SOME ASPECTS OF ADAPTATION IN DESERT MAMMALS

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(Opening Address by the Symposium President)

I should like first to explain by means of an analogy the somewhat odd fact of my occurrence before you tonight.

As mammalogists, you will all be familiar with the story of the evolution of the mammalian middle ear, which is referred to in one well-known textbook as "an example of the lack of design in adaptive structures". You will recall that three separate elements which functioned first as gill bars, then as parts of the jaws or as struts attaching the jaw to the cranium, became incorporated as ear ossicles one at a time during the course of vertebrate evolution. Each of these changes was innocuous enough by itself, but each led on to further changes which in sum produced the remarkable situation in which three bones, the malleus, the incus, and the stapes, which were originally articular surfaces or struts, now function in a completely different way as components of a sense organ.

During the planning of the present symposium there occurred, again, a series of apparently harmless decisions; the first was to hold the symposium in Salisbury, the second to ask the head of the local Zoology Department to act as President, and the third to have a Presidential Address. Each decision by itself seems not unreasonable, but we can now with hindsight discern the dreadful inevitability of a process, the culmination of which you see before you, in which your Symposium President who is by nature an arthropod physiologist is called upon to perform a most unlikely function, namely to address an audience of mammalogists.

The textbook referred to above suggests that the articular bone was pressed into service as an ear ossible because it was lying about at the right place at the right time with nothing else in particular to do. I do not want to press the analogy as far as this.

Having by this over long introduction attempted to recruit your sympathy, and to blunt your critical faculties, I should like to say something in a rather unsystematic way about adaptation to environment, mostly in desert mammals. There does not appear to be anything in our programme of papers during the next few days on this subject, so that the likelihood of immediate contradiction is mercifully remote. I certainly do not intend a complete survey o this very large field. I propose rather to present a rather personal *pot pouri* by referring to one or two aspects that have caught my attention, either as significant developments which open up the field for further work, or as gaps in our knowledge which urgently need filling.

Commentators who persist in pointing with righteous indignation to opportunities for research which are not being exploited can become more than a trifle tiresome; for one is often very well aware of the need for work in a particular field—the matter is a question of priorities in respect of man-power and finance. In my own defence I can only plead absence of indignation and righteousness. I am a little encouraged too, by the thought that since

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mammalogy covers such a wide field of enquiry, there may be mammalogists who are only a little less ignorant of my small corner of it, than I am of most of it.

First, a word about "adaptation" itself. This term, which is often used without much discrimination, is nevertheless appropriate in describing certain conditions and processes which are of interest to all biologists if only because their explanation must form the basis of any satisfactory theory of organic evolution.

P. B. Medawar (1951) drew attention to an important aspect of this problem when he pointed out that many adaptations which are genetically built in may be copied, as it were, in the same or other animals by responses to particular environmental stresses. Thus, thickening of the skin on the sole of the human foot, and flexure lines in the palm of the hand, both arise during foetal development; while thickening of the skin as a response to mechanical abuse (as in gardening) and expression lines on the face, are developed only in response to environmental stress. The pattern of callosities with which camels, ostriches and warthogs (for example) are provided, would presumably develop in response to these animals' habits of life. But in fact they develop in the embryo almost as if in response to some future need.

These sorts of adaptations, which are genetically obligatory, but which are closely paralleled by responses to the environment, are those which seem to fit well with a Lamarckian interpretation. The effect of using an organ, you will recall, was held by Lamarck to be transmitted to succeeding generations, so that by bending my hand in a particular way I contribute something to the pattern of creases on the hands of my children.

Other adaptations of the skin, however, as Medawar pointed out, such as its transparent nature where it covers the eye as the cornea, cannot conceivably receive a Lamarckian explanation in terms of use or disuse. No amount of peering through opaque skin is going to make it transparent.

Waddington (1959) then took the problem of the apparently Lamarckian adaptations further, and showed in experiments on fruit flies that characters induced by the environment may, if the selection pressure is high enough, become built into the obligatory developmental machinery. In terms of camels' callosities his explanation of this effect would run somewhat as follows:

Let us invent a proto-camel whose callosities develop only in response to abrasion of the skin. In these animals biochemical machinery for producing the thickening is clearly present. If, now, there is a great advantage in developing appropriate callosities quickly, natural selection will ensure the production of gene complexes which permit the response to be more and more readily initiated, until even a slight abrasive stimulus will set the whole developmental machinery in motion. When fully developed, the chain of biochemical processes leading to the production of callosities (in the appropriate areas) is like a gun all set to go off—it is necessary only to squeeze the hair-trigger.

Now, Waddington suggests, it is not improbable that a random gene mutation may modify developmental processes in some near-by region of the embryo in such a way that this takes over the function of the external pressure, operates the biochemical trigger, and sets off the development of callosities. Such a mutation once it had occurred would, of course, be selected, since it is clearly advantageous to possess your callosities in advance.

Now it seems to me that this hypothesis is very significant for evolutionary theory, and should provide a theoretical framework for much experimental research. So far as I know it has never been tested on mammals, though, as I shall try to show later, the opportunity is there.

So much for the theory of adaptation. I should now like to comment on one or two practical examples, the first of which are adaptations concerning water and temperature relationships which are so important for desert mammals.

Most of you will be familiar with the work of Schmidt-Nielsen and his school (1952, 1956) on the adaptations of camels to desert life. One among many of these animals' remarkable facilities, you will recall, is the ability to suffer a much greater degree of dehydration than, for example, a man or a dog can; and in part at least this is due to its ability to lose water, if it must, from parts of the body other than the blood, so that increased blood viscosity (which would lead to "explosive heat death" in the words of Adolf, 1938) is postponed or avoided. Macfarlane, Morris and Howard (1963), have recently compared camels, cattle *Bos taurus*, kangaroos and merino sheep in respect of their water economy and confirmed the earlier evidence by showing that a much smaller proportion of the total water lost during dehydration comes from the blood in camels than it does in merino sheep. They suggest in fact that most of the water lost by camels comes from the gut contents rather than the cells and intercellular spaces. Now there is nothing very mysterious about this if there is more water in the lumen of the gut than in the cells and tissue spaces, because an equivalent rise in salt concentration in both areas would imply that an absolutely greater volume of water had been derived from the gut. What *is* still mysterious is the mechanism of differential loss from the blood and from the rest of the body, for this must set up an osmotic gradient between blood and tissues.

Elucidation of this problem would be of great general interest, and might also pay dividends in terms of ranching and farming in arid lands. One suspects that the property is not confined to camels but may well be present in several other mammals from arid areas—gerenuk, for example, addax *Addax nasomaculatus* and oryx *Oryx leucoryx*. Some comparative work on African mammals is indicated.

Another field in which camel physiology has, I believe, led the way, concerns nitrogen metabolism. Camels, as Schmidt-Nielsen and his co-workers showed, when on a low protein diet, adapt by excreting in the urine only a small fraction of their urea production. The remainder is transferred to the stomach where, owing to the presence of an appropriate microfauna and flora, urea is converted to usable amino and fatty acids. This process is now known to occur in a number of animals, and it is clearly of great importance for stock raising in arid areas.

It is in fact well known that domestic cattle may be fed some of their protein requirements in the form of urea. If in addition some breeds of cattle can adapt themselves to low protein diet in the camels' way—by retaining urea from the urine—they would clearly be at an advantage in arid areas during the dry season.

The Schmidt-Nielsens' work on camels and kangaroo rats (1948) has been followed up in several laboratories. Kirmiz (1962), for example, has recently published very full data on the water economy of the Egyptian desert jerboa *Dipus aegyptius*. The jerboan kidneys, like those of the kangaroo rat *Dipodomys*, can concentrate urine to a remarkable extent (the maximum concentration in *Dipodomys* is nearly four times that in man), and this, together with the absence of sweat glands, low skin permeability and other adaptations, permits these animals to live indefinitely on a completely dry diet, the necessary water being obtained as a metabolic product. Not all desert mammals can live on dry diets, however; the American *Neotoma* and the African sand rat *Psammomys* are animals that cannot do so.

Comparative work on these arid-living mammals emphasises the importance of size in water economy. Clearly a large animal like a camel has the advantage of a large volume to surface ratio. It cannot very well live in burrows but it can afford to sweat. *Dipus* and *Dipodomys* on the other hand, can and do live in burrows, thus mitigating the effect of the often hot, dry environment, but they cannot afford to sweat. As a last resource these animals will salivate copiously—but they cannot keep it up for long.

Some recent work of Carpenter in America is interesting in this respect. He has worked with *D. merriami* (an extreme desert rat) and *D. agilis* (from relatively mesic coastal ranges). After measuring temperatures in their burrows throughout the year, Carpenter (personal communication) concludes that the "difficult" aspect of the environment of both these animals is not heat at all, but cold. They both have better thermal insulation than other mammals of equivalent size, and this means that their thermal neutral zone (within which thermogenic metabolism is minimal) extends down to an environmental temperature of 20° C. We are, perhaps, sometimes inclined to forget that deserts can be extremely cold as well as hot. Probably the sheer range of daily and annual fluctuations imposes more of a challenge to animals that live there than either of the temperature extremes does.

Reverting to larger species, there are scattered bits of information—often hearsay—about (in particular) addax, oryx and gerenuk, concerning the extent to which they can live without free water. The truth is probably (as Bourlière, 1955, and others believe) that these animals cannot go without water indefinitely any more than camels can, but their needs are very limited. Certainly they feed on succulent plants such as water melons when these are available, and certain antelopes such as duikers are known to lick the copious morning dew from leaves of plants and thus to survive in areas devoid of standing water.

In short, it seems that we are, with a very few exceptions, shockingly ignorant about the water and heat relationships of African mammals, if donkeys and camels (both domesticated) are excepted, and I am sure that this will be a fruitful field for future research.

Dr. Ledger and Mr. Norm Smith have, I understand, been working along these lines at the E.A.A.F.R.O., Animal Husbandry Laboratories at Maguga, and we look forward eagerly to the publication of their results.

Information, I believe, is necessary both at the "gross animal" level and also at the physiological "mechanism" level. We need to know, for example, *how* water is retained, and it so happens that there is an interesting lead on this. Sperber (1944) and others have found remarkably long kidney papillae, extending well down into the ureter in desert rodents. Wirz (1954) and B. Schmidt-Nielsen and Odell (1961) have evidence that concentration of the urine increases by outward extraction of water as it passes along the terminal portion of the kidney tubules, by a "counter-current" mechanism. If this is so, then it is tempting (as Chew, 1962, points out in a recent review) to relate length of nephron with degree of concentration. Certainly the nephrons of *Psammomys* are *all* long while those of a man are nearly all (97 per cent) short.

In the matter of reproduction, desert animals also show some interesting adaptations. The problem here, of course, is to ensure that breeding and production of young occur at the right time. Volcani (1952) studied the reproductive physiology of camels in the Negeb (S. Israel) and found that both the rutting season (January to March) and the time of birth after a 12-month gestation period, coincide with the short flush of green vegetation. Lactation lasts for a further three to four months, so that reproduction occurs only once in two years—a remarkable adaptation to desert conditions.

In sheep and most mammals the breeding rhythm is largely exogenous (affected by environmental factors), so that these animals when transported from the northern to the southern hemisphere soon adapt their breeding cycle to the reversed conditions. In some desert animals, however, the rhythm appears to be more firmly fixed. Bodenheimer (1953), for instance, points out that when camels from a winter rains area are transported to the summer rains region of the Sudan, they cease almost entirely to reproduce.

Certain North African gazelles behave similarly. Several species when kept in the Cairo Zoo and fed continuously, nevertheless retained the reproductive rhythm appropriate to the rainy seasons in their various areas of origin. Thus *Gazelle dorcas* from Beersheba (where rains fall in March) gave birth in April, while *G. ruficollis* from Khartoum, with August rains, gave birth in September.

It is a little difficult to see the advantage to desert animals of such rigid rhythms—one would have thought that a little manoeuvrability might be useful. Certainly such rigidity is not characteristic of all desert mammals. In a good year, for example, some gerbils (*Meriones* and *Acomys*) are capable of continuous breeding, but reproduction is usually confined to the short spring and seems to be triggered by abundant fresh food.

This is true of the Levant vole *Microtus guentheri* which, as shown by Bodenheimer, has an extremely high reproductive potential but whose population density fluctuates violently each year because it is fertile only if the diet contains fresh green plant material.

Our knowledge of these matters is indeed scrappy, and it will not have escaped notice that I have had to go outside Africa for several of my examples. Here, then, is another gap in our knowledge about African mammals.

Let us turn now to a brief consideration of another form of adaptation, namely acclimation. Like "adaptation" itself, this term (and the alternative "acclimatisation") has been used in various ways. Here "acclimation" is used to mean an adaptive physiological change in an individual in response to climatic stress during its own lifetime. In addition there is, so far, an unfortunate division between the work of those interested in the acclimation of poikilothermic animals, and those whose interests lie with homiotherms. At first sight there does appear to be a real difference. If we consider acclimation to temperature (about which most information is available), it seems that what happens in poikilotherms is as follows. There is, in these animals a more or less profound effect of body temperature upon the rate of various metabolic and physiological processes, such that, if the temperature is rapidly changed, the animals function inefficiently at high or low extremes. But the effect of exposure to rather high or low temperature for a long time is to reduce the extent of change in the rate of these processes. For example, cockroaches kept at 20° C. have a very high standard metabolic rate at 30° C., but if they are kept at 30° C., they become acclimated and the metabolic rate falls. In other words the animals are more tolerant of temperature extremes after acclimation at comparable temperatures.

In homiotherms, however, there is no greater tolerance of high and low *body* temperature after acclimation. Body temperature remains constant, and what alters is the ability successfully to maintain the body temperature in the face of difficult environmental conditions. Similarly, after exposure to high sub-lethal temperatures, the lethal temperature itself rises.

Basically, I believe (though without much evidence) that these two kinds of acclimation are mediated by similar processes, and that common factors will be found at the enzyme level, although the mechanism is still unclear. However this may be, both kinds of acclimation are clearly adaptive, and the point to be stressed at present is that acclimation (to temperature and to other factors) is proving to be of such importance in the lives of all animals that its effects must be taken into account by mammal physiologists, ecologists and ethologists. It may indeed be quite misleading to accept the results of work on a species living at 3,000 feet as being applicable to the same species at 4,000 feet. Similarly, attempts to assess the part played by climatic factors in limiting the distribution of an animal species are liable to error unless information is available about the performance of individuals over the whole specific range.

So far, work on acclimation in mammals has been confined to domesticated ones. It would seem that wild deserticolous species, exposed as they often are to very wide ranges of environmental conditions, are worth investigating in this connection.

Before leaving the subject of acclimation I should like to refer to my earlier remarks about the genetic assimilation of environmentally induced adaptive responses. Acclimation is an adaptive response which we think of as occurring only as a result of environmental stress. Yet similar differences in temperature/rate relations, temperature tolerance, and so on, are found as genetic differences between allopatric populations at all taxonomic levels. It seems possible, then, that Waddington's (1959) model for the incorporation of adaptive structures in the genetic make-up may also be valid in relation to the evolution of physiologically different sub-species and species by means of genetic fixation of an acclimated state.

It would be very interesting to test this experimentally in mammals in the same way that Waddington did with fruit flies. One would choose a rapidly breeding species (e.g. a mouse) and preferably start with a wild population to get maximum genetic variability. These animals would be acclimated, perhaps to high temperatures, and individuals which showed the maximum response would be selected for several generations. If genetic assimilation occurred one would find eventually that some individuals were being born fully acclimated.

An entirely different group of adaptations is considered by Wynne-Edwards (1962) in an interesting theory developed in his book on *Animal Dispersion in Relation to Social Behaviour*. The adaptations here are essentially forms of social behaviour (in a very wide sense) which lead to the regulation of the population of each species at an optimal level. The author points out that direct physical competition between members of a species for inadequate food resources is generally a bad thing since it leads to violent fluctuations in numbers, perhaps even to extinction and often to permanent damage of the resource itself. Such direct physical competition, he believes, is avoided by substituting relatively harmless social competition, one of the forms of which is territorial behaviour, where the size of each territory is appropriate, so far as food resources are concerned, for the support of the unit (be it a breeding pair, or a social group).

The various forms of social assembly and the displays that are often associated with it (swarms of gnats, calling of birds, herding of mammals, aggregation of locust hoppers) all serve the purpose of "letting the other fellow know you are there". Social competition (not physical fighting) may then lead to the dominance of some individuals (the number being nicely adjusted to the resources of the environment) and to the exclusion of others for whom there is no living space. The latter then perish or migrate. In its most highly evolved form such social behaviour leads to organised migrations, as in locusts, bees and lemmings. Wynne-Edwards would account in similar terms for the fact that some individuals in a herd of mammals migrate while others remain on the home range.

I do not propose to assess the validity of this theory, but there is little doubt in my mind that it is extremely provocative for all students of biology, and particularly for mammalogists, for mammals include some of the best examples of social aggregation and other forms of social behaviour. It might be very difficult indeed to prove the theory by experiment, but it may well stimulate valuable observations on mammalian behaviour in relation to numbers and to food resources. One recent piece of work which seems to fit the theory well is that of Buechner (personal communication), who found an interesting form of territorial behaviour in the Uganda kob *Adenota kob thomasi*, where each male has its own well defined stamping ground. But, significantly, such behaviour he believes occurs only when the population density is high.

This sort of observation, valuable as it is in itself, begins to make even more sense, I suspect, when seen in the context of Wynne-Edwards's theory, to which I have certainly not been able to do justice in the present brief reference. Doubtless those interested will refer to the original text.

Let me say in conclusion that I started to write this address with considerable disquietude. This feeling has in no way decreased, but at least the exercise has made me a little more aware of the attractions of mammalogy as a branch of biology.

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