# SECTION A. PHYSIOLOGY AND BEHAVIOUR

# K. R. L. HALL

# Professor of Psychology, University of Bristol (Section Leader's Introductory Address)

The behaviour of mammals, as of other animals, cannot be scientifically studied without close reference to the collateral sciences of ecology and physiology. There are numerous instances of this interdependence in the mammalian literature, but there are very few studies indeed of a mammal species, from any part of the world, upon which a sufficiency of data has been obtained on all these three major aspects. So few, indeed, are the major biological studies of mammals that it is worth referring briefly to four examples which, each in its different way, illustrates the extent of coverage and the various methods and techniques of enquiry that may be necessary in dealing with such diverse species.

The first is Kaufmann's (1962) two-year study of the coati Nasua narica on Barro Colorado Island, Panama. The second is the series of studies on the southern elephant seal Mirounga leonina by Carrick and others (1962) in the Antarctic. The third is the work being done by Goodall (1963, etc.) on the chimpanzee Pan troglodytes in Tanganyika. The fourth is Neal's (1948) study of the badger Meles meles in the English countryside.

These investigations have been carried out by people with different training and interest, but all show clearly the degree of concentration and effort needed to put together an adequate sample of data on mammalian species. It goes without saying that the natural history anecdote type of study, exemplified for all time by Romanes' (1886) interesting but inaccurate compendium, falls far short of modern standards, suggestive though anecdote may be of hypotheses for further investigation. Further, the methodological requirements of field observation are basically the same as those required of experimental study in the laboratory, namely objectivity and accuracy in observing and recording, the classification and quantification of data, and flexibility in moving on from stage to stage of the investigation.

I will comment briefly, under four headings, on these requirements in relation particularly to behaviour studies.

(1) In order to obtain sufficiently representative data, the species has to be sampled both extensively and intensively. This means, in effect, that data on feeding habits, mating and births, ranging and so on, should be obtained on the animals at different areas of their distribution where ecological conditions may vary. While it is obvious that some mammals are very restricted in habitat, others are now known to be highly adaptable, in the sense of surviving in widely differing environments. These different environments may produce corresponding variations in the number and spacing of the animals and, so it seems, in the constitution of groups. And these variations will, in turn, produce a diversity in the social behaviour of the species, as shown perhaps by differing frequencies of aggression or mating, even by non-occurrence of certain behaviour patterns, and by qualitative differences in the dynamic relations between individuals of a group.

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The variety of natural conditions thus sets up a series of continuing experiments for the species, and the variations are likely to be greatly extended by human agency in habitat destruction or encroachment. While, therefore, there is, as it were, a foundation of built-in physiological characteristics which sets a limit to species adaptability, mammalian species vary enormously in the degree to which these characteristics are conditionable by environmental circumstances.

But extensive, areal sampling is, of course, not by itself sufficient. It is necessary to concentrate observation and experiment upon one or a few groups of the species over a sufficiently long period of time to be able to trace seasonal variations in behaviour and variations due to changes in the social structure. Thus, obviously, one must know the breeding characteristics of the species—whether there is a period of rut, a limited season of mating and births, or little variation with time of year. And, further, one must be able to follow up the developmental stages of the animal, from birth to maturity, and to note how the social pattern may change as younger animals come to compete with the older in groups where dominance behaviour is characteristic.

Thus, both areal sampling and time sampling are necessary for the building up of the accurate account of the species, and what is "typical" or "average" for the species is determined only by an accurate knowledge of the range of variations that can be observed in all aspects of behaviour.

(2) This question of sampling is fundamental to all other problems of method in mammalian studies or in the studies of any animal, including man. And it brings in its train a number of related problems, all of which, again, are relevant to any kind of animal study, and the only justification for referring to them in this context is that the mammals and, especially, the primates seem to require a rather special and methodical attention to the standards of scientific investigation.

For example, adequate sampling of data can be vitiated by poor observational technique, or slipshod method in field note-taking, or the use of a "loaded" terminology. All such technical and methodological problems have been fully dealt with elsewhere (for example, in Schneirla 1950, and in Hall 1963), and it is only here necessary to emphasise that training in the techniques and methods of behaviour study must be as thorough and as rigorous, whether the study is of the animal in its natural habitat or in a zoo or in a laboratory, as it is in physiological investigations. In fact, it probably needs to be even more thorough, for the simple reason that the profusion of data to be gained from observing a complex group of mammals gives more latitude for perceptual bias or error.

(3) This emphasis upon technique and method must not be taken to imply a rigidity in the approach to mammalian behaviour study. On the contrary, good technique and method, as are adequate ways of ordering and quantifying one's observations, are simply the necessary aids that must themselves be directed by a flexibility of judgement and decision. For example, in attempting a field study of a so-far unstudied species, the general guides from other mammalian studies may suggest some outline plan. But, as the investigation proceeds, the quality of what comes out in the final account begins more and more to depend upon critical decisions. These decisions may relate to ways of obtaining more accurate data, as by marking individuals, or ways of dealing with particular problems which cannot be solved by field observation alone. In this, as in other respects, field observation differs only in degree and not in kind from what goes on in experimental study. In either case, a strict adherence to a preformulated plan will prevent the investigator from perceiving what is new and significant and steering the aids of method and technique along a different course.

(4) Every behaviour study is, or should be, linked with physiological investigations. Mostly, this can only be done by a team approach, by a close arrangement of field and captivity observation. Obvious examples concern the study of the sexual reproductive physiology of a species, of its sensory acuities and discriminations and of its neuro-endocrine and central nervous systems. Many behaviour investigations of an experimental kind are also close to the physiological level of approach as, for example, the study of stimulus-complexes that release species-characteristic behaviour patterns and the study of basic forms of learning, such as habituation and imprinting (see Thorpe 1956, and Zangwill and Thorpe (eds.) 1961). In most instances, however, we find these types of research far better represented in studies of invertebrates and the lower vertebrates than at the mammalian level, where there has been much less integration between field and experimental approaches.

These are all general points or problems which affect all studies of animal physiology and behaviour in some degree, but are perhaps of some special relevance to mammalian studies in Africa, now that many of us are considering how to make the best scientific use of the magnificent opportunities for naturalistic researches that are still available on this continent and on the island of Madagascar. So far, in Africa, the major research efforts in the field have been directed at the social behaviour and ecology of non-human primate species. In addition to Goodall's work, there have been two other studies of chimpanzees, one major study of the mountain gorillas, three major studies of Papio species (Kenya, Southern Africa and Ethiopia), and two are in progress on Cercopithecus aethiops, as well as at least two studies on the lemurs in Madagascar. There have been very few studies, comparable in length of time spent on observation and in the amount of data collected, upon the non-primate African mammals, and only now are a few of the ungulate species beginning to receive sufficient research attention, while the larger carnivores and smaller mammals, such as rodents, hyraxes, otters and mongoose, have no observational data on them in any way comparable to Kaufmann's coati study. Thus, while the monkey and ape studies may, it is hoped, produce data on social behaviour which can be linked more closely than at present with physiological work, it is also to be hoped that these studies will lead more and more to radiations of interest, so that the non-primate mammals will receive their due attention. There is little doubt, one may suppose, that, for complexity and variety of social behaviour, the elephant, the hyaena and the hunting dog, will give us data of at least equal interest to that available on the primates. And, as these other studies come in, then meaningful comparisons can, for the first time, begin to be made within the whole mammalian range in Africa.

Finally, in order that really thorough and long-term studies of the behaviour and physiology of the African mammals can be carried out soon, it is necessary that there should be more team projects or research units established for at least three or five year programmes, preferably for longer. Many of the most vital and interesting research problems cannot be solved in the

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course of one Ph.D. student's research, and some continuity of programme is necessary both in co-operation with existing university departments or research institutions and by the setting up of new field stations. Fundamental researches of this kind, linked inevitably with ecological studies, may do much to facilitate the work of scientific conservation and management.

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