant, but after a couple of years he had acquired a quite distinctive repertoire of imitated calls of other birds (a normal development in this species) which included the Redwing Francolin Francolinus levaillantii, Helmeted Guineafowl Numida meleagris, Redwing Starling Onychognathus morio and Bokmakierie Shrike Malaconotus zeylonus. None of the species calls could have been acquired locally by the robin in Winterskloof, but the particular combination is common in the cave sandstone belt of the Drakensberg foothills, the remnant forests of which are well populated with Chorister Robins. Assuming that this bird had come from such an area, he would have had to cross at least two forested scarps in the Natal midlands in which other populations of Chorister Robins reside.

Cossypha natalensis Natal Robin

The Natal Robin is a polytypic species with a widespread distribution in Africa. It is usually considered to be a lowland forest bird though it shuns the non-seasonal rain forest of the Congo basin. Populations everywhere seem to be involved in seasonal

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movements except perhaps those resident in littoral areas. The subject has been reviewed by Britton (1971) on the basis of collected specimens, and it is clear that little is known about the majority of the movements except their occurrence. However, two migration patterns are reasonably clear in south-eastern Africa and both are relevant to this text.

In Natal, Cossypha natalensis is characteristically a bird of the dune forest of the littoral and of lowland forest remnants and evergreen thickets of the coast hinterland. The species breeds in these haunts in the period October to February, but is more numerous in winter than in summer. It also breeds in riparian thickets well inland along the major river systems and their tributaries, but is present in these valleys only during the summer months of October to March. There is a seasonal movement inland along the river valleys in spring and coastwards in autumn. Natal Robins ringed in winter in suburban gardens in Durban and environs disappear in summer and return again the following winter. Although the movement inland is along incised drainage lines, altitudinal increment inevitably results and some birds are found breeding in wooded gullies some 1100 m a.s.l. The density of cover in such localities fluctuates markedly between summer and winter due to the dominance of deciduous elements in the flora and the dryness of the habitat in July and August. To a cover-loving species such as the Natal Robin, this factor may well be a significant one; certainly it is more important than food availability which is unlikely to be limiting (Oatley, 1970). It is possible that this sort of movement is quite widespread and by no means confined to Natal. In the Chipinga area of eastern Rhodesia at 910 m Scott (1972) records that it breeds in riparian forest and thickets but is possibly not resident.

In the same region, near the southern end of the highlands, lies the Mt.Selinda forest. Lying at an altitude of 1,200m it is not typically montane, and in the summer months it supports a respectable breeding population of Natal Robins. In the winter months most (but not all) of these birds have moved out, and collections during the same period on the Mocambique plain have yielded birds of the race C.n.hylophona to which these highland populations are attributed. Because Selinda is a proper evergreen

forest, the movement here is analogous to that described for other species under this heading.

Cossypha caffra — Cape Robin

This species is very widespread in South Africa, but north of the Limpopo River becomes restricted to the bracken-briar fringe of montane forest and the ericaceous woodland above 1,700 m. In Natal it is one of the notable altitudinal migrants, appearing on the coast in the winter months only, and moving into the warm, dry river valleys in considerable numbers at the same time. It is nevertheless resident in its breeding haunts throughout the year, and a high proportion of the altitudinal migrants are young birds in their first year. The phenomenon is not confined to Natal but has been recorded by the writer in the eastern Transvaal, at Gorongosa Mountain in Mocambique and at Malanje Mountain in Malawi. In the latter two localities the species is common on the upper levels of the mountains above 1,700 m, but individuals were encountered near the bases of the massifs in April and May respectively.

Pogonocichla stellata — Starred Robin

The Starred Robin extends from the Knysna region of the southern Cape Province in South Africa to the mountains of the southern Sudan. It is a characteristic species of montane forests in the eastern half of the African continent (excluding those in Abyssinia) and is also one of the most notable expondents of altitudinal migration.

In central Natal this species breeds in the period October to December in temperate evergreen forest mainly above the 900 m contour. From February to April there is a marked movement of these birds downwards towards the coast, mainly along drainage lines; in September and October a comparatively concentrated movement is to be observed back up again. This movement is diurnal, and it is not unusual to observe Starred Robins working their way through plantations of exotic pines or through wooded gullies in thornveld areas.

Like other species aforementioned, the Starred Robin is a winter visitor to the Lebombo range, where it was first collected

by the late Dr Austin Roberts and named by him as a distinct subspecies. However, it does not breed there, and the visitors may derive from the Ngome forest which is the nearest known breeding haunt of any consequence. Unlike species such as the Chorister Robin and the Bush Blackcap however, Pogonocichla does not stop at the Lebombo range. It has been recorded down on the Tongaland plain along the forested banks of the Mkuze, Pongolo and Usutu Rivers, and also in the dune forest on the littoral east of Lake Sibayi. Birds have been recorded in Lourenco Marques in winter (Lamm 1955) and from Chimonzo near the Limpopo (Clancey and Lawson 1967). These localities are more than 160 km from the nearest breeding stations with intervening country characterised by hot, dry Mopane woodland of the Limpopo system. In the latitude of Gorongosa Mountain, the Starred Robin has now been recorded on the eastern side of the Urema trough in the forests of the Cheringoma plateau at about 300 m by K.L.Tinley (pers. comm.) in May.

Altitudinal migration is similarly practised by members of other subspecies to the north (Benson and Irwin, 1967; Oatley,1966). In all cases the migration is partial in that some individuals are always to be found in the main breeding forests in the non-breeding season.

SYLVIIDAE

Bradypterus barratti — Barratts Scrub-warbler

A cover-loving species of afromontane forest and its fringes, extending in Leucosidea scrub to altitudes of 2,133m in Natal. There is a strong altitudinal movement in winter, possibly total from the highest levels, to forests between the 900 m contour and the coast. There are few records in the literature, but this species is so skulking in habit that it is hardly ever seen, and only its ratchet churr note betrays its presence. It is one of the species recorded by Irwin (1957) as being involved in altitudinal movement in eastern Rhodesia.

Seicercus ruficapillus — Yellow-throated Warbler

Like the last, recorded by Irwin as an altitudinal migrant in the eastern highlands of Rhodesia. A regular altitudinal migrant

from the high forests of Natal and Zululand to lower levels, reaching the coast where suitable forest exists.

MUSCICAPIDAE

Batis capensis Cape Batis

Like the last species, widespread in Natal, and short distance altitudinal movements which do occur tend to be masked by resident populations at all levels. Northwards it becomes increasingly restricted to evergreen forest above 1,400 m and Irwin (1957) records it as an altitudinal migrant in the eastern Rhodesian highlands.

DISCUSSION

The examples given for both forest and non-forest birds have been restricted to those species which exhibit a regular and unfailing seasonal movement. There are species such as the Drakensberg Siskin Serinus tottus which only appear at lower levels after exceptionally heavy snowfalls, and such examples of occasional movement in response to extreme conditions are widespread in animals as mobile as birds.

In the case of the majority of non-forest birds, the regular migration is a necessary adaptation to the severe climatic conditions pertaining in the high mountains of Lesotho during the winter solstice. By contrast, the Natal midlands, to which a lot of the Lesotho populations move, are relatively mild with severe frosts only occasionally experienced. Light snowfalls are irregular, seldom exceed 100 mm in depth and usually do not lie for more than a few days. Such snowfalls appear to have little effect on the invertebrate fauna; the snow is frequently supported a few centimetres above the ground by the grass cover, and holes poked through it have revealed insects such as grasshoppers to be fairly active beneath the mantle (B.R.Stuckenberg, pers.comm.).

For the forest birds involved in altitudinal migrations there are no obvious environmental factors (with the exception of the one quoted for Cossypha natalensis) which can be invoked in a causative

or contributory role. In the Natal forests the chief seasonal difference lies in the soil moisture content and, to a lesser extent, the density of cover (due to a number of deciduous elements in the flora). The lower temperatures and relative dryness of the winter months may be expected to inhibit the mobility and availability of invertebrate prey of insectivorous birds, but 75% of species of the avifauna of these forests are entirely resident, and it seems unlikely that food supplies are limiting for the species which indulge in migration.

It is tempting to look to the past and to conclude that the vicissitudes of climate in Africa, which have undergone a full cycle of change in the last 20,000 years, have been responsible for giving rise to a migratory pattern which persists today under much less severe climatic conditions than those pertaining as little as ten thousand years ago (see Moreau, 1966). Certainly it is known that there were periods synchronous with the ice ages of the northern hemisphere when temperatures were lower than they are now by several degrees, and that this temperature lowering was highest at high altitudes and lowest in the lowlands. Such climatic change could plausibly have initiated altitudinal migration, even in equatorial regions with sufficient topographic relief, but cannot alone account for the fact that only one species in four is so affected.

A little speculation is necessary here if any sort of tenable hypothesis is to emerge. It has already been suggested that the partial aspect of migrations observed in the species which are involved in altitudinal movement can be accounted for by intrinsic genetic factors such as dimorphism for sedentary or migratory habit (Oatley 1966). Such factors can play important roles in speciation and a consideration of this subject is relevant.

Various hypotheses have been put forward to account for the several features of species diversity of wet tropical lowlands. MacArthur (1969) has recently discussed these and proposed one himself, which is based on the importance of species interactions, particularly predation and competition, and has the virtue of being both simple and mathematically sound. He likens the tropical environment to a balloon which resists immigration in proportion

to its content but which can always hold a little bit more when necessary. There is always a tendency for its contents to escape to areas of lower pressure.

With this analogy in mind, it is interesting to envisage a primeval lowland forest contiguous with a cooler montane forest area. Competition is intense in the lowland habitat and individuals are forced into peripheral, 'unsuitable' montane habitat, there to attempt to breed. For some such individuals the lack of competition will outweigh the disadvantage of unfamiliar environment and there will be reproductive success. However, the montane habitat is more seasonal than the lowland forest, and after breeding the tendency is for return to the more comfortable and familiar lowland habitat. An initial pattern of movement may well be evolved in this manner, and with little competition and fewer predators enhanced reproductive success in the more temperate habitat will ensure its perpetuation. In the process a highly specialised species will have become less specialised and better fitted to survive in times of climatic vicissitudes. Some montane forest species could have evolved in this way. The other more passive way would involve forest species 'staying put' in periods of temperature decline and evolving slowly with the habitat from a lowland warm to a montane cool adapted existence.

In both instances extinction rates may be expected to be high. For the montane birds that evolved, there would be two main evolutionary paths open. On the one hand, a tendency to descend to lower levels will connote ability to exploit a variety of ecological niches at different seasons and in different habitats and would improve opportunities to find and colonize other montane areas. On the other hand, specialization to the montane environment will result in a tendency to shun lowland conditions, which in turn will lead to isolation in montane refuges and, in the event of severe climatic change, to extinction.

The above is of course a gross simplification of the complexities of the interplay of species dispersal and changing habitats in times of climatic instability, and one would expect these basic simple trends to be modified in many ways, which in fact they are. In the previous review (Oatley 1966) it was pointed

out that forest birds which practised altitudinal migration were generally widespread in range, and that the most localised and rare species were notable for their abstention from any sort of movement. Since then the Atlas of Speciation of African Passerine Birds has been published (Hall and Moreau, 1970) and it is instructive to examine the distributions of the forest birds here mentioned.

In terms of MacArthur's hypothesis, it might be expected that some lowland forest species under pressure had 'escaped' to seasonal woodland habitats in addition to seasonal montane ones. In this regard the mapped distribution of Coracina caesia superspecies is significant, even to the extent that the woodland C.pectoralis exhibits seasonal movements in west Africa. Maps of the distribution of species confined to southern Africa show them to be members of superspecies groups which enjoy widespread distribution in the continent, even to the very isolated highland regions of West Africa.

Seen in this light, the altitudinal migration of forest birds seems less of a mystery. Its persistence may still be advantageous in maintaining gene flow between populations in fragmented habitat relicts in southern Africa. There is not enough data yet to either support or refute this possibility, but the characters of some allopatric populations, particularly of Pogonocichla stellata, suggest that it may be substantiated.

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