ADAPTATION OF **CROCIDURA HIRTA** PETERS TO VARIATION IN MOISTURE CONDITIONS IN SOUTHERN AFRICA

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Shrews are amongst the most widespread local small mammals and different species of shrews can be found in every part of Southern Africa except the extremely arid Namib desert. This is no doubt at least partly due to the adaptability of these animals to a variety of different environmental conditions.

Probably one of the most vital factors affecting the distribution of many animals in Southern Africa is water. Not only is the presence of water imperative for the survival of many animals, it also, by determining to a certain extent the distribution of plants, indirectly affects the spread of the herbivores dependent on these plants, as well as their predators.

Only one shrew, Crocidura hirta deserti *(Schwann) has been reported from the Kalahari Gemsbok Reserve (Davis, 1958, 186). In this form and the closely-allied C. h. hirta Peters, it is possible to discern a marked degree of adaptation to environmental conditions, and particularly to the wide range of moisture conditions to which C. hirta is subjected in different parts of its range.

The localities from which the two subspecies of C. hirta in Southern Africa have been recorded are listed in table 1, with loci indicated after the system used by Davis (1949). In fig. 1 these localities are plotted, those of hirta by means of squares and those of deserti by means of triangles. Furthermore the limits of the zones with mean annual rainfall less than 200 mm. and more than 600 mm., are indicated by means of dotted lines.

It appears that C. h. hirta extends from north of the Zambesi through Southern Rho'desia, Moçambique and the Transvaal to Durban in the east and Bothaville, northern Orange Free State, in the west.

C. h. deserti extends from north of the Cunene, whence it has been recorded from Capelongo, Angola and Shangombo, Barotseland, to Ngamiland in

C. deserti is commonly regarded as a distinct species. The inclusion of this form under C. hirta is based on results obtained in an as yet unpublished revision of the taxonomy of Southern African Crocidura.

South West Africa and southward to western and southern Bechuanaland Protectorate and the extreme northern Cape Province.

The two subspecies differ very markedly in colour. Typically hirta is much darker than deserti, cinnamon-brown above and silvery grey below, while deserti is much paler, dorsally pale fawn and ventrally off-white or creamy, with very little grey. For the most part these colour differences are so striking that it would be tempting to regard the two forms as distinct species. However, colour is somewhat variable, so that extremes are hard to distinguish and sometimes actually overlap. For example, specimens of hirta from Bothaville are so pale that Roberts (1928, 322, 1935, 193) regards them as deserti. Similarly, in a fairly long series of hirta from Pretoria, and another from Bulawayo, specimens occur which are extremely pale while the darkest specimens from these localities are darker than average. The palest specimens from Pretoria overlap in colour with deserti. Further overlapping specimens have been collected at Montrose Estates, Zoutpansberg; Blinkwater, Mopani; Rhodes Drift and Balovale, Barotseland. Similarly a specimen of deserti from Shangombo, although decidedly belonging to this form, overlaps in ventral colour with hirta. Further overlapping specimens of deserti have been collected at Quickborn, South West Africa.

Certain significant points arise from the above. First, there appears to be a relationship between the western extreme of the range of C. hirta and rainfall conditions in that area. As shown in fig. 1, the species has been collected at only one locality, Kij-Kij waterhole, in the below 200 mm. mean annual rainfall zone. Elsewhere the range of the species remains in the above 200 mm. zone, and extends further to the west where the edge of this zone recedes westward in northern South West Africa.

It may be noted in passing that the reason for the restriction of the range of C. hirta in the south is not clear. The species is clearly very adaptable, as witness its occurrence in such diverse regions as the eastern escarpment of Southern Rhodesia on the one hand, and the Kalahari and Ngamiland on the other. No barriers of physiography, rainfall or vegetation appear to limit its southward spread, and in fact the eastern coastal strip is a common dispersal route for small mammals as well as many other animals. Its failure to range further south along this strip or any other route is therefore hard to understand. In this respect it is interesting to note that a number of snakes, e.g. Aspidelaps scutatus, the shieldnose snake, and Psammophylax tritaeneatus, the striped skaapsteker, have very similar distribution patterns. Not only are their ranges restricted in the south in a very similar fashion to that of C. hirta, but in the west also their ranges are limited in much the same way as that of this species (Dr. V. FitzSimons, in litt.)

To return to the relationship between the range of C. hirta and rainfall distribution, there appears to be a much more striking correlation when the

two subspecies are considered independently. Fig. 1 shows that the range of C. h. hirta is restricted almost entirely to the above 600 mm. mean annual rainfall zone. The only localities falling outside this zone are Bothaville; Crecy; Moorddrift, Waterberg; Blinkwater, Mopani; and Rhodes Drift. Most of these are only just outside this zone, while Rhodes Drift, which lies further away from it, is along the Limpopo River, where presumably a moisture-restricted animal should be able to extend into an otherwise dry area. In the north-eastern Transvaal, the southern part of Southern Rhodesia, and Moçambique there is an intrusion of the dry 200-600 mm. mean annual rainfall zone encountered further west into the eastern higher rainfall zone. C. h. hirta has not been recorded from any locality in this area except Rhodes Drift. Apparently the low rainfall conditions encountered here are responsible for a gap in the distribution of this form.

Similarly, deserti appears to be largely restricted to the 200-600 mm. mean annual rainfall zone. As noted above only one locally, Kij-Kij waterhole, falls in the below 200 mm. zone. For the rest it occurs in the above 600 mm. zone at only three localities: Maschi River, Caprivi; Shangombo, Barotseland and Capelongo, Angola. Of these Maschi River falls only just outside the 200-600 mm. zone, and the single specimen from Shangombo overlaps in ventral colour with hirta.

As shown above, extreme specimens of hirta have been collected at Bothaville, Pretoria, Blinkwater, Rhodes Drift, Bulawayo and Balovale. All these localities except Balovale fall along the margin of the above 600 mm. mean annual rainfall zone, or just outside it. Similarly, a specimen of deserti from Shangombo, outside the rainfall zone normally inhabited by this form, overlaps with hirta. In fact therefore, transitional specimens of both subspecies are known from localities which are marginal not only in relation to the range of the form concerned, as is to be expected, but also in relation to the rainfall area inhabited by each form.

It is obvious therefore that in C. hirta in Southern Africa colour adaptation is closely linked with geographic variation in rainfall, to the extent that not only does the paler subspecies occur in the more arid area, but the ranges of the two subspecies seem to be determined to some extent by the rainfall zones they inhabit, and transitional specimens between the two forms are likely to be found in the area of transition between these rainfall zones. Besides this, the degree of colour change is of a magnitude more often associated with species than subspecies differences. It appears therefore that C. hirta represents a most dramatic illustration of Gloger's rule, that animals living in warm, humid areas are more melanic than those living in cool or arid regions.

Nevertheless it is necessary to qualify this statement in respect of the distribution of the two subspecies north of the Zambesi and Cunene. C. h. hirta occurs extensively in Northern Rhodesia and elsewhere, while deserti is known

from Shangombo and Capelongo. Both localities fall in the above 600 mm. mean annual rainfall zone, as does Balovale, from whence a series of hirta has been collected that overlaps in colour with deserti. If the relationship between colour and rainfall had been as close here as in Southern Africa, not only should deserti not have occurred, but hirta should have been much darker. It is obvious that here other factors determine the limits of the two subspecies and that rainfall distribution is not of the adaptive significance that it is in Southern Africa.

This point is important in considering the next question: If colour variation in C. hirta is the consequence of environmental factors, what reason is there to assume that the two subspecies distinguished on this colour variation are genetically based, and do not merely represent direct physiological adaptations to these environmental conditions?

Unfortunately it has not been possible to obtain live deserti in order to

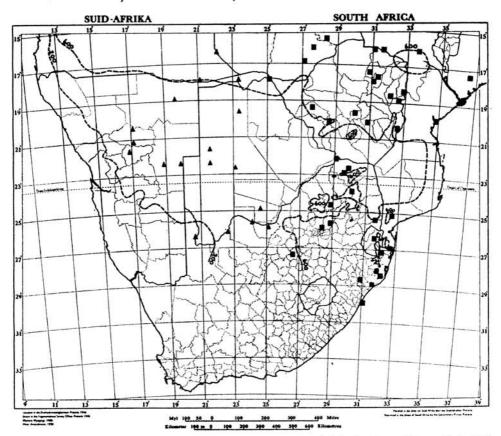


Fig. 1. Localities from which Crocidura hirta has been recorded in Southern Africa. C. h. hirta indicated by means of squares, and C. h. deserti by means of triangles. Limits of zones with mean annual rainfall below 200 mm. and above 600 mm. indicated by means of dotted lines.

ascertain whether they change colour under more moist conditions in the laboratory, or whether their progeny, born and reared under moister conditions, are any darker than the parents, collected in dry areas. However, the evidence of the Shangombo and Capelongo material is suggestive. Here one is in fact dealing with deserti living under moister conditions, yet colour is apparently not much affected, as would be expected if adaptation had been non-genetic. So it can be tentatively concluded that in C. hirta this colour change is genetically based.

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TABLE 1.

Localities plotted in fig. 1, with loci indicated after the system used by Davis (1949)

Locality	Locus
Crocidura hirta	
Balovale, Barotseland, (Extralimital, not plotted)	1323Ca
Chilanga, Northern Rhodesia (extralimital)	1528Cb
Monze, Northern Rhodesia (extralimital)	1627Ba
Choma, Northern Rhodesia (extralimital)	1627Cc
Junction, Messenguez and Zambesi rivers	1631Aa
Msusa, Zambesi river	1631Ba
Tette, Moçambique (extralimital)	1633Ba
Kazungula, Northern Rhodesia (extralimital)	1725Cc
Concession, near Salisbury, Southern Rhodesia	1730Bd

Bindura township, near Salisbury, Southern Rhodesia Rhodesia	1731Cb
Salisbury, Southern Rhodesia	1731Cc
Villa Pereira, Boror, Moçambique (extralimital)	1736Bc
Vumba, Southern Rhodesia	1832Bd
Rusape, Southern Rhodesia	1832Ca
Palmerston, Umtali lands, Southern Rhodesia	1832Dc
Gwaai siding, Southern Rhodesia	1927Bc
Selukwe, Southern Rhodesia	1930Ca
Beira, Moçambique	1934Dd
Bulawayo, Southern Rhodesia	2028Ba
Fort Victoria, Southern Rhodesia	2030Bd
Chipinga and Mount Selinda, Southern Rhodesia Rhodesia	2032Bc
Rhodes Drift, Transvaal/Rhodesia border border	2229Aa
Blinkwater, Mopani, Transvaal	2229Db
Montrose Estates, Zoutpansberg	2229Dc
Tzaneen, Transvaal	2330Cc
Geluk Camp, Crecy, and Moorddrift, Waterberg, Transvaal	2428Db
Pretoria District, Transvaal	2528Cd
Rhenosterkop, Elands River, Transvaal	2528Db
Hectorspruit, Transvaal	2531Bc
Magude, Moçambique	2532Ba
	2631Bc
Ranches Ltd., Swaziland	
Ranches Ltd., Swaziland Maputa, Zululand	2632Dc
Maputa, Zululand	2632Dc
Maputa, Zululand Ingwavuma, Zululand, and Tete Pan, Ubombo	
Maputa, Zululand Ingwavuma, Zululand, and Tete Pan, Ubombo Angra Pequina, Bothaville, O.F.S	2732Aa
Maputa, Zululand Ingwavuma, Zululand, and Tete Pan, Ubombo	2732Aa 2726Ba
Maputa, Zululand Ingwavuma, Zululand, and Tete Pan, Ubombo	2732Aa 2726Ba 2830Db
Maputa, Zululand Ingwavuma, Zululand, and Tete Pan, Ubombo	2732Aa 2726Ba 2830Db 2831Bb

Crocidura hirta deserti.	
Capelongo, Angola (extralimital, not plotted)	1415C
Shangombo, Barotseland (extralimital)	1622A
Maschi River, Caprivi strip	1723Cc
Gangongo, Western Caprivi strip	1721Cc
Karakuwisa, South West Africa	1819Da
Shorobe, near Maun, Bechuanaland	1923Cb
Waterberg, South West Africa	2017Ac
Road from Okahandja to Amatako, South West Africa	2116Db
Quickborn, South West Africa	2117Aa
Gemsbok Pan, Ghanzi dist., Bechuanaland	2121Da
Gobabis, South West Africa	2218Bd
Karolinenhof and Sandfontein, South West Africa	2219Bd
Okwa, Bechuanaland	2221Bc
Kaotwe Pan, Ghanzi dist., Bechuanaland	2223Ca
Kiri Pits, 50 miles N.W. of Noshapa, Bechuanaland	2424Dc
Molopo River, Bechuanaland	2524Ca
30 miles W. of Mafeking, Cape Province	2525Cc
Kij-Kij waterhole, Kalahari	2620Bc
Molopo river, W. of Morokwen, Cape Province	2622Ba

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