ENVIRONMENT AND AMPHIBIAN DISTRIBUTION IN ZULULAND

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Although the fauna of north-eastern Zululand has yet to be fully surveyed, our present knowledge shows that this area is populated by an essentially East African assemblage (e.g· Poynton 1961). To the south and west of this area, however, the tropical fauna becomes markedly thinned out and it is progressively replaced by a non-tropical fauna. Consequently the region provides exceptional opportunities for studying the controlling effect of environmental factors on a zoogeographical change of major importance.

Work on the amphibian fauna of this area has shown that these opportunities are matched by enormous heuristic difficulties. The aim of this paper is to outline the difficulties encountered, and to suggest possible openings for future work. For the sake of convenient presentation, the paper will be primarily concerned with the southward subtraction of the tropical fauna and its gradual replacement by a non-tropical fauna. The westward transition inland will be considered mainly in relation to the southward transition down the coast.

The faunal change-over along the coast is represented graphically in Figure 1. The species composition of the tropical and non-tropical assemblages is given in Poynton 1964. Fig. 1 shows that the zone of steepest tropical subtraction lies between latitudes 28 and 29 degrees south, that is, between the northern end of Lake St. Lucia and Mtunzini. In this region the Mozambique Plain continues into rolling coastal lowlands without any abrupt physiographic or climatic changes, and consequently the abrupt faunal change is unexpected. To try to explain the existence and geographical location of this transformation, all possible environmental factors have to be considered. These can be treated under the headings Physical Factors and Biotic Factors.

PHYSICAL FACTORS

1. *Geology, topography and water types.* A single geological formation underlies most of the Mozambique Plain, and where it narrows down towards the south it presents a pattern to which the subtraction of the tropical amphibian fauna conforms. But while there is an obvious correlation between the pattern of distribution and the pattern of surface features, a direct causal relationship within this correlation is difficult to establish. To the north of Zululand, the greater westward spread of tropical species does not conform to the topography or the underlying geological formations, and consequently it is not possible to explain the pattern

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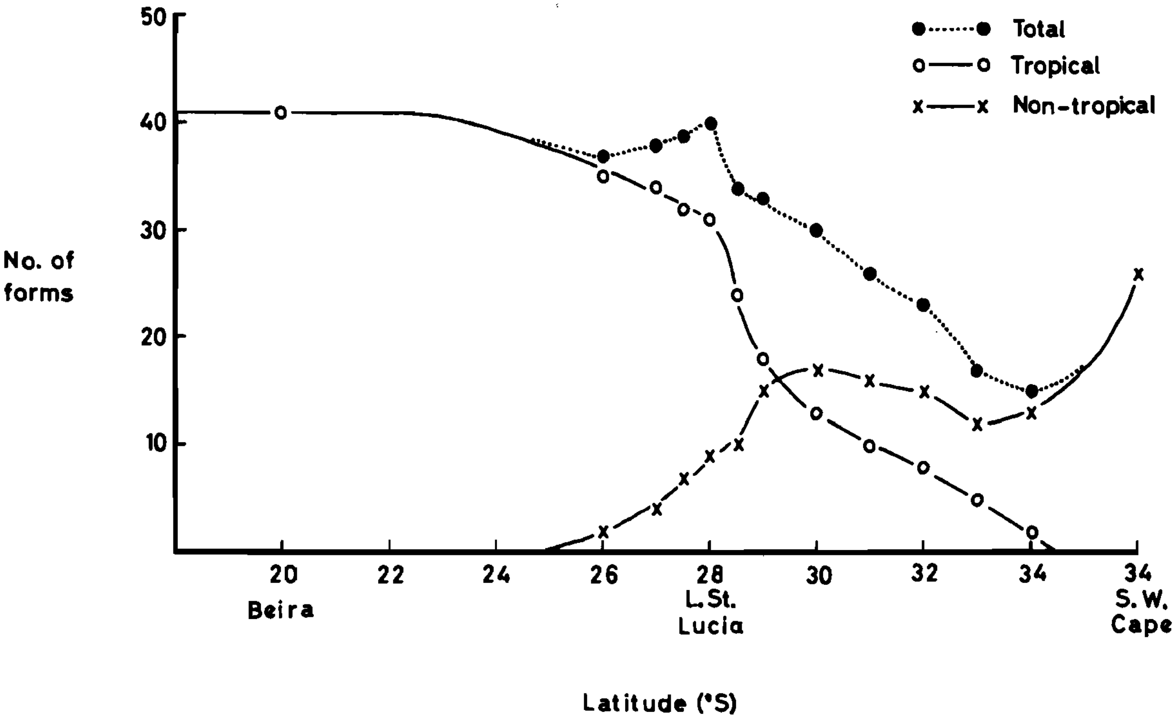

FIGURE 1

Succession of amphibian faunas along the eastern and southern coastal strip of Southern Africa.

of distribution in Zululand directly in terms of topography: there must be other factors in this area which are causing the distribution pattern to follow the topographical pattern, at least to the west. To the south the topographical changes are so slight as hardly to constitute a 'pattern', and gross habitats do not appear to be affected.

The fresh waters in Zululand are mainly slightly alkaline, and no major changes in the pH occur until the southern Cape is reached, by which time the tropical subtraction is almost complete.

2. *Rainfall and evaporation.* Rainfall and saturation-deficit show no marked change from north to south along the Natal coast, although a slightly wetter area (above 1250 mm. or 50 ins. per annum) should be noted south of Lake St. Lucia (see for example Schulze 1965). The absence of the bullfrog *Pyxicephalus adspersus* Tschudi and also of *P. delalandei cryptotis* (Boulenger) from the area between southern Zululand and the Kei River might conceivably be due to the higher rainfall in this area (see maps 25 and 26 in Poynton 1964). These burrowing frogs are more characteristic of dry areas, although they do occur in middle Mozambique, where the rainfall is high (over 1000 mm.). This possibility has not yet been investigated ecologically, but at first sight it does not seem particularly likely. This matter is considered further in the discussion.

3. *Seasonality.* The differentiation between summer and winter becomes greater with increasing latitude, particularly with regard to day-length. A resulting hormonal effect could therefore be looked for, which in the field could be reinforced by an accompanying southward decrease in temperature. However, this possibility has yet to be explored, and it would be of relevance only to the southward subtraction of the tropical fauna, not to its subtraction westwards.

4. *Temperature.* There is a very gradual decrease in temperature with increasing latitude. The extent of this decrease is indicated by the mean annual temperatures of the following stations: Cape St. Lucia 21.5 ± 7.9°C; Durban 20.5 ± 8.3°C; Port St. Johns 20.0 ± 6.5°C. There is a much more rapid decrease in temperature as the land rises westwards.

Testing the relationship between the westward spread of a tropical species along 29°S and the southernmost extension of its range yields a slight correlation ($r = +0.59$). This suggests a tendency for the species which extend the furthest south also to extend the furthest west into the cool uplands. Temperature is the only climatic factor that varies in the same fashion, but the correlation is not particularly significant, and it offers no causal explanation for the distribution pattern. Temperature will be considered further in the discussion.

5. *Physical history of the area.* The coastal plain has been periodically flooded by the sea, and this flooding appears to have been particularly frequent during the Pleistocene (King and Belderson 1961). Consequently the present pattern of distribution on the plain cannot be regarded as long established, not only because of this marine factor but also because of the effect of Pleistocene climatic oscillations. The marine factor might very well account for the precipitous southward subtraction of tropical freshwater fishes in Natal (e.g. Poynton 1961), but anurans are so mobile that the same explanation cannot be used for this group. Even the markedly aquatic platanna (*Xenopus*) moves extensively over land.

The influence of competing species is a factor that could be expected to prevent the pattern of distribution from closely following the overall climatic and physiographic changes, and this possibility will be considered later under the biotic factors. But the physical history of the coastal plain itself gives no explanation as to why the transition pattern shown by the Anura occurs where it does, or why it is so abrupt.

It is also not possible to account for this pattern in terms of the recent upheavals caused by man. For example, the Mtunzini area (29°S) possesses an undisturbed island in a region of intense cultivation, yet the anuran fauna there shows no deviation from the overall pattern.

BIOTIC FACTORS

1. *Vegetation.* In north-eastern Zululand the vegetation consists of a complex of tropical communities. The tropical flora becomes impoverished and progressively replaced to the south by non-tropical elements (Poynton 1961). But this botanical transformation is not accompanied by physiognomic changes that could affect the diversity and availability of anuran habitats. Anuran habitat preference resolves itself essentially into a forest/non-forest choice, and this preference stops largely at the presence or absence of close tree cover; the actual botanical composition of the plant community appears to be without much significance provided the basic physiognomy is suitable. Therefore the phytogeographical change occurring

in this area does not seem to be responsible for the anuran pattern of change. Recent interference with the natural vegetation due to cultivation and settlement also cannot be regarded as an important factor, since wide ecological tolerances have enabled the amphibian fauna to live successfully in cultivated regions and even in urban areas. Disturbance is most marked where forest has been destroyed, resulting in the replacement of the small sylvicolous fauna (Poynton 1964) by the savanna fauna; or where plantations have been established, adversely affecting the savanna fauna.

2. *Predators and prey.* In spite of the very general zoogeographical transformation that takes place from the St. Lucia area southwards, at present there is no evidence to show that this transformation affects the overall balance of either predator species or the type and availability of prey. The stability of this balance is due to the great variety of predators and prey involved. The amphibian fauna makes a very broad ecological contact with its surroundings, and consequently the biogeographical changes that take place in this area, however profound and general, do not appear to be a direct cause of the anuran pattern of change. The causal factors evidently lie behind the general biogeographical change rather than within it.

3. *Competition between tropical and non-tropical species.* The steep southward subtraction of the tropical species occurs in an area where the tropical fauna overlaps the non-tropical fauna. There is good reason for assuming that the tropical fauna is at present tending to expand southwards (Poynton 1964) and if this is the case, then in areas where the expanding fauna is competing with an established non-tropical fauna, it is likely that the rate of colonisation and overall movement of the tropical fauna will be impeded. This effect would be particularly likely to occur in ecologically marginal areas such as are encountered at the edge of the range of a species, where the stress of competition from other species is likely to be more severe than in an ecologically central area. The resulting 'friction zone' in the area of overlap would show on a graph as a steep tailing off in the number of tropical species, coupled with a reversed falling off of non-tropical species, as is in fact shown in Fig. 1.

This 'friction zone' theory has been applied as a promising hypothesis to account for the observed pattern of distribution, but in practice it does not find much supporting evidence. As a background to discussing the hypothesis, it should be noted that the pattern is shown mainly at the species level: only two genera, *Phrynomerus* and *Chiromantis* (each with only one species), reach their southernmost limit in Zululand, and neither are replaced by ecologically equivalent non-tropical genera or species.

The genus *Ptychadena* is a typical case illustrating the weakness of this hypothesis. This is a genus that can be regarded as a tropical counterpart of the essentially non-tropical genus *Rana*. Six species enter Zululand down the Mozambique Plain. Only two of these species pass beyond Durban. A third reaches the Tugela Basin, and the remaining three reach their southern limits between 28 and 29 degrees south. None of these species appears to be ecologically replaced by the two species of *Rana* that succeed in reaching into north-eastern Zululand. *R. fasciata* Smith is a winter breeder in Zululand, and is rarely found in summer when *Ptychadena* is breeding. *R. angolensis* Bocage is much more widespread than is *fasciata*, even though it is absent from most of the Mozambique Plain, and it tends to breed throughout the year. But in northern Zululand these frogs are more common at the edges of streams than at the edges of pools and swampy areas where *Ptychadena* normally breeds and consequently, although there is a fairly broad geographical overlap, competition between *R. angolensis* and the *Ptychadena* species is limited by different habitat preferences.

Seven other tropical genera become thinned out in the same way as *Ptychadena*, apparently without being ecologically replaced by non-tropical species.

In the case of three other genera, the genus is represented in northern Zululand by one tropical species and one non-tropical species. In the aquatic genus *Xenopus*, the tropical *muelleri* (Peters) extends as far south as the Charters Creek area of Lake St. Lucia (28°15'S), and the non-tropical *laevis* (Daudin) overlaps the range of *muelleri* at least as far north as Bela Vista (26°20'S). In the completely terrestrial genus *Arthroleptis*, the replacement between the tropical and non-tropical species takes place at Lake St. Lucia, with no known geographical overlap. The tree-frog genus *Leptopelis* shows a broad geographical overlap of the tropical and non-tropical species in the region between Richards Bay (28°50'S) to Lake Sibayi (27°25'S). In the case of *Leptopelis*, differences in habitat preference probably reduce ecological competition, since the tropical species occurs in open tree savanna while the non-tropical species tends to occur in forest. But there might be head-on competition in the case of *Arthroleptis* and *Xenopus*, and the ecology of the *Xenopus* species pair is at present being investigated.

It is clear from these examples that the situation in the 'friction zone' is extremely complex, there being strong indications of competition between some tropical and non-tropical species, but no suggestion of competition being a limiting factor in other tropical species. The latter condition appears to be more general, particularly as the non-tropical fauna is composed of fewer species than the tropical fauna (Fig. 1), and so these non-tropical species do not replace the tropical species in a strictly numerical sense: indeed the dwindling tropical fauna leaves some habitats unoccupied to the south, and appears to relieve pressure on others. This appears to be a feature of tropical subtraction. However, the full picture is still far from clear because numerical population data are not available: even if there are fewer non-tropical species than tropical species, it is not yet known whether this numerical decrease also applies to the number of individual frogs per unit area. But in the present state of knowledge there is little promise that the 'friction zone' hypothesis has any general application in accounting for the overall pattern of distribution in Zululand.

We are grateful to Mr. B. R. Stuckenberg for the suggestion that the small size of the populations in this narrow coastal strip could accentuate any 'friction zone effect', and could conceivably help to explain why the pattern of transformation occurs in the area where it does. Clearly there is a very large and seemingly most rewarding opening for population ecology studies in this area.

DISCUSSION

As noted above, physiography is an obvious physical factor to be considered because of its close correlation with the pattern of distribution, but the factor or factors causing this correlation in this particular area must be sought beyond the topography itself. These primary factors appear to be climatic. Regarding temperature, a correlation of a sort between the mid-winter month temperature and the pattern of amphibian distribution has previously been pointed out (e.g. Poynton 1964), and the 18°C mean mid-winter month isotherm chosen by Köppen to demarcate a tropical climate is convenient for demarcating a tropical centre of the amphibian fauna (Poynton 1964). But this correlation is not held to represent direct causal relationships: mid-winter temperature conditions may be useful indicators of a whole climatic complex that controls distribution, but they are not necessarily in themselves the ecologically effective factors. They are to be considered as indicator or marker factors of use in a geographical context, but not necessarily effective factors in an ecological context. There is in fact no perceptible correlation between the pattern of southward tropical subtraction and the pattern of extreme minimum night temperatures as shown in Schulze 1965, Fig. 77. This is not surprising, since amphibians tend to hibernate in winter, particularly during the coldest spells.

A closer relationship is indicated between distribution and night temperatures during summer. This temperature pattern can be expressed as the frequency of tropical nights (nights with a minimum temperature above 20°C) as in Schulze 1965, Fig. 83. These conditions typically occur when the air is humid and the sky overcast—conditions which appear to be optimal for amphibian breeding. The frequency of these nights decreases from ninety to five per annum between northern Zululand and the southern Cape, and this great decrease could be expected to have some bearing on the tropical subtraction in this area. It is also worth pointing out that the southern Cape and eastern highlands fall into the same area with a frequency below five tropical nights per annum, which accords very well with the distribution of the temperate amphibian fauna in this area. However, a causal relationship between the frequency of breeding and the frequency of presumed optimal breeding nights for the various species has not yet been established, and indeed a demonstration of a causal relationship will not be possible until an observer can spend at least one full breeding season in the study area. The effect of geographical variation in the length of the possible breeding season is undoubtedly a most promising avenue for investigation, and deserves attention in the study of all animal groups in Zululand.

In considering other ways in which temperature could affect amphibian distribution, it should be noted that workers on north-temperate anurans give evidence to show that there are relationships between the type of spawn mass laid and the temperature tolerance of the eggs (Savage 1961). But in the highly diversified anuran fauna of the Zululand coast, it seems that whatever the environmental effect on the type of spawn might be, it is largely overshadowed by taxonomic characteristics: the various species keep to the typical habits of their particular genus or subgenus, regardless of whether they are tropical or non-tropical in distribution. Small variations within the gross spawning pattern, however, have not yet been looked for.

Moore (1942) has shown that the rates of tadpole development are a direct adaptation of the species to its environment, and doubtless a similar adaptation is present in southern African amphibians. But even if such an effect is to be shown, the problem still remains as to why so many different species should have a similar temperature reaction. This difficulty remains with all the possible temperature-influenced factors: a demonstration of one general range of temperature tolerance in tropical species and of other ranges in non-tropical species still does not touch on the evolutionary and zoogeographical problem of why there is such a marked clustering of the various species into these groups.

Moreover, even if temperature is shown to be the main determining factor of amphibian distribution, it still has to be explained why the abrupt subtraction of the tropical fauna should occur in an area that shows no abrupt temperature gradient. Some biotic factors that could conceivably augment the temperature effect have been discussed above under the heading of competition. Another possible factor to be noted is that in the area between 28 and 29 degrees south, an increasing rainfall gradient overlies the decreasing temperature gradient. Furthermore, this rainfall gradient passes beyond the level that is normal for the Mozambique Plain. It has already been noted that the southward subtraction of tropical *Pyxicephalus* species in this area might possibly be related to the southward increase in rainfall. As the tropical fauna as a whole is apparently at the end of its optimal thermal range in this area, a more general effect of increasing rainfall must be borne in mind, however unlikely it may seem at first sight. The increase in rainfall appears to have no appreciable effect on the availability and composition of gross habitats, and so at the moment this factor appears to offer no help towards solving the problem.

Clearly historical factors must have as much bearing on the problem as has the present environmental pattern: the dramatic zoogeographical change can receive a full explanation only in the light of a faunal pattern that continues to shift with oscillations in the climatic pattern over a great period of time. At present, precise historical information is almost entirely lacking.

In Zululand the effect of human activity is all too obvious in the case of mammals and many types of birds. But the upheaval has not yet become so catastrophic as to interfere seriously with the distribution of all elements of the fauna. If the heuristic problems encountered during this present study are anything to go by, the full elucidation of the controlling effects of environmental factors on animal distribution in Zululand promises to be a lengthy undertaking. It can only be hoped that good progress is made before the effect of human settlement and cultivation finally becomes the single factor determining plant and animal distribution in Zululand.

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SUMMARY

In Zululand an essentially East African fauna becomes progressively replaced by a non-tropical fauna. Subtraction of the tropical amphibian species is heaviest between 28° and 29°S, and as this area shows no abrupt physiographic or climatic changes from north to south, the abrupt faunal change is unexpected. Possible effective environmental factors are considered, and particular note is made of an apparent relationship between temperature, the frequency of optimal breeding nights and distribution. Possible competition between tropical and non-

tropical species is seen as a 'friction zone' impeding the expanding tropical fauna where it comes into contact with the established non-tropical fauna. In practice this 'friction zone theory' appears to have at best only limited application.

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