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To cite this article: J.M. Winterbottom (1973) The Relationships of the Avifauna of the South West Arid Area of Africa, *Zoologica Africana*, 8:1, 83-90, DOI: [10.1080/00445096.1973.11447468](https://doi.org/10.1080/00445096.1973.11447468)

To link to this article: <https://doi.org/10.1080/00445096.1973.11447468>



Published online: 02 Oct 2015.



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THE RELATIONSHIPS OF THE AVIFAUNA OF THE SOUTH WEST ARID AREA OF AFRICA

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Some years ago, I discussed (Winterbottom 1959) the limits of the zoogeographical district well named by Chapin (1923) the South West Arid and extended it eastward to include the highveld grasslands of the Transvaal and Orange Free State which Chapin had excluded. Later, I (Winterbottom 1966) considered its north-eastern limits and pointed out that there existed a broad transitional zone along the western border of Rhodesia, through the Caprivi Strip and northern Botswana to the Okavango valley of north-eastern South West Africa. In a subsequent paper (Winterbottom 1967), I briefly discussed the relationships between the avifauna of this South West Arid District and that of Chapin's Somali Arid District. The present paper is an attempt to carry this analysis further. Since then, however, I (Winterbottom 1970) have divided the original South West Arid into two, splitting off the Macchia, Karoo and Highveld as the South Temperate District. Nevertheless, since the faunas of the two districts are related, I propose here to treat them together.

As a beginning to this analysis, I drew up a list of 90 characteristic species of the South West Arid District, i.e., all those species peculiar to the South West Arid and those species whose range in southern Africa fell entirely, or almost entirely, within that district or within that and the South Temperate District; but did not include species confined to the Macchia or the Highveld. The full list is set out in Table 1.

As I have pointed out (Winterbottom 1967), without any claim to originality in doing so, there can be little doubt that a corridor of arid country, linking or almost linking the South West and Somali Arid Districts, must have been present several times during the Pleistocene. Clark (1959) lists three Pleistocene dry phases between the Pleistocene pluvials, of which the first and third were "very dry"; in addition, there appear to have been two periods subsequent to the last (Gamblian) pluvial when the climate was drier than at present. These findings suggest that there must have been at least two, and possibly as many as five, periods when the close approach of arid conditions from the south-west and north-east allowed of an exchange of fauna.

Geographical considerations suggest that the original avifauna of southern Africa probably came from the north; zoological facts suggest that African birds must have evolved within the continent, with little interference, for a considerable period—probably at least the whole Pleistocene, though the Somali Arid, like the Sudanese Arid further west, must have been in touch with the Palaearctic faunas at least at times. In respect of the South West Arid District, there must have been long periods during which it was isolated from other arid areas by better-watered savanna and forest country.

If we seek to analyse the present avifauna of the South West Arid, we find that 12 of the species are represented by different subspecies or groups of subspecies in the north-east (Table 2) and 22 (Table 3) are represented there by species to which they are most closely allied. Of the remainder, 24 species are most nearly allied to others which occur to the east in southern Africa, often overlapping at the edges of their range. The remaining species I have been unable to place in any of these three categories and they may be discussed individually hereunder. They offer clear proof of the distinctness of the South West Arid District from any other.

TABLE 1

CHARACTERISTIC SOUTH WEST ARID BIRDS

A=South-West Arid; T=South Temperate; B=Both Districts

<i>Struthio camelus</i>	B	<i>Cercomela tractrac</i>	T
<i>Tadorna cana</i>	B	<i>C. sinuata</i>	T
<i>Poliohierax semitorquatus</i>	A	<i>Myrmecocichla formicivora</i>	B
<i>Melierax musicus</i>	B	<i>Erythropygia coryphaeus</i>	T
<i>Circus maurus</i>	T	<i>E. paena</i>	A
<i>Francolinus levaillantoides</i>	T	<i>Camaroptera subcinnamomea</i>	B
<i>F. adspersus</i>	A	<i>Eremomela gregalis</i>	T
<i>F. hartlaubi</i>	A	<i>Cisticola subruficapilla</i>	T
<i>Otis kori</i>	B	<i>Achaetops pycnopygius</i>	A
<i>O. ludwigii</i>	B	<i>Prinla flavicans</i>	B
<i>Eupodotis vigorsii</i>	T	<i>P. substriata</i>	T
<i>E. ruficrista</i>	A	<i>P. pectoralis</i>	B
<i>E. afra</i>	B	<i>Parisoma subcaeruleum</i>	B
<i>Cursorius rufus</i>	B	<i>P. layardi</i>	B
<i>Rhinoptilus cinctus</i>	B	<i>Namibornis herero</i>	A
<i>Pterocles namaqua</i>	T	<i>Melaenornis mariquensis</i>	A
<i>P. burchellii</i>	A	<i>M. infuscata</i>	T
<i>Poicephalus rueppellii</i>	A	<i>M. silens</i>	T
<i>Agapornis roseicollis</i>	A	<i>Batis pririt</i>	B
<i>Colius colius</i>	B	<i>Stenostira scita</i>	T
<i>C. indicus</i>	B	<i>Laniarius atrococcineus</i>	A
<i>Tockus bradfieldi</i>	A	<i>Malaconotus zeylonus</i>	T
<i>T. monteiri</i>	A	<i>Lanioturdus torquatus</i>	A
<i>Miraфра africanoides</i>	A	<i>Eurocephalus anguitinens</i>	A
<i>M. sabota</i>	B	<i>Onychognathus naboroupp</i>	B
<i>M. passerina</i>	A	<i>Spreo bicolor</i>	T
<i>M. aplata</i>	B	<i>Nectarinia mariquensis</i>	A
<i>Certhilauda albescens</i>	T	<i>N. fusca</i>	B
<i>C. burra</i>	T	<i>Bubalornis albirostris</i>	A
<i>C. albofasciata</i>	B	<i>Plocepasser mahali</i>	B
<i>C. curvirostris</i>	T	<i>Philetairus socius</i>	B
<i>Galerida magnirostris</i>	T	<i>Sporopipes squamifrons</i>	B
<i>Ammomanes grayi</i>	T	<i>Passer motitensis</i>	B
<i>Eremopterix verticalis</i>	B	<i>P. melanurus</i>	B
<i>E. australis</i>	T	<i>Ploceus rubiginosus</i>	A
<i>Calandrella conirostris</i>	B	<i>Amadina erythrocephala</i>	A
<i>C. starki</i>	B	<i>A. fasciata</i>	A
<i>C. sclateri</i>	T	<i>Uraeginthus granatinus</i>	A
<i>Anthoscopus minutus</i>	B	<i>Estrilda erythronotos</i>	A
<i>Turdoides melanops</i>	A	<i>Vidua regia</i>	A
<i>T. bicolor</i>	A	<i>Serinus atrogularis</i>	A
<i>T. gymnogenys</i>	A	<i>S. alario</i>	B
<i>Pyncnonotus nigricans</i>	B	<i>S. flaviventris</i>	B
<i>Monticola brevipes</i>	B	<i>S. albogularis</i>	T
<i>Cercomela schlegelii</i>	T	<i>Emberiza impetuani</i>	B
			<i>E. capensis</i>	T

In a number of cases of species-pairs, however, the intervening area is inhabited by another closely related species. Thus between the ranges of *Eremopterix verticalis* and *E. signata* is *E. leucopareia*, considered by Hall & Moreau (1970) to be a member of the same superspecies; similarly *Erythropygia leucophrys* and *Myrmecocichla nigra* are interposed between the species-pairs in these genera listed in Table 3. In these cases, therefore, it is possible that the close resemblances between the south-west and north-east species are due to convergent evolution under similar climatic and ecological conditions of a species which broke up into three closely-related species; or to the lesser divergence of the two end-links in a chain of populations in which the central population became adapted to other environments.

TABLE 2
SOUTH-WEST-NORTH-EAST SPECIES

<i>Poliohierax semitorquatus</i>	<i>Nectarinia mariquensis</i>
<i>Francolinus levaillantoides</i>	<i>Passer motitensis</i>
<i>Eupodotis ruficrista</i>	<i>Ploceus rubiginosus</i>
<i>Rhinoptilus africanus</i>	<i>Amadina fasciata</i>
<i>Mirafra africanoides</i>	<i>Estrilda erythronotus</i>
<i>Turdoides melanops</i>	<i>Serinus atrogularis</i>

I now comment on the more puzzling species of the South West Arid. Though I have not always followed them, my debt to Hall & Moreau (1970) in respect of the passerines is obvious and gladly acknowledged.

The black harrier *Circus maurus* may be a dry-country derivative of the African marsh harrier *C. ranivorus*, but this is far from certain.

The black korhaan *Eupodotis afra* appears to have no close relative among African Otididae, though the female plumage suggests that it is perhaps nearer to *E. ruficrista*, itself a South West Arid endemic, than any other. If so, *afra* must have been an early immigrant of *ruficrista* stock, which became isolated in the south. *E. ruficrista* itself is a much more recent arrival, being closely related to *E. gindiana* of the north-west (Table 3).

The rosy-faced lovebird *Agapornis roseicollis* is considered by Moreau (1948) to be intermediate between the two groups into which the other species of this genus fall and must therefore have arrived in the South West Arid before this splitting occurred.

Monteiro's hornbill *Tockus monteiri* may be most closely related to *T. pallidirostris*, but not very closely.

The karoo lark *Certhilauda albescens* and the long-billed Lark *C. curvirostris* are clearly closely related to one another; and their nearest relative is probably the spike-heeled lark *C. albofasciata* (see Verheyen 1959). The latter, with a subspecies in central Angola and a recently-discovered one in central Tanganyika, appears to have evolved in the South West Arid but to have left these relict populations behind as arid conditions waned. White (1961) and Hall & Moreau (1970) consider the red lark "*C.*" *burra* to be closely related to *C. albescens* and Lawson (1961) has gone so far as to place it as a subspecies of that bird. I am doubtful about the first and

quite unable to accept the second of these suggestions (see Winterbottom 1960). The red lark may be related to *Alaemon grayi* of the Namib. The only other species usually placed in *Certhi- lauda* is *C. somalica* of the north-east, which does not seem to be particularly closely related to any of the foregoing and Hall & Moreau (1970) group it with *Mirafra africana*. White considers that *C. albescens* and *C. curvirostris* should be placed in the genus *Mirafra*, a view strongly criticised by Verheyen (1959); and resurrects the genus *Chersomanes* for *C. albofasciata*. Hall & Moreau believe *curvirostris* might form a superspecies with *chuana*, but as this is a highveld endemic, it throws no light on the origins of *curvirostris*.

The black-eared sparrow-lark *Eremopterix australis* seems to be a comparatively isolated member of a genus essentially south-west to north-east in origin. Hall & Moreau consider it forms a superspecies with *E. leucotis*, with which it overlaps slightly in the Orange Free State. If so, it must represent an earlier invasion of the south-west by a stock which subsequently gave rise to *leucotis*, whose presence in the south-west is therefore a second invasion by this stock. I am not entirely satisfied with Hall & Moreau's grouping of the *Eremopterix* species, however. It seems to me that *leucotis* is more similar, in size and plumage pattern, to *verticalis* than to *australis*.

TABLE 3

"SPECIES-PAIRS" IN THE SOUTH-WEST AND SOMALI ARID DISTRICTS

<i>Tadorna cana</i>	<i>T. ferruginea</i>
<i>Melierax musicus</i>	<i>M. poliopterus</i>
<i>Otis kori</i>	<i>O. arabs</i>
<i>Eupodotis vigorstii</i>	<i>E. humilis</i>
<i>E. ruficrista</i>	<i>E. gindiana</i>
<i>Cursorius rufus</i>	<i>C. cursor</i>
<i>Pterocles namaqua</i>	<i>P. senegallus</i>
<i>P. burchellii</i>	<i>P. decoratus</i>
<i>Colius colius</i>	<i>C. leucocephalus</i>
<i>C. indicus</i>	<i>C. macrourus</i>
<i>Mirafra sabota</i>	<i>M. gilletti & M. poecilosterna</i>
<i>M. passerina</i>	<i>M. cantilla</i> ^{ns}
<i>Galerida magnirostris</i>	<i>G. fremantlii</i>
<i>Ammomanes grayi</i>	<i>A. deserti</i>
<i>Eremopterix verticalis</i>	<i>E. signata</i>
<i>Myrmecocichla formicivora</i>	<i>M. aethiops</i>
<i>Erythropygia paena</i>	<i>E. hamertoni</i>
<i>Parisoma subcaeruleum</i>	<i>P. boehmi</i>
<i>P. layardi</i>	<i>P. lugens</i>
<i>Laniarius atrococcineus</i>	<i>L. erythrogaster</i>
<i>Spreo bicolor</i>	<i>S. albicapillus</i>
<i>Uraeginthus granatinus</i>	<i>U. ianthinogaster</i>
<i>Vidua regia</i>	<i>V. fischeri</i>
<i>Serinus flaviventris</i>	<i>S. donaldsoni</i>

The *Spizocorys* group of *Calandrella* appears to have evolved three species (*conirostris*, *starki* and *sclateri*) in the south-west; there is a single species (*obbiensis*) in the north-east but whether this represents the ancestral form, from which three successive invasions of the south-west took place, or whether the group evolved in the south-west either from a single or a multiple invasion from the north; or whether *obbiensis* represents an invasion of the Somali Arid from the south, it is not possible to decide. Discussion is hampered by paucity of information about *obbiensis*. From the fact that *obbiensis* appears to be exceedingly rare and local and to combine characters of *starki* and *sclateri*, it may be that it represents an ancestral form that has had its day and is on the road to extinction. Nevertheless, on the whole it appears more likely that the *Spizocorys* group differentiated from other species of *Calandrella* in the South West Arid. It may be added that Hall & Moreau tentatively group *obbiensis* with *C. dunni* of the southern border of the Sahara and *C. personata* of the Kenya desert and not with the *Spizocorys* group. It may also be mentioned that Maclean (1969) would remove *starki* from *Calandrella* and put it into *Alauda*.

The bare-cheeked babbler *Turdoides gymnogenys* is likewise a rather isolated species in its genus with no special affinities but nearest to *T. jardineii*.

The pied babbler *T. bicolor* is considered by Hall & Moreau to be an outlying member of the *jardineii* species-group but it has clearly been isolated from the others for some considerable time and probably represents an early invasion of this stock.

The tractrac and sickle-winged chats *Cercomela tractrac* and *C. sinuata* seem to be closely related, the second connected with *C. schlegelii* by the sickle-shaped first primary (but see Meinertzhagen (1950) on the significance of this). The form of tractrac inhabiting the Namib desert shows astonishing convergence in plumage and size with the local subspecies of *C. schlegelii*. The origins of these three forms must remain unexplained but *C. schlegelii* may be related to *C. sordida* of the East African mountains, as suggested in Table 2. Hall & Moreau, however, regard all three as links between *Oenanthe* and *Cercomela*. Although all three are sympatric over most of the karoo, *sinuata* extends further onto the highveld and into the macchia (i.e., into higher rainfall areas) than either of the others; and *tractrac* alone extends into the Namib desert, with *schlegelii* only along the edges and *sinuata* considerably further inland. The possibility, therefore, of ecological and climatic factors being responsible for speciation must be born in mind.

The Karoo robin *Erythropygia coryphaeus*, while obviously related to other species of *Erythropygia*, does not appear to be closer to one than to another. In the absence of rufous pigment and the poor quality of its song, it suggests an early isolate of *Erythropygia* stock. It may possibly be nearest to the brown robin *E. signata* of the south-east; or to the black bush-robin *Cercotrichas podobe* of the southern Sahara, Somaliland and Arabia. If the latter, it would confirm the views of those systematists (e.g., White 1962) who fuse the genera *Erythropygia* and *Cercotrichas*; and would afford another example of a "species pair".

The cinnamon-breasted warbler *Camaroptera subcinnamomea* is rather doubtfully placed in this genus but Hall & Moreau (1970) consider it "a divergent member of the *C. fasciolatus* superspecies".

The Namaqua prinia *Prinia substriata* is not unlike *P. maculosa* in appearance but its biology is quite different; and rather similar comments apply to the rufous-eared prinia *P.*

pectoralis. Neither of them seems to have close relatives in the north-east, but Hall & Moreau believe *substriata* may be related to *P. robertsi* of the forest fringes of Rhodesia.

The fiscal flycatcher *Melaenornis silens* is not placed by Hall & Moreau in any superspecies or species-group and its nearest relative is obscure. Its present plumage pattern would appear to have evolved to give it a resemblance to *Lanius collaris*; and this mimicry suggests that it may be closest to the similarly mimetic black flycatcher *M. pammelaina* and its allies.

The Herero chat *Namibornis herero*, the fairy flycatcher *Stenostira scita* and the white-tailed shrike *Lanioturdus torquatus* all represent monotypic genera of uncertain affinities and show no connection with the Somali Arid or anywhere else. The flycatcher may be nearer to *Batis* than to any other genus; the shrike is perhaps related to *Prionops* (see Roberts 1946); but the connection is doubtful in both cases; and the chat Jensen & Jensen (1971) regard as intermediate between *Cercomela* and *Melaenornis*.

The nearest relative of the pale-winged starling *Onychognathus nabouroup* is uncertain. There is no particular Somali Arid counterpart with which it can be paired and it is as much like its nearest neighbour *O. morio* as any other species in the genus.

Hall & Moreau believe the dusky sunbird *Nectarinia fusca* to form a superspecies with the coppery sunbird *N. cuprea*, in which case it falls into the class of species most nearly allied to others which occur to the east and north.

As isolated as any species mentioned above is the social weaver *Philetairus socius*. No guess can be made as to its origins.

The cape sparrow *Passer melanurus*, like *Onychognathus nabouroup*, seems to have no particular species in its genus to which it has special affinities; and the same is true of *Emberiza impetuani*, the lark-like bunting, though Hall & Moreau group this last with *E. capensis* and *E. tahapisi*, as being nearer to them than to the *flaviventris* group. However, it differs from the others in the absence of the black and white head pattern and in its gregarious habits.

The red-headed finch *Amadina erythrocephala* may represent a first invasion of the stock which subsequently gave rise to the cut-throat *A. fasciata*, now existing in different subspecies in the north-east and south-west. Hall & Moreau put them in one superspecies.

The black-headed canary *Serinus alario* is probably nearer to the *mozambicus-atrogularis-citrinipectus* group than to any other; though it has also some characteristics of *S. canicollis*. But its very different plumage suggests long isolation and it has no Somali counterpart.

The white-throated seed-eater *Serinus albogularis* is another isolate. Hall & Moreau group it with *flaviventris* and *sulphuratus*; but I am not at all sure that its nearest relatives are not *S. gularis* of the African savannas and *S. leucopterus*, confined to the Macchia of the south-western Cape, which, like it, lack yellow pigment (except on the rump in *albogularis*).

The Damara rockjumper *Achaetops pyncnopygius* is not included in the total of isolates since, although perhaps meriting generic separation, it is clearly related to *Sphenoecus afer* of the South African mountains.

It is clear from the above analysis that there has been an interchange of forms between the South West Arid and Somali Arid Districts; that this interchange has occurred several times; but that a complete intermingling of the avifaunas is highly unlikely ever to have taken place in view of the five peculiar genera present in the south-west (*Namibornis*, *Stenostira*, *Achaetops*, *Lanioturdus* and *Philetairus*) and four (*Pseudalaemon*, *Speculipastor*, *Dinamellia* and *Rhyncho-*

struthius) in the north-east. These views obtain support from the analysis of some of the birds common to, or closely related in, the two districts.

It would appear probable that the ancestral forms of *Namibornis*, *Lanioturdus*, *Philetairus*, *Certhilauda*, *Stenostira* and *Camaroptera subcinnamomea* evolved *in situ* from unknown ancestors which may or may not have had Pliocene representatives in the north-east; that the ancestors of *Circus maurus*, *Agapornis roseicollis*, *Tockus monteiri*, *Calandrella (Spizocorys) spp.*, the three *Cercomela* species discussed above, *Erthropygia coryphaeus*, *Onychognathus nabouroup*, *Passer melanurus*, *Serinus alario*, *S. albogularis* and *Emberiza impetuani* similarly evolved in the South West Arid, probably from more generalized form which subsequently radiated into other species elsewhere; and that most of the remaining characteristic South West Arid species represent two or more waves of invasion from Somali or more local speciation from stocks represented by forms widespread elsewhere in South Africa. But the possibility of speciation in the south and subsequent invasion of the north (e.g., in the *Spizocorys* group) cannot be ruled out, particularly in view of the age of the southern deserts. It is tempting to attribute the "species-pairs" to an earlier and the common species to a later invasion but this makes no allowance for differential rates of evolution and is therefore purely speculative.

A number of the South West Arid species have a marked association with rocks—e.g., *Francolinus hartlaubi*, *Achaetops pycnopygius*, *Namibornis herero* and several others. In the case of the three species named, extension of their range eastward would be prevented by the interposition of the sand-covered Kalahari desert. Why they do not extend further south, however, is not clear, but none reaches further than 23°S. In the case of other rock-lovers, such as *Monticola brevipes*, *Camaroptera subcinnamomea* and *Onychognathus nabouroup*, they extend too far south for the Kalahari to form a barrier to their dispersal, but for the first and third of these, the areas to the east are occupied by related species which would presumably exclude them.

I have not discussed here Macdonald's suggestion (1957) that the difference between winter and summer rainfall might be a factor in speciation because, with the possible exception of *Pycnonotus capensis*, I can find no evidence that the ranges of any species-pair bear any relation to the rainfall changes.

It should not be thought that the phenomenon here discussed is peculiar to birds. "Species-pairs" exist in mammals (e.g., *Oryx gazella* and *O. beisa*) and so do conspecific species with one population in the south-west and another in the north-east (e.g., *Otocyon megalotis*—see Meester 1965); and Dr. R. F. Lawrence (*pers. comm.*) has drawn my attention to similar cases among spiders as observed by him (Lawrence 1927) and by de Dalmas (1920).

I am deeply indebted to Mrs. B. P. Hall for criticism of the draft of this paper, correcting errors and making stimulating suggestions. She must not, however, be held responsible for the opinions expressed.

SUMMARY

The avifauna of the South West Arid Area of Africa is made up of three parts:

1. Species identical with, or closely related to, those of adjacent areas to the east and north;
2. Species identical with, or closely related to, those of the arid regions of north-east Africa;
3. Indigenous species of doubtful affinity.

Possible derivations of these last are briefly discussed.

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