WILD ANIMALS IN CAPTIVITY

An outline of the biology of Zoological Gardens
The town pit, a forerunner of the modern zoological garden. The moat at Berne used for enclosing deer.
WILD ANIMALS IN CAPTIVITY

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Foreword

The title of Professor Hediger's book 'Wild Animals in Captivity' immediately focuses attention on one aspect of zoological gardens that is often under discussion; captivity—a word which at once arouses sympathy and calls to mind the Prisoner of Chillon, the Count of Monte Cristo, and other famous captives of romance. The pacing to and fro of some of the larger carnivores, especially near feeding time, is identified with that of the prisoner in his cell, and some extremists regard even the most up to date zoological gardens as little better than prison establishments. This view completely ignores the fact that the great majority of these animals are far healthier and better fed than those in the wild, and also have a longer average life. A large proportion of all newly arrived animals at the London Zoo are infected with various parasites which are gradually eliminated as a result of treatment and absence of re-infection. The famous hunter F. C. Selous said that he could always distinguish the skin of a menagerie lion from that of a wild one because it was healthier and had a longer and glossier coat. It is obvious that no animal with defective teeth would have much chance of surviving in the wild, but in captivity such animals may be fed with suitable food and live for years. It is more difficult to assess the comparative length of life, but the available evidence certainly supports the view that the average length of life of animals in captivity far exceeds that of animals in nature. To give only one example, the Long-tailed Field Mouse, Apodemus sylvaticus; it has been shown by H. P. Hacker and H. S. Pearson (1946) that in nature very few individuals—in some years none—survive from one winter season to the next, whilst in the Rodent House at the London Zoo they often live for three to four years.

We take great pleasure, therefore, in drawing the attention of all true animal lovers to the present work which may help to correct some of the mistaken notions concerning the conditions of animals in captivity, most of which are the result of an anthropomorphic approach to the subject.

One of the most widespread ideas concerning wild animals is that in nature they are fancy free and able to range at will over wide areas. Nothing could be further from the truth. The great majority of animals, including not only mammals but other groups, are confined to very restricted territories—in many cases extremely so. Indeed, as a general rule, it is doubtful whether lack of space is a very serious consideration
when providing suitable accommodation for animals, and it is noteworthy that species which do range over wide territories, such as elephants, the larger ungulates, and birds of prey, are among the easiest to keep in menageries and generally live to a ripe old age. Moreover, it is well known to aviculturists that birds usually do far better in small cages than in large aviaries. Fear of man is a far more important factor, but fortunately most animals gradually overcome this fear and eventually seem to take an interest in the spectators.

A very controversial topic is introduced by Professor Hediger in his chapter on the training of animals. One of the problems in all zoological gardens is the difficulty of providing suitable occupation for captive animals, for in nature they are constantly preoccupied with the impulse to avoid enemies and to seek food—factors which suddenly disappear after capture. This monotony can be broken in a pleasant way by training which provides new interests for the animal, and in the words of the author is 'healthy, expedient and good'. The blind opposition to the training of animals, except so-called domestic species, is considered to perform a real disservice to them, and is based on a mistaken notion of 'natural treatment'. Training for captive animals may be regarded as corresponding to some extent with sport and athletic activities for civilized man. In zoological gardens only simple occupational training is possible; performances of a high standard may be left to the circus for which the author obviously has the highest respect. The more complex an animal's organization the more it feels enforced lack of activity and the sooner it tries to do something for itself. Begging represents one of the misdirected forms of occupation and is often shown, especially by bears. Chimpanzees are notorious for their performances and at the London Zoo there is nearly always at least one individual which uses various devices to attract a crowd.

With reference to the wider question as to the desirability of maintaining zoological gardens, surely no one would deny the very great pleasure which is given to a large section of the population by the opportunity of seeing living animals. Even the best examples of the taxidermist's art are a very poor substitute for the grace and beauty of the living form. Theoretically, of course, the best way of seeing living animals would be to see them in their natural surroundings, but the practical difficulties are often overlooked. With the exception of deer, a few rodents, the hedgehog and possibly the weasel, how many readers have ever seen any of our native mammals in the wild? The fox may perhaps have been seen at a hunt; but if it were not for zoological gardens the beautiful pine marten, the retiring badger, the graceful otter and many other wonderful and interesting animals, even of our own countryside, would remain completely unknown except to a favoured few with sufficient means and leisure to search them out in their native haunts. This argument applies with even greater force to
animals from foreign countries, some of which would have disappeared from the earth without ever having been seen by more than a handful of people if it were not for the shelter afforded by zoological gardens and parks.

The maintenance of these collections, however, requires a wide knowledge and involves certain responsibilities, and the present work is the first attempt by a trained zoologist to collect the available information on the subject. It is hoped that it will help to break down the prejudice of those who maintain that conditions in captivity are unnatural as a matter of course, and that any deductions drawn from them are not valid for the interpretation of natural behaviour. The author is well known for his many publications dealing with animal psychology, based mainly on a study of the wild animals in his care, first at the Dählhölzli Park, Berne, and subsequently as Director of the Basle Zoological Gardens. He has also studied animals in nature during the course of zoological expeditions to Morocco, Central Africa, Australia, New Guinea and the Pacific Islands. The knowledge thus acquired is united with wide practical experience in the handling of animals in captivity, and his book will be invaluable to all interested in their proper care.

Edward Hindle

January 1950
Introduction

A comprehensive literature exists on how to manage domestic animals, dealing at length with every conceivable detail. Feeding, breeding, transmission of hereditary characters, pedigree, distribution, market value, pathology, training and so on have long been the subject of profound research, and have become the specialized departments of an impressive science. On the other hand, the study of how to keep wild animals in zoos can hardly boast of even the most general outlines; all it has to show is a collection of more or less disconnected pieces of advice and some facts. In this book, therefore, an attempt will be made to sketch out a few essential lines for preliminary study. It is neither possible nor advisable to discuss at length individual species; that would furnish the subject matter for an exhaustive textbook on zoo management; our concern is rather to lay the foundations and nothing else.

Curators of zoos and private collectors may perhaps find in this short work some stimulus; they will certainly find many gaps. It is because of these that definite results may be expected from this work. It should persuade all who are interested in wild animal management to look for the frequent omissions, and fill them in as quickly as possible. Only by the cooperation of all who are interested can this rough, imperfect outline be improved and completed, and a practical plan emerge, of use in the management of zoos throughout the world, as well as for biological research, and for the welfare of the animals themselves. These points have been borne in mind during the production of this book, and for this reason scientific terms used are often explained. It is to that extent aimed at the real animal lover, at those, that is, who are interested in the biological aspects of the problem. Here their view that the animal’s welfare can be assured only by fundamental knowledge of animals will find support.

The biology of zoological gardens opens up such a complex field of study that it is no easy task for a single individual to get a complete view. It ranges, for example, from zoology to human psychology, from ecology to pathology. The present outline aims at showing, or at least at suggesting, the relationship between the most important of these aspects.
INTRODUCTION

The main biological problems of zoos can be grouped under the following headings:

1. Space
2. Food

The subject matter has therefore been arranged to fit this threefold division. It deals first and foremost with vertebrates, and the higher ones at that. The problems of the animal captured wild will be dealt with more thoroughly than those of the animal bred in captivity, in spite of the fact that the numbers of the former are always far fewer, and should remain so. The problem of the animal bred in captivity is in one respect obviously simpler than that of one born wild; the abrupt, decisive change from freedom to captivity is absent. No rupture with an existing environment, entailing laborious re-creation of a fresh one, arises.

Man's first efforts to keep wild animals in captivity date back to prehistoric times. There is reason to suppose that his attempts are almost as old as himself; that is, if we consider those beings which emerged at the time of greatest differentiation to be human; when the creature that was destined to become man ceased to be an animal among animals; when he succeeded in gaining that unique mastery over the great beasts which is the first indispensable requisite for the emergence of human culture.

When we examine the long evolution in the keeping of wild animals by man, from the first hints in palaeolithic times to the beginning of the twentieth century, we find once more three main divisions:

1. The Age of Cults. The bear cult of the Stone Age; animal divinities in Ancient Egypt; development of the first domestic animals from sacred motives
2. The Profane Age. The chief considerations being:
   a. Usefulness
   b. Entertainment (animal fights; hunting as a prerogative)
3. The Scientific Age. The interests being mainly:
   a. Systematic and anatomical
   b. Biological and psychological.

This outline does not mean that there is a hard and fast division between the various phases. It is simply meant to show that the emphasis in man's attitude towards animals has been gradually shifted and re-oriented. This is not the place to go into the history of the keeping of animals, however fascinating and instructive that story may be. The fact is merely stressed that such a story does exist, has had a regular development, and should not be neglected nowadays. This period of thousands of years of evolution implies a responsibility which should be taken seriously. A modern zoo nowadays is not only a local place of
popular entertainment, but an institution which has always been indebted throughout its development to scientific inquiry, and must keep in active touch with it. It is impossible today to build a hospital, for example, and to disregard precedents and contemporary standards, or to run it in ignorance of the present state of medical knowledge. It is just as inconceivable to try to run a zoo on lines dictated by personal whims and fancies.

It is not too much to claim that today the zoo is a cultural element of prime importance. Since the beginning of the scientific age in the sixteenth and seventeenth centuries it has decisively influenced the whole trend of world natural history. Two examples only need be given: the fundamental biological law that only living things can generate living things, *omnis vivum ex vivo*, was discovered in the seventeenth century by F. Redi in the course of experiments on animals in the Florence menagerie. In the same century W. Harvey immortalized himself by his discovery of the circulation of the blood. He got his knowledge partly through examining dead and living animals in Windsor Park (G. Loisel (1912) ?31).

The rapid development of comparative anatomy is closely connected with the growth of zoological gardens; so in fact is animal psychology, which gained powerful impetus through W. Köhler keeping anthropoid apes purely for scientific purposes. In fact his setting up of the experimental station at Teneriffe may be considered the real beginning of the biological and psychological work of the Scientific Age. Since then the stimulus given to comparative psychology by zoos can no more be estimated than can their artistic inspiration to the world. The relations between the zoo and comparative psychology are mutual, and nowadays zoos may expect great help from the results of the psychological investigation of animals. For this reason the various links between zoo biology and animal psychology have been stressed throughout this work. Since they can only be referred to in passing, the authorities have been given not in full but enough for those bent on more detailed study to find the necessary information without waste of time.
**Territorial Requirements in the Wild State**

A proper appreciation and understanding of life in captivity must be based on the closest possible study of life in the free state. Yet until recently very little was known about the lives of animals in their natural state. So long as this initial drawback existed the problems of life in captivity had to remain insoluble. It was usually assumed that an animal in natural conditions enjoyed absolute freedom of place and person. This idea, authoritative until lately, was based upon a fundamental error. Consequently, all arguments founded on it must be completely revised. However paradoxical it may sound, the truth is actually this: the free animal does not live in freedom: neither in space nor as regards its behaviour towards other animals. This basic truth cannot be repeated too often, since it contradicts all previous ideas and is vital for the arguments that follow.

It might be worth while to take those factors which form the main outlines of the free animal’s spatial and individual limitations one at a time.

### Geographical Range

Every species or race is known to have a definite geographical distribution. This range, according to R. Hasse (1934), is bounded by lines joining the most distant places where the species is found (Figure 1). As a rule the whole area is not inhabited by the species, but more often consists of insular districts of a definite nature—the biotopes. Those interested in the geographical distribution of animals

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**Territorial Requirements in the Wild State**
know of some species with a wide range and others with limited range. The Komodo dragon (*Varanus komodoensis*) is confined to a small part of the Lesser Sunda Islands, and the lizard *Cricosaura* (Barbour 1934) to a narrow strip of the coast of Cuba near Cape Santa Cruz, its range consisting of a few dozen acres. In contrast to these, deer, many birds of prey, or snakes (*Vipera berus*) have extraordinarily wide ranges, and so do some species artificially transplanted by man, such as the brown rat, the house mouse, or the common sparrow, which have become cosmopolitan. We must not imagine, however, that these cosmopolitans 'enjoy the run' of their enormous territory in the sense that they travel from end to end of it. The development of so many local varieties that the systematist finds himself in serious difficulties points to the fact that even these animals tend to keep to definite limits within their main range. Even the most obvious vagrants, migratory birds or fish, e.g. the eel, can never enjoy the whole of their widespread habitat. These vagrants are wrongly called free-roaming, and are regarded as typical carefree wanderers. Yet these very creatures are the victims of forces they cannot control. Their range is peculiarly limited in space and time. A set timetable drives them from one end of their territory to the other, in strict obedience to laws. The seasonal movements of migrant birds should not be thought of as pleasure trips; these birds are in fact compelled to go on their exhausting migrations by a fixed rhythmic cycle and many fall a victim to the dangers and hardships. J. von Uexkull (1940) states that every year the migrations of birds involve the extermination of countless numbers of individuals that are not equal to these fearful ordeals, and this is true. Swifts sometimes abandon their last brood unceremoniously under the urge to migrate. The periodic journeys of bird and animal migrants are done under compulsion, and bear no resemblance to pleasure trips. As F. Lucanus (1929) says, *Der Zugvogel zieht, weil er ziehen muss* ('Migrating birds go because they must').

Many ideas about the limits of range are wrong; these limits are not always necessarily natural obstacles like mountains, valleys, rivers,
TERRITORIAL REQUIREMENTS IN THE WILD STATE

lakes, seas etc. Temperature, humidity and vegetation, as well as air pressure, can act as surprisingly effective boundaries and so can certain psychological factors. The capacity for extensive range of a migrant, whether a bird or a butterfly largely independent of physical obstacles, does not depend on its technical flying capacity, since this bears no direct relation to geographical freedom of movement. In this connection neither birds, bats, nor butterflies should be thought of as more or less efficient flying machines capable of extensive distribution, but as living creatures linked to particular localities. A striking illustration of this is the distribution of certain island birds in the South Seas. These find safety and isolation in narrow inlets of the sea a bare hundred yards across. Yet they are exceptionally good fliers and could cover a far wider range with ease. The same phenomenon is sometimes seen in some continental birds, where R. Hesse remarks ((1924) 131) that among birds, the cracid Oreophasis derbyanus is found only in the volcanic forests of de Fuego in Guatemala, 10,000 feet above sea level; among certain species of humming birds a very restricted territory is not unusual: thus Oreotrochilus chimborazo typicus is known only from Chimborazo, and Erionenmis glaucopoides from Valle Grande in Bolivia. These are just a few examples of minimum range. Among butterflies we sometimes find similar minute ranges. Nearly two hundred varieties of the genus Zygaea are known, all very similar, according to R. Hesse; nearly all inhabit the Mediterranean, often in restricted localities. For instance, the flying area (i.e. the range) of Zygaea seriziata near Philippeville is only eight to ten yards wide in places*. In freedom, too, railings and glass panes are not always needed to keep a creature in one particular spot; often psychological factors act as curbs or powerful restraining influences.

The Biochore or Habitat

As we have already said, a species does not as a rule occupy the whole of its range, but simply those districts within the range which meet particular needs (Figure 2). Thus a forest dweller, for example, a squirrel, is found only in wooded districts; the otter only along watercourses; the house rat only in places inhabited by man etc. The boundaries between different biochores are often remarkably distinct. The partridge is never found in woods, nor the squirrel on the adjacent potato patch.

The Biotope or Ecological Niche

According to R. Hesse ((1924) 141), the biotope is the primary topographical unit, also described by him as the 'house' or 'living

* 1 ft = 0.3048 cm; 1 yd = 0.914 m

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Figure 2. Bioniche of Moroccan fiddler crab; tidal zone of estuaries with sandy or muddy bottom

Figure 3. Biotope of Moroccan fiddler crab
Figure 4. Territory of an individual crab

a. Crab at entrance to its home

b. Self-registering tracks radiating from the home
THE BIOTOPE OR ECOLOGICAL NICHE

place' (Figure 3). The home is the basis of the whole ecological structure, just as the species is the unit for the systematic classification of living things. Forest animals inhabit a distinct section within their biochore; the biotopes are often separated from each other by a few yards or even inches. There are some wild animals, deer for example, that never leave the ground; others such as squirrels, in their natural surroundings, hardly ever set foot on the earth.

The sharp delimitation of biotopes is strikingly seen in districts where the whole living space contains a maximum number of species and individuals, as for example among reptiles in the South Sea Islands (H. Hediger (1934) 540). There are some lizards (Scincidae), for instance, that live only on the shore itself (Lygosoma atrocostatum); others again live only among the woods, but here only on the ground (Lygosoma johiene) or in the root area of large trees (Sphenomorphus varius), up which they climb to a maximum height of nine feet. Lygosoma martagilitum, on the other hand, climbs up the tallest trunks. Some species live only at the edge of the woods (Lygosoma cyanurum), others again only in the grass (Lygosoma fuscum). Lygosoma solomonis, it is true, also lives on grassy ground, but in the earth, not on it.

The species is thus to some extent confined to its biotope; outside it, the necessary conditions for existence are not found. In an analysis of the concept of biotopes, Corti (1941) 544), not without reason, even ascribes to the biotope the characteristics of an imprisonment for the animal confined to it.

The Territory

The concept of territory, the individual’s living area, is taken from ornithology, and is probably due to J. B. T. Altum (E. Mayr 1935). Whilst the area, the biochore, and the biotope belong to the whole species, the territory belongs only to a single individual, to a pair, or to a social unit; that is, to the group represented by the chief individual. Although an animal’s specific character may permit freedom of movement within the whole biotope, in most instances it will be prevented from this by individual characteristics. The biotope is usually inhabited by several individuals of the same species, which must somehow or other manage to share it. This arrangement generally works through strict obedience to the rules.

The smallest subdivisions of the biotope are called territories (Figure 4, a, b, and Figure 5). These are clearly defined by a variety of factors (optical, acoustic, olfactory, or various combinations of these). In a short article on the territories of mammals and their demarcation (H. Hediger 1949) a summary of examples was given showing how certain parts of the body, as in the fiddler crab (Uca), or even the whole body, as in the giraffe, are used in visual demarcation. We might
call this demarcation static-optical when the result is achieved merely by the presence or appearance of the animal’s body in the area, as with the giraffe; or dynamic-optical when a specially adapted signalling apparatus, such as the claw of the fiddler crab, functions with a typical movement—as when the crab waves it about.

Territorial demarcation by acoustic means occurs in many animals—from amphibia to monkeys, though many invertebrates, especially insects (e.g. grasshoppers), use the acoustic method too. The croaking of many species of frogs apparently acts as an acoustic delimitation of living space. Reptiles with acoustic demarcation seem to include the alligator (Alligator mississippiensis), whose bellowing roar has been described by E. A. McIlhenny.

Most ornithologists nowadays accept without question that the song of many birds during the nesting season is a sign of demarcation of territory. S. C. Kendeigh (1941), for example, clearly showed that demarcation, or defence, of territory occurs in the wren (Troglopsis) exclusively through song. According to C. R. Carpenter (1942) acoustic means of demarcation play a prominent part in the howler monkey (Alouatta) as well as the gibbon (Hylobates) and siamang (Symphalangus). He says that coincident with the approach to, or entry of, the territory of one howler group by another, the barking roars of this species are normally exchanged between the two groups. A truly vocal battle between the males of the groups, supported by whines of females and young, ensues and continues usually without actual fighting until one group retreats. Most often the retreat is made by the encroaching group i.e. the home team usually wins. The territory is defended and inter-group dominance is asserted through the medium of strong and persistent sound production.

The same conditions of inter-group competition provoke the loud serial calls of the gibbon or the reverberating hoots of the siamang, and the vocal patterns in these types as in howlers serve to regulate and coordinate the spacial relations of groups.

These relatively loud inter-group calls of monkeys and apes in natural groups serve as a sound buffer which is a substitute for, or actually prevents, fighting which would often result in the wounding and killing of group-members. The impressive noises emitted by the proboscis monkey (Nasalis larvatus) and the orang-outang can doubtless be interpreted as acoustic demarcation of territory (H. Hediger 1944) as can the roaring of stags etc.

In view of the fact that most mammals, except monkeys and seals, belong to the macrosmatae it is no wonder that their favourite method of demarcation is the olfactory one. For this either excrement or urine is used or else the various scents produced from special glands. The significance of micturition and defaecation in many animals goes far beyond a purely physiological metabolic function (H. Hediger 1944).
THE TERRITORY

Special anatomical arrangements are often present to ensure a liberal sprinkling of scent in the territory and this may lead to a regular impregnation with the scent. The glands may occur in any part of the body from the nose to the tail. As a rule the secretions are deposited at definite places in the territory, at which the scent is continually renewed. This upkeep of scent marks is almost exclusively the prerogative of the males, the glands and corresponding auxiliary organs (e.g. tail bristles in the hippopotamus and Choeropsis) being therefore much more developed in the males than in the females. Most females in fact lack these secretions.

Frequently a territory is simultaneously marked by several means e.g. acoustic and olfactory in the alligator, olfactory and optic in the brown bear etc.

Territory may be represented as an area which is first rendered distinctive by its owner in a particular way and, secondly, is defended by it. Various writers have recently given definitions of territory. The best and simplest is G. K. Noble's (1939): 'territory is any defended area'. Naturally this very general definition with which W. H. Burt (1943) agrees, can be modified in individual instances. E. Mayr (1935) gives a more detailed one, namely that territory is an area occupied by one male of a species which it defends against intrusions of other males of the same species and in which it makes itself conspicuous. A full report on various types of bird territory has been given by W. Meise (1935), (1936). He distinguishes them (1936) according to function (display, food or nesting territory) or according to the number of birds permitted in them (single, pair or family territory) as well as according to length of occupation and to the relationship with the total living space. Thus the hawk (Accipiter gentilis) has a territory as large as its total living space, whereas with the blackbird (Turdus merula) the territory includes only the nest, display area, and part of the food area, a considerable part lying outside it, on neutral ground. What is meant here is what many other writers, including H. Hediger, call the neutral zone, lying between the territories of many species of animals. W. H. Burt (1943) also makes a clear distinction between territory and home range in mammals. He quotes observations on the chipmunk (Tamias), whose home range extends to a radius of one hundred yards or more round the nest while the territory proper only forms a fifty yard circle about the nest. Here too these outer circles, in many cases overlapping, might just as well be considered as belonging to neutral zones. In the author's opinion the differentiation and classification of various types of territory has gone rather too far. At all events it is not our concern to go into details here. Clearly what emerges in this connection is the simple fact that even in so-called freedom the animal is not free but spatially bound to its conquered territory which it marks and defends. As a rule this defence is left to the male, principally
against rivals of its own species; more seldom, or not at all, against animals of other species. The presence of hyenas in his living area is more or less a matter of indifference to the lion but he will never tolerate a rival of his own race. The ostrich ignores the guinea fowl, the crocodile the lizard, and so on. O. Heinroth (1941) describes this state of affairs very vividly in another way: 'The remote connection between the animals, the more their living areas overlap'.

Within the biotope, individual A cannot enter the territory of B or C, other members of its own species, without a fight, and vice versa. If a territory falls vacant it is at once seized by a member of the same species, which till then has had to make do with a less favourable territory. This is as true for the trout as for the tiger. It is well known that individual animals live in the same territory for years. Two winters running, for instance, B. Berg (1934) came across and photographed the same pair of tigers in Bengal on the same territory and along the same tracks.

A biotope, as has been shown, may contain several territories in the same way as a biochore may contain several biotopes, and an area several biochores. As with the larger types of space, the territories are often so sharply defined that they can be plotted accurately, as H. E. Howard (1920) has for the first time done for some birds.

In his unique work, S. C. Kendeigh (1941) reports on the territory of the house wren (Troglodytes aedon). For nineteen years, from 1921 to 1939, this first rate observer accurately recorded the distribution of Troglodytes territories over a fifteen acre plot, and card indexed them. In this way 215 territories were examined. Their average size was one acre. L. T. Evans closely investigated the territories of a lizard (Anolis sagrei) and also kept record cards. Today there are territorial analyses of many invertebrates, as well as of vertebrates from fish to monkeys. This widespread characteristic is a primitive display of property ownership and may be traced right through to mankind, as W. H. Burt (1943) rightly remarks. Consequences, important for the treatment and handling of animals in captivity, follow from these investigations on territory; their cage or enclosure must be arranged so that the animal accepts it as its territory i.e. as its personal property, and consequently marks and defends it as such.

It is understandable that small animals generally have a small territory but that large ones should have a large territory. A lizard owns a territory of only a few square yards but a tiger one of many square miles. We already know a great deal nowadays about the size of territory of a variety of species of animals; examples will be found in Table II.

Further it is understandable that the territories of predatory animals must be measured on a different scale from those of their plant eating
prey. The number of herbivores serving as food for the predators should not be continually decreased by periodic decimation but kept at least at the same level. Thus in the territory of a lion there must be many antelopes and zebras; in the antelopes' territory even more small rodents etc. In such a way, whole 'pyramids' of territories may be formed, all on the same patch of country. We shall instance only one example from A. Leopold (1939) of the Santa Rita Range Reserve, Arizona.

In one square mile occurred:

<table>
<thead>
<tr>
<th>Species</th>
<th>Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>coyote</td>
<td>1</td>
</tr>
<tr>
<td>roadrunners</td>
<td>20</td>
</tr>
<tr>
<td>gambel quails</td>
<td>75</td>
</tr>
<tr>
<td>horned owls</td>
<td>2</td>
</tr>
<tr>
<td>cattle</td>
<td>25</td>
</tr>
<tr>
<td>scaled quails</td>
<td>1,280</td>
</tr>
<tr>
<td>antelopes</td>
<td></td>
</tr>
<tr>
<td>blacktail jackrabbits</td>
<td>25</td>
</tr>
<tr>
<td>cottontails</td>
<td>6,400</td>
</tr>
<tr>
<td>kangaroo rats</td>
<td></td>
</tr>
<tr>
<td>red tail hawks</td>
<td>2</td>
</tr>
<tr>
<td>wood rats</td>
<td>1,280</td>
</tr>
<tr>
<td>Allen's jackrabbits</td>
<td>45</td>
</tr>
<tr>
<td>Neotoma</td>
<td></td>
</tr>
<tr>
<td>skunks</td>
<td>15</td>
</tr>
<tr>
<td>Dipodomys</td>
<td></td>
</tr>
<tr>
<td>Allen's jackrabbits</td>
<td></td>
</tr>
<tr>
<td>Neotoma</td>
<td></td>
</tr>
<tr>
<td>4-S</td>
<td></td>
</tr>
<tr>
<td>cottontails</td>
<td></td>
</tr>
<tr>
<td>wood rats</td>
<td></td>
</tr>
<tr>
<td>mice, spermophiles</td>
<td>17,948</td>
</tr>
<tr>
<td>and other rodents</td>
<td></td>
</tr>
</tbody>
</table>

A. Leopold (1939) says that in California about 360 deer occur to one puma. From these data it is clear that:

1. The territories of large numbers of species overlap
2. Small animals possess small territories, large animals large ones
3. Predators must have a far bigger territory than herbivores.

They must, in fact, as self providers, have such large herds of prey at their disposal that they can feed well without decimating them. If a puma 'owns' 360 deer, it can 'consume' at least 30 per cent, or a good hundred head annually i.e. one every three or four days. Of course, pumas do not live exclusively on deer nor on the other hand are deer stocks reserved exclusively for pumas. These figures therefore should not be taken too literally, but they give an idea of the numbers concerned.

L. E. Hubert's estimates (1947) of the density of various species of big game in the Albert National Park, Belgian Congo, are interesting. According to him, there is one lion to every three or four sq km, three hippopotamus per sq km, three buffaloes to two sq km, one warthog (Phacochoerus) to every six sq km, and one elephant to every eight sq km. In 1931 the game in it was distributed as follows: twelve topee antelopes, twenty four cob antelopes, and two reedbuck per sq km. Other calculations gave one waterbuck per sq km, one bushbuck per two sq km, one warthog per sq km, one lion per five sq km, one spotted hyaena per four sq km, one leopard per twelve sq km.

Here, too, the predators' territories naturally appear considerably larger than those of the herbivores. Of course, the size of territory cannot always be estimated from the mere number of individuals present in a given country. Yet valuable evidence may often emerge from density of population figures.
TERRITORIAL REQUIREMENTS IN THE WILD STATE

Table II
Examples of extent of territory

<table>
<thead>
<tr>
<th>Species</th>
<th>Locality</th>
<th>Approximate Size</th>
<th>Authority</th>
<th>Year</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Howler monkeys</td>
<td>Panama</td>
<td>300 acres</td>
<td>Carpenter</td>
<td>1934</td>
<td>46</td>
</tr>
<tr>
<td>Cougar</td>
<td>California</td>
<td>20 sq miles</td>
<td>Leopold</td>
<td>1939</td>
<td>234</td>
</tr>
<tr>
<td>Tannier</td>
<td></td>
<td>100 yds diam</td>
<td>Burt</td>
<td>1943</td>
<td>349</td>
</tr>
<tr>
<td>Lion</td>
<td>Kruger National Park</td>
<td>13 sq miles</td>
<td>Bigalke</td>
<td>1939</td>
<td>145</td>
</tr>
<tr>
<td>Giant Panda</td>
<td>Chinese Tibet</td>
<td>Approx 1 sq mile</td>
<td>Schaefer</td>
<td>1938</td>
<td>21</td>
</tr>
<tr>
<td>White-tailed eagle</td>
<td></td>
<td>Av. range of 2 miles</td>
<td>Alverdes</td>
<td>1925</td>
<td>109</td>
</tr>
<tr>
<td>Buteo buteo</td>
<td>Speewald</td>
<td>Approx 1 sq mile</td>
<td>Meise</td>
<td>1930</td>
<td>60</td>
</tr>
<tr>
<td>Cinclus aquaticus</td>
<td>Germany</td>
<td>½ mile riverside</td>
<td>Meise</td>
<td>1930</td>
<td>59</td>
</tr>
<tr>
<td>Mute Swan</td>
<td></td>
<td>Approx ½ sq mile</td>
<td>Heinroth</td>
<td>1941</td>
<td>11</td>
</tr>
<tr>
<td>Galapagos heron</td>
<td>Galapagos Islands</td>
<td>Less than 400 sq yds</td>
<td>Beebe</td>
<td>1924</td>
<td>78</td>
</tr>
<tr>
<td>Lizard (Anolis sagrei)</td>
<td>Cuba</td>
<td>37 sq yds</td>
<td>Evans</td>
<td>1938</td>
<td>123</td>
</tr>
</tbody>
</table>

1 acre = 0.405 hectares 1 sq mile = 2.59 hectares

Space and Time Pattern

The traditional idea of the wild animal roaming more or less aimlessly and at random about the world is far from the truth. 'No wild animal roams at random over the country', said E. T. SETON as early as 1909. This roaming does not in fact occur even in the limited section of the field we call territory, nor is this individual living space of the animal homogeneous, but highly differentiated. This is clearly shown in those animals which follow definite tracks, as any hunter of rodents, beasts of prey or ungulates well knows. Cursorial birds are also given to using regular beats, and so trapping is rendered easy. Even such excellent fliers as birds of prey do not fly aimlessly about in the air, but keep to certain localities for soaring on up-currents. H. KRIEG (1940) says of the South American vulture (Coragyps) that they are sluggish birds that hover high up in circles, and on sunny days delight to float on the up-currents. They may be seen in great flocks soaring on the
SPACE AND TIME PATTERN

rising columns of air, or, when these die away, planing down with slow wing beats. When one of them encounters a fresh air-lift, it at once starts circling, thus attracting its fellows. Since such upward currents are formed only at certain times of day, Krieger found a connection between the periods of activity of species that made use of them (1940: 132). Many other observers confirm this, as for example B. Berg (1931: 70), during his observations on Lammergeyers in the Himalayas. He states that there was a regular vultures' highroad, where one only had to lie in wait with a camera and shoot at the right moment to get as many pictures as one liked. He observed that the Lammergeyer knew very well that air that had been warmed during the day rose up the mountain flanks. This bird and others not so strong on the wing had their own paths along which the air currents carried them. Although these varied according to wind and time of day, yet they had as definite tracks up aloft as men and goats on the slopes below.

Even fish, amphibians and reptiles may have regular beats inside their living area. C. Darwin mentions a turtle (Testudo nigra) that he came across on the Galapagos Islands (quoted in W. Beebe 1924: 'When I landed at Chatham Island, I could not imagine what animal travelled so methodically along well chosen tracks. Near the springs it was a curious spectacle to behold many of these huge creatures, one set eagerly travelling onwards with outstretched necks, and another set returning, after having drunk their fill.'

The fact that an animal's living space is not homogeneous but differentiated e.g. criss-crossed by definite tracks, is of the utmost importance. The animal trusts himself to these tracks, in contrast to other parts of the area scarcely ever used by it, or even quite unknown. The beat has its origin in what J. von Uexküll (1934: 67) described in another connection as the familiar path, and vividly compares it to a thread of highly fluid medium within a viscous mass.

Apart from the well worn beaten tracks, the living area of a free animal contains countless other patterns e.g. the home, in the shape of a nest, cave, lair and the like, forming a place of maximum (relative) concealment. This is often the place to which the animal retires under threat of danger; where it rests and sleeps; and often, too, brings its young into the world and protects them in their infancy. The animal is not always in the position to seek out a first category home (Home 1) when circumstances demand; it must then make do with a second category home (Home 2), called a refuge in the language of Umwelt-biologists (in the fox or badger, a temporary earth). It may so happen that even this is not available, but that for the time being the animal must make do with an emergency cover, a home of the third category (Home 3). These home types, different in quality, are distributed throughout its territory and are often closely linked. They are graded like this only so far as, in a given situation, a home of the first category
offers the best conditions, while a home of the third category offers the worst. As soon as an animal can venture out, it tries to exchange a Home 3 for a 2 or a 2 for a 1. There is usually only one Home 1 available, whilst refuges and sanctuaries may be more numerous, or may even have to be improvised at need. These differentiations of territory apply to all representatives of vertebrate groups as well as to many invertebrates.

As Figure 5 indicates, in many species the home is surrounded by a protected zone i.e. in its immediate neighbourhood predators refrain from hunting and herbivores leave the vegetation alone and only feed on what is beyond a certain distance. The author has repeatedly watched the common marten (Martes foina) spare the dovecots and henruns closest to its home. In Africa, inhabited Orycteropus earths were found immediately next to and underneath intact termites' nests. It is well known too that many birds of prey only kill their prey beyond a certain distance from the nest i.e. outside the protected zone. J. Von Uexkull and G. Kriszat (1934) regard this to some extent as a protective device preventing the killing of their
SPACE AND TIME PATTERN

own young. A general explanation for the existence of these safety zones is not easy to give. With predatory animals it is conceivable that in the immediate neighbourhood of their home it may not be possible to work up a proper frame of mind for hunting. With herbivores it is likely that by stripping the surroundings the home would be dangerously exposed were it not for a protected zone for the vegetation. Many animals show a strong need for cover and perhaps that is why they refrain from destroying it where it is most needed.

With herbivores, too, this fact may play a part; the grass, leaves etc near the home, in the most used parts of the territory, that is, are so strongly impregnated with its own body scents that they have lost their food valency. In zoological gardens one can sometimes observe with many ungulates (dwarf goats, antelopes etc) that their paddocks contain a particular patch of grass that is not grazed by them. If these animals are given grass of the same sort, though not from their own enclosure, they will often eat it immediately. The questions arising from this fact need to be answered through experiment. A start has already been made on them at Basle Zoological Gardens.

It is important to differentiate between protected zones and neutral zones for a true understanding of the living conditions of the free living animal. The protected zone lies within the territory, round the home, and is characterized by a special (negative) connection with the acquisition of food, whether this consists of animals or plants. The neutral zones, on the other hand, always occur outside the territories and are characterized by special connections with the animals of a species, which here are not chased off or fought.

As far as situation of the home within the territory is concerned, two basic types may be distinguished. In most examples the home is more or less in the centre (concentric) and never peripheral. All the same there are homes situated markedly eccentrically e.g. in the hippopotamus, which has a pear-shaped territory. Its home in the water, where it spends the whole day, lies at the farthest end of the pear stalk, which, in the form of a narrow passage, often along a deep-sunk track, leads to the lake or river.

Besides the home, in many animals another differentiation is often met with, namely, places where special metabolic functions are performed. These may be places for the dismembering of prey among the predators, disgorging of pellets among raptorial birds, drinking places, and places for defaecation and urination, as well as spots at which certain gland secretions are deposited (scent marks) and larders. Bathing places and wallows are important, too, and so are rubbing posts etc. All these localities are connected in typical cases by well known paths and are normally visited at definite times.

The animal's personal living space or territory is seen as a system of biologically significant points connected in a characteristic manner by
TERRITORIAL REQUIREMENTS IN THE WILD STATE

means of definite tracks or beats (Figure 5). Moreover, movements within this geometrical system, so to speak, normally take place at definite times. A time system is coordinated with a space system. In other words, at definite times and places the animal must perform definite activities. Such a well known sport as shooting from a stand depends in practice on this everyday fact, and it has not until now been appreciated from its biological point of view. H. Brüll (1937) says that when hunting its prey a buzzard (Buteo buteo) adopted a particular observation post which might be a telegraph post, a pole or a hummock, and used this to take off from on its raids. It was remarkable how regularly these posts were used. M. Eisenraut (1937) remarks on the striking punctuality with which one of the bats that he was observing at the end of June used to emerge. For a week it was seen flying past one particular spot punctually every evening at the same time, 9.5 p.m. Confirmation of a similar nature may be found elsewhere in the literature on the subject. During a stay of some weeks in the summer of 1948 in the Parc National de la Kagera (Ruanda-Urundi), the author watched huge streams of bats pour out from holes in the roof of his rest house. They did this fairly punctually at 6.20 every evening, after sundry preparatory rustlings. C. R. Carpenter (1935) describes the characteristic behaviour of a group of spider monkeys observed in the open. For eight successive nights the animals returned to the same clump of 'nispero' trees. Throughout the day the group travelled, in general, over the same route from one food tree to another and to and from favourable places in the deep forest where the mid-day 'siesta' occurred.

In Greenland, A. Pedersen (1930) observed a certain blue fox that was regularly the first to arrive outside his hut at 2 p.m. prompt. G. Niethammer (1937) proved that free-roaming wild rabbits (Oryctolagus) not only kept to accurate times, but also to particular tracks. G. Shiras (1938) kept an individually recognizable tree porcupine (Erethizon) under observation for seven years. Its habits in freedom were of almost clocklike regularity. Evening after evening it would appear between seven and eight o'clock on its trail on the shore of a lake, where it was often photographed. Many other similar examples could be quoted (H. Hediger 1946).

In all these examples only portions of the whole of the animal's daily life are concerned. Unfortunately, investigations about such vital matters as the complete daily cycle in the life of the animal have, until lately, been strangely neglected (H. Hediger 1944), although information of this nature is of great importance to the biologist of zoological gardens. Apart from the fact that the necessary inquiry into this problem has been lacking, the reason for this state of affairs lies in the fact that observation of normal undisturbed behaviour in freedom is remarkably difficult and takes up an enormous amount of time. Excellent
field workers such as C. R. Carpenter and F. Darling have recently made successful progress as pioneers in present day investigations.

If the material at present available is used as a basis for observing the free animal's behaviour from the point of view of its space and time connection, the following facts emerge, of great importance for the proper treatment of the animal in captivity. Two space and time systems may clearly be distinguished, with a relationship to each other like that of the large and small hands of a clock. The lesser space and time system comprises in general all those activities of the animal which take place within twenty four hours inside its territory or the immediate neighbourhood. For example, the search for food, song, preening, bathing etc in the life of a song bird. Suddenly migration, a new urge of far longer rhythm, takes control of the bird. Now its accomplishment is the only thing that matters; all other activities give way or are completely abandoned. The greater space and time system thus includes seasonal activities of wide range that take the bird far beyond its territory, and affect it at much greater intervals, usually yearly.

The phenomena of the lesser and greater space and time systems can be clearly seen in invertebrates (swarm years of insects, palolo worms etc) as well as in vertebrates.

The Mosaic of Territories

Important practical research in recent years has too easily tempted us to think of nature as a gigantic mosaic of territories, each one simple in structure. For example, the diagrammatic representation of bird territories particularly lends itself to this conception, but is, in fact, valid only for single species. If we consider that within the territory of the golden eagle, not only jackdaws, nutcrackers, woodpeckers and owls may live, but also chamois, marmots and alpine salamanders, lizards and ring snakes, trout, voles and other creatures, we soon come to the conclusion that the territories of different species do not touch each other like adjacent pieces in a mosaic, but only the territories of individuals of the same species. For example, an accurate diagram of the territories of all the vertebrates within a golden eagle's territory would show a large number of lines criss-crossing. In nature, countless networks are interwoven in the most complicated manner, with endless ramifications cutting across each other. Investigation of this network would be a fascinating exercise in ecology, animal psychology, and other biological studies. Meanwhile, our present knowledge on the subject is more than scanty.

A. Leopold (1939: 230) remarks quite rightly that our knowledge of the inter relationships of animals is still very imperfect. Meanwhile J. M. Linsdale's excellent monograph on the Californian ground
squirrel ([1946] 65, et seq), with its careful analysis of this rodent’s connections with many other neighbouring species, is a model that promises well for the future.

In the example mentioned of the eagle territory there will be mosaics between which no relationships exist. If we assume as a rough guide that each species has a mosaic of a certain colour, separate unrelated colours will be found in the complicated system of overlapping mosaics. The eagle is hardly likely to bother with the alpine salamander, and may never even come across it, as the eagle is diurnal and the salamander largely nocturnal. There will also be definite regular connections between different colours. We know that eagles and chamois, even eagles and marmots, are linked by the captor-prey relationship: but what is the link between chamois and marmot? Furthermore, the relation between the eagle and the jackdaw is a peculiar one. The latter mob the robbers in the same way as little songsters mob owls. This curious relationship between certain birds has not yet been properly investigated. We know that roe deer have to give precedence to chamois when they meet (cf biological rank). The owl shows interest in the vole etc.

From all this it is clear that the most widely divergent species may become connected through the interweaving of territorial networks, and in regular contact. Not all species, even in a state of liberty, are able to get on together. Individuals may band together in associations and societies (F. ALVERDES (1925) 3) and help each other against enemies. Other species are presumably quite indifferent to each other. Others again live in symbiotic partnership, in competition with each other, or on a predator-victim basis. This background of sociability, or the opposite, in different species, of such importance for the animal student, may be an extremely complicated one, and still needs adequate analysis. In the following sections only two of the possible types of mutual incompatibility will be discussed; one the result of the predator-prey relationship, the other of biological rank.

Before that, however, we must return for a moment to the picture of the territories, with their pattern of networks. In nature, a simplified mosaic of this kind, of various colours, in which the living spaces of individual species neither cut across each other nor intermingle, but just touch, does not exist. Such an arrangement can only occur in the artificial conditions of zoological gardens, where railings and glass divide the living space of one species from that of another. But even here, in a simple framework, we may on closer inspection watch it occur through the mingling and interweaving of individual territories. We have only to think of those pests of every zoological garden, the rats and mice, which find the defences of all too many cages vulnerable. We shall return later to the important fact that large animals cannot be kept under sterilized conditions in zoological gardens.
Sociological Factors in the Wild State

The Predator-Prey Relationship

The relation of animal to animal is of fundamental importance for solving the problem of keeping wild animals; especially as man himself often plays the part of predator, in so far as he may be of danger to other animals, even to the largest and to those most capable of self-defence. Man is the universal enemy of nearly all animals in the free state, and as this is so we should not speak of the predator-prey, but of the enemy-prey relationship. The enemy may thus be either man or a beast of prey. The animal runs away from its enemy, and from man too, in whom it sees a dangerous enemy in the form of a superior beast of prey. Man is, as it were, the focus of the animal’s escape reaction.

The escape reaction is the animal’s normal response to an enemy’s approach, and all behaviour mechanism, including crouching down, is aimed at avoiding the enemy. The author has shown in detail elsewhere (1934), (1937), that in the presence of an enemy, an animal or bird does not simply run or fly away; the escape reaction is subject to definite laws, quantitatively and qualitatively. These facts, indispensable for understanding the following explanation, may be summed up like this: on suddenly encountering an enemy, the animal shows a characteristic escape reaction, specific for sex, age, enemy, and surroundings, as soon as the enemy approaches within a definite distance (the flight distance). The escape reaction may perhaps have the characteristics of an ‘Appetenz relationship’ in Lorenz’s sense, for M. Holzapfel (1940) 278) thinks it restores the animal to its relative state of rest, disturbed by the enemy. This state of rest can only be restored when enemy and victim are once more at a distance greater than the animal’s specific flight distance. The presence of an enemy within that distance produces a condition of violent disturbance.

In flight, the animal is urged by the impulse to escape from its enemy. If it is followed and gradually overtaken by the enemy, the animal’s flight reaction suddenly changes when the enemy comes within the animal’s defence distance. The attack resulting from this change, always with the character of self defence (emergency), is called the
defence reaction, and is characteristic for each species. Finally, it may be that owing to the presence of an enemy the animal wants to escape, but circumstances may prevent it; for instance, it may find itself cornered, or feel that it is. In such a situation it shows (again specifically) critical reaction the moment its enemy reaches the critical distance.

This critical reaction consists of an attack, with emergency characteristics. Flight, defence, and critical distances are specific, within certain limits, and may be accurately measured, often within inches.

By far the chief pre-occupation of wild animals at liberty is finding safety i.e. perpetual safety from enemies, and avoiding enemies. The be-all and end-all of its existence is flight. Hunger and love occupy only a secondary place, since the satisfaction of both physical and sexual wants can be postponed while flight from the approach of a dangerous enemy cannot. In freedom, an animal subordinates everything to flight; that is the prime duty of an individual, for its own preservation, and for that of the race.

The relationship between prey and predator is governed by certain laws in two respects:

1. In the characteristic behaviour of the prey towards its enemy (the predator) and
2. In the behaviour of the predator towards its prey.

The existence of these laws has been mentioned elsewhere (H. Hediger (1941) 38). Here it will only be necessary to emphasize that feeding, just like flight, is controlled by certain strictly observed rules. This is true of carnivores and herbivores, and does not simply consist in aimlessly capturing and devouring prey or swallowing at random masses of greenstuff. The intake of food in carnivores, herbivores and omnivores (flesh eaters, plant eaters and animals of mixed diet) depends on quality, quantity and time, and often also on space. It is connected with definite localities and territories (space-time pattern).

As regards quality of food, R. Hisse (1974) 15) distinguishes between euryphagous animals i.e. those that eat many different foods, or even anything edible, and stenophagous animals i.e. those that have a specialized diet. Generally speaking, we tend to think that a wild animal’s food is more restricted than it actually is. In other words, most animals are much more euryphagous than we suppose. Thus among the carnivores proper, purely flesh eaters are rare; so are purely plant or even grass eaters among ungulates, or purely seed eaters among birds. Only a few examples need be quoted. According to W. Schoenichen (1938) 38), the fox, apart from his own already highly varied meat diet, eats fish and crabs, worms, great green grasshoppers, and other insects, besides fruit and berries. On the other hand, F. F. Darling (1937) 7) observed in the field that red deer ate frogs, thus becoming temporarily carnivorous. Even animals that look least like rodents turn
THE PREDATOR-PREY RELATIONSHIP

vegetarian in exceptional cases. C. R. Carpenter (1934) recorded the plants eaten by free roaming howler monkeys (Alouatta palliata) between January and May 1932. He had each plant identified. In all there were fifty six different species belonging to twenty nine genera. Moreover this list was far from complete. A. Jacob (1931) mentions twenty two different species of flowering plants chosen by Scandinavian reindeer for their diet, although they have always been regarded as exclusively lichen-feeders.

A. Leopold (1939) is right in talking of the tremendous variety of foods eaten by most game species. Game eat a greater variety of species than humans do, the lack of refrigerators to the contrary notwithstanding. The author quotes a record of 1,659 investigations of stomach contents, according to which Bobwhite quails ate 927 different kinds of food. In Pennsylvania, deer were observed to browse on 113 shrubs, rabbits (cottontails) on seventy one etc. Th. Hubback (1939) quotes a detailed list of the food plants of the Sumatra rhinoceros, and H. Grote (1944) mentions the varied diet of the capercaillie.

A. Leopold (1939) distinguishes between the following four classes among free wild animals:

Preferred food or delicacies
Staple foods
Emergency foods, and
Roughage.

True monophagous animals, eating only one type of food are, contrary to belief, extraordinarily rare. Even specialized fish or egg eaters have a far wider range in their choice of food than would be supposed from the rigid classification found in textbooks. Among flesh and plant eaters, monotony of diet in the everyday meaning of the term is only to be found in books and zoological gardens. Too strong a warning cannot be given against over schematized classification of food, based on tooth structure and theoretically coordinated diet.

It is scarcely necessary to add that food consumption is also determined quantitatively; fundamentally, the danger of overfeeding is very remote in the natural state. The quantity of food taken at a meal is directly related to whether the animal can be classified as a continuous or an occasional feeder. Continuous feeders take relatively small amounts of food; occasional feeders on the other hand e.g. snakes, take large amounts at a time. Permanent feeders in the strictest sense of the word, with the possible exception of filter feeders e.g. shellfish and parasites, probably do not exist, since as a rule feeding activity is definitely regulated. Its rhythm of activity and repose causes an animal to take its meals during the day, in the night, or at twilight. Time of day is intrinsically less important here than suitable light intensity. Animals that shun the light are forced to feed in the dark just as
much as a diurnal bird of prey, for example, is compelled to seek its food only when the light is sufficient for its purpose. Feeding may also depend on internal rhythms: in the case of most snakes it is interrupted by the various phases of skin-casting; in the case of mammals, by hibernation, rutting etc in the case of birds (penguins) by moult. Only one requisite for seeking or eating food is usually necessary. The animal must be put in the food situation, to borrow a phrase from the Umwelt-biologists.

Internal changes are usually the cause of this stimulus, though in the case of some animals e.g. the European salmon, it can also be induced externally. By dangling a tempting bait in front of it, a salmon can be persuaded to snap at it, even when it is not able to swallow or digest it. The feeding of a ruminant presents a special case, divided so to speak into a temporary and a final phase, both resulting in situations completely different in time and place. Rapid snatching of food on exposed grassland is followed by a leisurely chewing of the cud in the comparative quiet of the resting ground. In chewing the cud, the number of movements made in masticating each mass of food sent up from the paunch into the mouth is specific i.e. characteristic for each separate species; it may be thirty in certain Cervidae (red deer), or in some Bovidae (species of cattle) over seventy. Likewise the rhythmic side-to-side movement of the lower jaw during rumination is often characteristic of each species. Owing to anisognathia (unequal width of upper and lower jaws) only half the lower jaw can come into contact with the corresponding half of the upper jaw during simple chewing. Whilst some species like the camels regularly alternate between both sides of the lower jaws (pattern—left, right, l, r, l, r, l, r), others like most antelopes chew with the left half of the lower jaw for a time, and then change to the right half (pattern, l, l, l, l, r, r, r, r). The way in which food is offered is of great importance. Bats will not take any prey that clings to a flat support; lizards ignore motionless prey. Not all ungulates are ground-feeders; giraffes and moose, for instance, find their food at a certain height above ground level; many birds cannot take hanging food, and so on.

**Biological Rank**

In the section on the mosaic of overlapping territories the many different ways that species living in freedom are bound to be interconnected were pointed out. One of the most important kinds of connection is obviously the enemy-prey relationship. In addition to the above, one other important type of relationship must be mentioned here, that of biological rank. It has been more fully outlined elsewhere (H. HEDIGER (1940)). Here it will simply be distinguished from the enemy-prey relationship, from which it differs fundamentally. Biological rank
means a hierarchy, based upon definite rules, among those species and
genera which closely resemble each other in their physical make-up
(e.g. ruminants, monkeys, cats, and bears), with areas and biotopes
overlapping. To some extent it implies a state of biological com-
petition. Generally, these competitors try to avoid each other; the
biologically inferior species as a rule gets out of the way of its superior,
to avoid a fight. When competitors do come face to face, the superior
has the advantage in every respect over the inferior, especially in
obtaining food, in freedom of movement, in choice of resting and
sleeping places etc. The following hierarchies may be used for illus-
tration:

ibex—chamois—roe deer
or mountain eagle—raven—jackdaw
or grizzly bear—American black bear
or gorilla—chimpanzee

e.tc. The freedom of the subordinate species is in every way greatly
restricted by this relationship; it must always yield to the superior and
give precedence to it. Usually it is clear from the outset which species
is the superior, and no fighting, real or pretence, is necessary to prove
it. On the other hand, there are cases among predatory animals e.g.
walrus—seal, in which it is difficult to distinguish this from an enemy-
prey relationship; in certain circumstances the walrus overpowers and
devours its biologically inferior relative, if the latter allows itself to be
captured. The seal is not the normal prey of the walrus, and is only
taken in exceptional circumstances.

Social Rank

Just as the species as a whole can form part of a strict biological hier-
archy, a single individual can take its place in a social hierarchy among
the animals with which it lives. Only in rare cases does a society of
related animals form either an amorphous (unorganized) group, or a
band of individuals equal among themselves. Far oftener a regular order
of precedence is established, of linear or complex type. There is a
comprehensive literature on this. The premier place (α-position),
which often involves all kinds of advantages for the animal concerned,
is occasionally linked with a particular sex in a single species. The
second place is called the β-position, the third, γ-position and so on;
the lowest individual in the social hierarchy is the ω-individual. The
premier place among most monkeys, the American bison, wild horses,
guanacos, pheasants, pigeons etc is always occupied by a male. Among
African elephants, kiangs, chamois, ibex, red deer, sparrows etc on
the other hand, always by a female. Further, the role of leader and of
guide in individual species (e.g. the chamois and capuchin monkeys)
Sociological factors in the wild state

may fall to one and the same animal, or (as in the moose) may be taken by two individuals. In a chamois herd on the move the α-female invariably leads; the α-elk never goes first but lets the so-called secondary stags, socially inferior to him, do so. Among the elephants, furthermore, male individuals ranking high socially act as a rearguard to the moving herd. In many animals specific marching order is observed. The criterion for position on the social ladder is not as a rule physical strength, but usually certain psychological characteristics. This factor is seen in the organization of a shoal of fish, and is of considerable significance in the animal-man relationship.

The status of the individual in the social order is of great importance for its whole existence. A definite ceremonial is assigned to each grade in intercourse with its fellows; any infringement of this ceremonial means rebuke or fighting. Recently R. Schenkel (1947) has given a vivid description of the wolf. Field workers have repeatedly had to emphasize that the popular conception of 'golden freedom' is purely a product of the human imagination, and is certainly not a biological fact. Neither the fish in its shoal nor the monkey in its troop is free as an individual. C. R. Carpenter significantly remarks (1942) that the monkey or ape in its natural group in the tropical forest has its freedom of movement strictly limited by the structure of its group. The behaviour-ceremonial is waived only in the case of very young animals, not yet socially important; these may be permitted almost any liberties towards the adults, but as they grow older they often suffer really harsh treatment. F. Goethe (1937) observed that immature herring gulls suffered when in the company of their elders. He remarks that these young gulls show unmistakable complexes in the presence of elder members of their species, so hard has been the school in which they have learned how to behave. He has often watched young gulls take fright and fly off when a nearby old gull moved just to preen itself, with no thought at all for the immature gulls. According to A. Pratt (1937), mother koalas when necessary give their own growing cubs cuffs on the posterior with their monkey-like hands. According to J. Beninde (1937), the red-deer calf's obedience is exacted if need be by hard and energetic kicks from the forelegs. Socially high ranking stags in male herds usually drive lesser rankers before them, as a safety measure so to speak. In so doing, they occasionally use their antlers if the weaker stags move on too slowly (ibid 203). The vigour with which rutting stags fight for their social position (and at the same time for the conquest of a territory and of the females included in it) is too familiar to mention. The stag is simply the popular example of similar fights of social significance among antelopes, elephants, primates and carnivores.

Socially conditioned fighting can also become violent among poikilothermous (cold-blooded) vertebrates; here it clearly shows the
Social Rank

aggravating effects of confined space. Thus R. MERTENS (1940) found continental lizards not so socially pugnacious as insular types, living together in more crowded conditions. Greater living density, where the animals have less room to spread out, increases social quarrels to the extent of open anti-social behaviour. This fact, through its connection with confinement of space, is of great importance for life in captivity. Every reptile lover knows from experience that it is quite impossible with most of the Anolis species to keep two or more healthy males in a terrarium, without the lizards fighting and wounding each other more or less severely (ibid 189). Elsewhere MERTENS states that the intolerance of lizards, obviously under the influence of confined space on islands, yet in complete freedom, is striking, and often develops into cannibalism. This anti-social effect of confinement, with increased pugnacity, has also been mentioned by F. F. DARLING (1937) in his comparison of red deer living in freedom and in parks. He comes to the conclusion that overcrowding, or confined space, leads to anti-social behaviour.

Mating Pattern and Reproduction Ceremonial

Among our earliest knowledge of animal sociology is the fact that animals show the most varied types of mating, from promiscuity to lifelong monogamy. Far less attention has been paid to the fact that mating or pairing is normally associated with a definite ceremonial, often so strict that it cannot take place if the appropriate ceremonial is in any way disturbed. The ceremonial sometimes consists of a series of complicated symbolic actions, which may require special objects, indispensable to their performance. Thus, as a necessary adjunct for mating, certain terns (Sterna) require a fish, with which the female is symbolically fed by the male at one phase of the complicated ceremonial (N. TIMBERGEN (1939) 224). Detailed accounts of the extremely complex pairing ceremonial of Anatinae (surface ducks) are to be found in K. LORENZ'S excellent investigations (1940), (1943).

The physiological idea of mating (coition to order), familiar through the keeping of animals for breeding purposes, should certainly not be applied to the pairing and mating of free wild animals. Even in closely related species the ceremonial may differ widely, as O. ANTONIUS (1937) has shown for various Equidae (members of the horse family). Finally, personal sympathies and antipathies often play a decisive role among wild animals. A meeting between a mature male and female of the same species, mammal or fish, does not invariably lead to pairing or mating. Unlike the case of domestic animals, the rutting period of wild animals is mostly confined to definite seasons.

In three consecutive years F. M. CHAPMAN (1939) observed the onset of heat in a free coati (Nasua). In 1935, the period began on
29 January, in 1936 on the 27th, and in 1937 again on the 27th. The period of heat came to an end as punctually in 1935 on 11 February, in 1936 on the 10th, and 1937 on the 18th. Among wild animals the foundation of a family, or the preparation for it, is often regularly dependent on a fixed ceremonial (display), a fixed time (rut), and often on a fixed place (mating ground) as well. Sexual behaviour is closely linked with the space-time pattern.
From Freedom to Captivity

Not all animals kept in captivity pass through this phase: many are born in captivity, so they know nothing of freedom. Meanwhile, year after year many wild animals are captured and have to get used to it. As experience shows, this is very often possible only at the expense of serious losses. The change over from freedom to captivity itself has a fundamental bearing on a proper appreciation of the wild animal's situation in its new state of captivity. For these two reasons we shall deal with this transitional phase a little more fully.

The transition of a wild animal from freedom to captivity is like a transplantation experiment, grafting part of one living organism on to the body of another animal.

The transplanted animal's behaviour may be of two different kinds, depending on its origin or the new locality. The second kind is usually seen in the undeveloped still adaptable young wild animal; it may fit the new environment and settle down in it. The first kind on the other hand occurs with the older wild animal already set in its ways and rigidly conditioned by its previous background. It has lost its plasticity and adaptability, and so must behave as it always has done. True, such individuals may often be kept in captivity for a time, but they never become properly adapted to the new situation. If they survive capture they usually linger in a chronic state of excitement generally caused by their uneasiness in the presence of man, and with a basically rigid attitude of mind, so to speak. This prevents any suitable treatment, even the taking of food; it may result in nervous disturbances, reduce resistance to disease and lead to death, psychologically caused. These animals correspond to grafting failures or grafts that refuse to heal in the above comparison. Among them are adult moose which, unlike their young, cannot get accustomed to captivity according to L. Heck's experience (1934).

The exceptional significance of capture for the wild animal can best be explained in J. Von Uexküll's terminology. According to him, each animal lives in its own specific world. The environment (milieu) offers as it were a reservoir of stimuli from which the subject constructs its own world. The building material consists of a variety of things of vital importance or biological interest to the animal. By capturing it we utterly destroy the animal's previous world, and put it into a different
The animal must construct an entirely fresh subjective world. This means an enormous task, and it is easy to understand that every individual cannot tackle it successfully. The animal must struggle with completely fresh and strange factors, in order to fit the new structure as harmoniously as possible into the new environment.

The actions of the free animal, as has been shown in the section on freedom, are constantly aimed at avoiding its enemies. Man, we saw, is the universal enemy of such an animal. It must flee from him above all others, until it is completely exhausted if necessary, and until heart and lungs fail. In order to avoid close approach to the animal, man has turned to the construction of all kinds of traps ever since palaeolithic times. In recent methods for capturing animals, analeptics and sedatives have been injected in order to lessen the shock of capture. Attempts have also been made hitherto, unfortunately without the sedative effect aimed at, to find a way of introducing some kind of anaesthetic into the body of the free animal e.g. by light shot, and so reduce to a minimum the upset and risk of capture. All these difficulties are caused through the presence of man, the universal enemy, from whom the animal tries to escape at all costs as long as it keeps the original flight tendency of the free wild animal. In the milieu of captivity the most important factor is man; apart from his immediate presence, the whole environment of the captive animal is as it were impregnated with man. Under such circumstances the most important behaviour pattern in freedom, flight from man, the enemy, becomes meaningless. In addition, the normal course of flight reaction is usually impossible through the narrow confines of the captive’s life. The main problem set the animal in the reconstruction of its subjective world to suit captive conditions is to fit man into the new set of circumstances. In a successful reconstruction man undergoes a complete change in significance in the animal’s world; the original negative enemy significance is replaced by a new positive one. Man gets as it were a change of sign—a ‘plus’ instead of a ‘minus’ (Figure 6). The particular nature of this new positive significance will be dealt with in the section on the animal-man relationship.
Once this change of significance of man in the animal's world has been accomplished, the reconstruction of their relationship may be considered successful. At the most important point the animal has fitted in with totally different circumstances, and thus the basis for an optimum existence is laid. This is conditioned on the one hand by the eph-harmony (R. Hess), that is, by the balanced interaction of all parts of the organism; on the other, by the harmonious state between animal and milieu. The life of an animal which has reached this double state of harmony in captivity is just as complete, or incomplete, as that of an animal at liberty.

For the animal born in captivity, as was mentioned in the introduction (p. 2), no such discrepancy between behaviour and environment exists; it is born into the conditions of life in captivity in which the eph-harmony is largely guaranteed from the start. Trifling disturbances may occur, for the simple reason that certain innate behaviour patterns, adapted for life in freedom, cannot develop properly under conditions of captivity, or be brought into play, through lack of appropriate stimuli. Finally 'Leerlauf' reactions may arise in K. Lorenz's sense (1935 210), possibly connected with the inability in captivity to satisfy the impulse to run away, so frequent in freedom. He suggests that it seems as though the bird expects to have to fly off, and indeed that it would be a relief to it if the enemy who never turns up were at last to appear. The 'Leerlauf' reaction consists of exaggerated fright at unimportant, petty things. This lack of balance is in striking contrast to the confidence such animals show in their keepers. In fact, Lorenz (ibid 211) thinks that it stands in inverse proportion to this confidence.

Apart from the psychological changes just mentioned, which the wild animal undergoes when transplanted into captivity, this latter naturally has many other consequences, ecological, physiological, climatic, geographical etc. Yet the psychological seem to be far and away the most significant. Let us return to the separate factors. For the moment we are concerned simply with influences that may sometimes result from geographical displacement. This, of course, only concerns animals when the place of capture is a long way from the place where they are kept and which show marked sensitivity about it. Often the journey that follows capture takes the animal into a completely different climate, sometimes into a completely different seasonal rhythm. For instance, penguins brought from the Antarctic via the equator to the northern hemisphere often need time to adapt their moulting and breeding periods to the new cycle, as T. H. Gillespie (1932 93) on the basis of his long experience with penguins points out in a most interesting manner.

There are only the vaguest clues as to whether and to what extent geographical displacement alone (not climatic or ecological) may affect an animal. Perhaps it plays a part for the North American pronghorn
antelope (*Antilocapra americana*), which has been mentioned previously ((1946) 255). At all events the investigations of E. Heller (1930) on this subject, which have only subsequently come to the knowledge of the author, do not contradict it. Amongst other things this writer points out that the zoos which are situated on the Atlantic coast of the U.S.A. are more than one thousand miles east of the natural range of pronghorns, and it is apparently a region very unsuitable climatically and quite deadly to pronghorns. As is well known, these remarkable antelopes have not yet been successfully kept in Europe for any length of time. At any rate, the effect of geographical transposition, though not so far explained in detail, may be theoretically conceivable. The so-called homesickness in man, certainly ascribable to more primitive biological phenomena, still needs further analysis.
Range in the Wild State

Compared with the revolutionary change in the subjective world just mentioned, all accompanying phenomena, all the consequences of captivity, are of secondary importance to the animal. With his anthropocentric tendency, man has always been apt to form a one-sided idea of the fate of a wild animal living in captivity. The chief factor of an animal's life in captivity, or at least its chief drawback, was supposed to be restriction of space. The amount of space at the animal's disposal has had too much attention while the quality of the space on the other hand has received too little. This false idea about the problem of space was based on the belief that the wild animal in freedom has a limitless amount of space to roam in, but in captivity only a restricted amount, of oppressive smallness. But in the ecological analysis of freedom it has been shown that the free animal has not got an unrestricted amount of space at its disposal; simply a territory of limited extent, varying in size from a few square yards to hundreds of acres, according to the species (cf Table II, p 12).

There would be no need to discuss the question of the amount of room in captivity if each animal in the zoological garden could be provided with a space the same size as its territory. This, however, is not usually possible. The space at the disposal of an inmate is necessarily less—from 100 to 16,000 times so—than its usual natural territory. The non-expert might think that in itself this confinement of space, that is, restriction of the freedom of movement would be the most important factor in captivity. It must be said here and now that this space restriction is of far less importance to the animal than certain secondary results of this diminution of space. We must therefore differentiate between:

1 Direct i.e. primary effects of space restriction—restriction of freedom of movement, or possibility of movement in the physiological sense (necessary muscular activity etc)

2 Indirect i.e. secondary effects of space restriction; as, for example, hypertrophy of values ('Valenz' in the sense of W. Fischel); lack of diversion and occupation; impoverishment of the subjective world; liberation of energies that were pent up in freedom (through avoidance of the enemy etc); impossibility of suitable differentiation of space; impossibility of free choice
RANGE IN THE WILD STATE

of food; impossibility of choice of optimum micro-climate; hypersexuality; anti-social behaviour; impossibility of avoiding members of its own species at will, and increase in danger from infection and re-infection.

We shall come back to the discussion of these indirect or secondary results of confinement dependent upon captivity when considering quality of space. First of all we must take a close look at restriction of space itself, in its direct effects upon the animal.

The Space necessary physiologically and psychologically

It has just been shown that in freedom the wild animal has the urge to escape from an enemy, especially from man, as soon as the flight distance of the animal concerned is exceeded. The animal tries as quickly as possible to put its flight distance between itself and its enemy and with all the means in its power. Not until it has succeeded can the animal achieve a state of rest, or harmony. If it cannot get far enough away from its enemy, that is, beyond the flight distance, it must remain in a state of tension; it may sometimes show defence or critical reaction, accompanied by maximum excitement.

Since flight reaction is the most significant behaviour pattern of the wild animal’s life in freedom, it must be a prime concern in captivity to give normal play to this vitally important reaction. This means giving the animal the chance to get away from man himself, at least to beyond its flight distance. The smallest cage in theory must thus be a circle of a diameter twice the flight distance (Figure 7). In such a cage the animal could retreat to the centre from a man of enemy significance standing on the perimeter. Here it would be separated from its enemy by the flight distance, and could (theoretically) achieve rest in it.

Figure 7. Plan of space psychologically necessary for a wild animal in captivity. The circular cage must have a diameter at least twice the critical distance of the animal concerned. Only at the centre H (Home) of this minimum theoretical cage would the animal be separated from surrounding spectators by its flight distance, and thus be able to find rest there.
It is obvious that in practice enclosures of such dimensions are seldom available for captive animals. Moreover, we should not be able to see them any better than in freedom. On the other hand we must realize that any cage that has a diameter of not less than twice the flight distance of the animal inside it is too small, in terms of animal psychology. In the presence of man, the enemy, outside the cage, the animal is not able to take food offered to it, owing to the critical distance in such a cage (Figure 8).

Figure 8. Plan of the situation of a newly caught wild animal. Because of the presence of man beyond the bars of the (psychologically) too small cage, and so within the flight distance, the animal is unable to take the food offered it.

The animal would have to go even nearer to man, who has already stepped inside the limit by approaching the bars. The wild animal cannot settle down in a cage where the size is less than that theoretically determined. Since in practice, however, it is impossible to fit the size of the cage to the flight distance of the wild animal, only one possible solution remains: to make the flight distance fit the cage, that is, to neutralize the animal's desire to escape and reduce its flight distance to zero. This is possible by taming, and has been fully discussed elsewhere (H. HEDIGER (1935)).

By way of demonstration, we give a few examples in Table III, taken from the literature on flight distance. It must be emphasized that the flight distance is based on full visibility of the enemy, that is, of man.

The flight distance of the free animal varies not only according to the species, but in the same species according to intensity of pursuit in different areas: it may also show individual fluctuation in the same animal, varying with the enemy, or the animal's temperament. In spite of all this, a definite, unmistakable specific distance exists within fixed limits, as will be seen from Table III.

A wild animal which by taming has lost its urge to run away from human beings, and the flight distance of which is therefore zero, settles down in a much smaller space than its untamed companion, as has been said before. A thoroughly tame animal put into a small box that hardly allows it room to turn round, will not be disturbed by the approach of man, it will more likely press against the wires to be fondled. In contrast to the untamed one it feels ideally no biological urge to run away at the approach of a visitor, or to make desperate attempts to escape. Man is no longer able to cause extreme agitation by his close presence,
### Range in the Wild State

**Table III: Examples of Flight Distance**

<table>
<thead>
<tr>
<th>Species</th>
<th>Flight Distance</th>
<th>Further Details</th>
<th>Author</th>
<th>Year</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mammals</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Howler monkey</td>
<td>20–30 yds</td>
<td>In trees</td>
<td>Chapman</td>
<td>1939</td>
<td>172</td>
</tr>
<tr>
<td>Giraffe</td>
<td>150 yds</td>
<td>For men</td>
<td>Kearton</td>
<td>1929</td>
<td>101</td>
</tr>
<tr>
<td>Giraffe</td>
<td>25 yds</td>
<td>For motor-car</td>
<td>Kearton</td>
<td>1929</td>
<td>101</td>
</tr>
<tr>
<td>Giraffe</td>
<td>About 200 paces</td>
<td>Grassland with no human beings</td>
<td>Schillings</td>
<td>1920</td>
<td>129</td>
</tr>
<tr>
<td>Kiang</td>
<td>200–350 yds</td>
<td>For men on horseback</td>
<td>Schaffer</td>
<td>1937</td>
<td>135</td>
</tr>
<tr>
<td>Prong-horned antelope</td>
<td>500 yds</td>
<td></td>
<td>Heller</td>
<td>1920</td>
<td>2</td>
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<tr>
<td>Chamois</td>
<td>100–200 yds</td>
<td>In the Carpathians</td>
<td>Coaster</td>
<td>1929</td>
<td>101</td>
</tr>
<tr>
<td>Oryx</td>
<td>150–200 yds</td>
<td>Not very timid</td>
<td>Roosevelt</td>
<td>1910</td>
<td>291</td>
</tr>
<tr>
<td>Kudu</td>
<td>About 200 yds</td>
<td></td>
<td>Maydon</td>
<td>1927</td>
<td>207</td>
</tr>
<tr>
<td>American bison</td>
<td>250–400 yds</td>
<td>District not hunted</td>
<td>Garrettson</td>
<td>1928</td>
<td>103</td>
</tr>
<tr>
<td>African buffalo</td>
<td>About 80 yds</td>
<td></td>
<td>Maydon</td>
<td>1932</td>
<td>290</td>
</tr>
<tr>
<td>Red deer</td>
<td>50–100 yds</td>
<td>When being fed</td>
<td>Darling</td>
<td>1937</td>
<td>72</td>
</tr>
<tr>
<td>Red deer</td>
<td>600 yds</td>
<td>When irritable</td>
<td>Darling</td>
<td>1937</td>
<td>109</td>
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<tr>
<td><strong>Birds</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bustard</td>
<td>500 yds</td>
<td></td>
<td>Heinroth</td>
<td>1924/18</td>
<td>117</td>
</tr>
<tr>
<td>Flamingo</td>
<td>400 yds</td>
<td></td>
<td>Peney</td>
<td>1926</td>
<td>25</td>
</tr>
<tr>
<td>Ostrich</td>
<td>150 yds</td>
<td></td>
<td>Kearton</td>
<td>1929</td>
<td>138</td>
</tr>
<tr>
<td>Hermit gull</td>
<td>15–20 yds</td>
<td>For man</td>
<td>Goethe</td>
<td>1937</td>
<td>44</td>
</tr>
<tr>
<td>Hermit gull</td>
<td>30 yds</td>
<td>For wolfhound</td>
<td>Goethe</td>
<td>1937</td>
<td>44</td>
</tr>
<tr>
<td>Sarus crane</td>
<td>30–40 yds</td>
<td>Not very timid</td>
<td>Champon</td>
<td>1934</td>
<td>41</td>
</tr>
<tr>
<td><strong>Reptiles</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Clemmys leprosa</td>
<td>15 yds</td>
<td></td>
<td>Hediger</td>
<td>1935a</td>
<td>4</td>
</tr>
<tr>
<td>Natrix piscator</td>
<td>2 yds</td>
<td></td>
<td>Mell</td>
<td>1929</td>
<td>241</td>
</tr>
<tr>
<td>Eumeces guttulatus</td>
<td>5 yds</td>
<td></td>
<td>Dimars</td>
<td>1932</td>
<td>201</td>
</tr>
<tr>
<td><strong>Fish</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Periophthalmus</td>
<td>20–30 yds</td>
<td></td>
<td>Harms</td>
<td>1929</td>
<td>277</td>
</tr>
<tr>
<td><strong>Invertebrates</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fiddler crab</td>
<td>10 yds</td>
<td></td>
<td>Hediger</td>
<td>1933</td>
<td>388</td>
</tr>
</tbody>
</table>
and the tame animal feels at home in man's company. Thus the
smallest box, in the purely psychological sense, is big enough for the
tame animal. Let us assume that this animal is kept permanently, not
temporarily, in such a box. It would be bound to suffer serious damage
to health, through the impossibility of being able to move about, of
enjoying a minimum of activity. Thus from the physiological point of
view the box is obviously too small. The well-being of the captive
animal doubtless depends on the possibility of satisfying those occasional
activity needs that are essential to the species. The space that gives this
satisfaction is physiologically big enough, but is often greatly over­
estimated; its size is extraordinarily variable from species to species.
We might suppose that the dimensions of the space physiologically
necessary must at any rate be several times the overall length of the
animal concerned. That may be true for most animals, but it would be
too much for many, as for example, snakes, especially the largest
species. F. Werner (1939) rightly pointed out in one of his
recent works that the snake has no real need to stretch out to its full
length. There are even some boas (giant snakes), as for instance
B. constrictor, which cannot make their bodies stretch straight out. In the Basle Zoo
we bred the python P. molurus in a terrarium, in which the parent snakes
could not stretch out.

It has already been said that the space available for the animal in
captivity is much less than its natural territory. Experience in running
zoological gardens teaches us that many animals thrive for years, for
decades, even for a hundred years or more, during which they even
reproduce. There is no doubt that many species flourish in zoos, des­
pite seemingly cramped quarters. In view of this the question at once
arises—why are the territories of free-roaming animals so extensive?

This is easy to answer. The free animal has to forage for itself. In
contrast to the zoo inmate (or the domestic animal) the necessary food
is not regularly provided for it by man; it has to get the required quan­
tity of food on its own. This may consist of animal or vegetable matter,
and the animal can only live on the surplus provided by its territory;
it may not recklessly despoil and wastefully plunder. In other words,
the size of a territory must be such that the inhabitants' food consump­
tion is balanced by the food produced in it. A lion in a district short of
game needs a larger territory than one in a place where it is more
plentiful. The lion population in the latter may thus be greater than in
the former. In the zoo where the lion gets enough meat, the territory
can be far smaller, the population far greater. Thus food supply deter­
mines density of animal population, states R. Hesse (1924) 250),
speaking as an ecologist. In the cowshed, with artificial feeding, cows
can be kept in greater density, flank to flank; but out in the fields they
need, as temporary self-supporters, a considerable area.

The most important of the different factors determining the size of
RANGE IN THE WILD STATE

territory is obviously the amount of food required. However much we may dislike it, we must put biological facts before anthropomorphic ideas about the animal in freedom. Even the eagle, that typical example of free and unrestrained flight in boundless space, does not fly about at will in its territory, which, because its prey is scattered, is bound to be large. It is driven chiefly by the urge to get food; if this urge disappears, it gives up distant foraging expeditions, just as the lion does on his extensive trails over grassland.

It is inconceivable that lions and other large carnivores can be kept over twenty years, bears thirty, baboons, condors, eagles and vultures twenty, thirty four and forty, even more than one hundred years, elephants forty, giant salamanders fifty five, and alligators fifty four years, and for them to breed in captivity and be in perfect health if the space allotted to them is too small; especially if the physiological conditions are insufficient. Significantly enough, and contrary to popular ideas, the largest and most skillful fliers among the raptorial birds, the eagles and vultures, are among the longest lived inmates of zoological gardens. The oldest inmate in Basle Zoo is a male condor, bought in 1900 and still in full health. Most likely the maximum span of life of many animals is attained in zoological gardens and not in the wild state. In freedom, very few animals indeed die of old age, but quite a number do so in captivity. In these conditions they can as it were exhaust their latent capacity for living, but practically never in freedom, as E. Mohr (1938) pertinently remarks in his work on

Table IV
Comparative Ages of Four Common British Birds, from 'How to Study Birds' by Stuart Smith

<table>
<thead>
<tr>
<th>Species</th>
<th>Greatest age (Aviary)</th>
<th>Greatest age (Wild Conditions)</th>
<th>Average age (Wild Conditions)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Song thrush</td>
<td>17 years</td>
<td>9 years</td>
<td>15 years</td>
</tr>
<tr>
<td>Blackbird</td>
<td>20 years</td>
<td>10 years</td>
<td>16 years</td>
</tr>
<tr>
<td>Starling</td>
<td>15 years</td>
<td>9 years</td>
<td>14 years</td>
</tr>
<tr>
<td>Robin</td>
<td>20 years</td>
<td>11 years</td>
<td>15 years</td>
</tr>
</tbody>
</table>

rodents. This fact is beginning to be generally accepted. A. Portmann (1944) states that we must adopt the view that nowadays animals attain their true age limit far more often in captivity than in the wilds and that from the new evidence of zoological gardens we may draw certain conclusions about the animals’ potential longevity. Zoological garden biologists have S. S. Flower to thank (1931 and following years) for some extremely valuable and at the same time critical reports on the life span of various vertebrates. We must not forget in
this connection that few mammals, indeed few animals, can ever reach or surpass the average age of man.

The attainment of ripe old age in captivity is no guarantee of biologically correct treatment. We may indeed regard the long span of life of many isolated cage birds as unnatural, for isolation itself is unbiological. On the much discussed problem of solitary confinement, with its long but obviously unnatural mode of life, F. BRAUN, in his Essentials of Aviculture (1924) 36, especially the discussion on Rausch’s double-sprung cage), emphasizes that M. RAUSCH is no doubt right to keep on emphasizing that the hedge-sparrow and bastard nightingales (Luscinia major), that were kept according to his method, often reached a far more advanced age than can ever have been the lot of their free relatives in the struggle for existence. One might with justice argue that such captives led an existence that could hardly be described as living, with all that life implies in vigour and fullness. He goes on to say that for this reason he has never got much pleasure from keeping pedigree song birds on their own in cages. He always feels they are too much cut off from natural conditions.

There is, in the author’s opinion, only one criterion for suitable biological conditions and that is success in breeding. To the zoo biologist this is like arithmetical proof to the mathematician. When breeding does not occur, something is wrong with the methods of keeping the animals; if breeding does occur, it is a guarantee that the conditions are essentially right, since regular breeding presupposes, at least among the higher animals, a certain measure of well-being in the parents.

In practice successful breeding is not necessarily proportional to the amount of space at the animal’s disposal. The opposite is often the case. Hence it may be inferred that amount of space is not vital for success in breeding i.e., for correct biological conditions. It is of far less importance than the outsider generally assumes. F. SCHMIDT-HOENSDORF (1931) points out that travelling menageries breed lions and even tigers in their cramped wagon-cages, and astonishing results are often attained in small zoos. The ant-eater at Niill’s Zoo in Stuttgart gave birth to eight cubs all told; and H. LANDOIS bred wild hares in a restricted space at the Münster Zoo. G. RAAK (1940) reports successful breeding in a pair of flying foxes that were kept in a cage of 9 cu ft (1 cu m) capacity, and in which they were quite unable to fly. He rightly adds that here is clear proof that suitable treatment, not size of quarters, is essential to the well-being and reproduction of animals in captivity. In Basle, flying foxes have bred several times in a cage measuring two yards by two yards by three yards.

Flying animals especially are thought of as creatures that need room for moving about. But they usually take to this fatiguing type of locomotion only when compelled, for instance, to escape or to seek food. Among the Chiroptera (Macro- as well as Microchiroptera), flight is
remarkably easily dispensed with. Neither in birds nor Chiroptera (bats) has any damage to health been shown through lack of opportunities for flying. In the small park at Brienz (Bernese Oberland), a pair of golden eagles lived in a small cage for more than forty years and repeatedly brought off a brood. In many other zoos as well the greater raptorial birds have bred successfully. It has often been the experience with them that they do not make use of all the space available. They simply have no need to fly. A similar state of affairs occurs with species of geese and ducks that breed regularly in zoos in spite of being pinioned.

In birds of prey and Anatidae, a need to fly, in the sense of a physiologically necessary activity, does not exist. We must realize, however, that in individual species, ceremonial flights are essential components of mating ceremonies. N. Tinbergen (1939), for example, describes the ceremonial flight of the tern. It is not certain whether it is essential here for mating behaviour, as it apparently is with the grey lag goose, dealt with later. If it is, such birds must naturally be given the necessary opportunities for flight, if their treatment is to be biologically sound.

In Switzerland, the fairly wide spread Alpine swift (Micropus melba melba) is one of the birds the life flight of which has unusual significance, as it is only able to take food on the wing. Even the nesting material is obtained preferably in the air e.g. falling bud-scales. It is believed by many ornithologists that in this bird, which cannot rise from a flat surface, coition invariably occurs during flight. However, H. Arn (1945), an excellent authority on this bird, states that this is not always the case, but that mating may take place at the nest.

A certain amount of opportunity for flying seems necessary for breeding flamingoes. At any rate, it is a striking fact that this favourite ornamental bird has not been known to breed in any zoological garden in the world. This may be due to the vast and a typical space-time system of this handsome bird that visits definite breeding places only every few years. Perhaps too because these birds are not usually kept in aviaries, but free with clipped wings. This may, perhaps, be the reason why the male, through this obstacle to flight, is unable to tread the long legged female. Certainly other factors must also be responsible for the persistent lack of success in breeding e.g. the fact that flamingoes are not able to get highly concentrated salt water and the particular kind of slime found in nature, and finally that their food substitute is not always adequate. E. Gallet (1949) has given us a clear insight into the biology of the African and Mediterranean species.

Activity from Internal Motive and External Cause
The need for flying is the most striking form that the need for movement takes, and one that most deeply impresses man. In typically
anthropocentric manner he transfers it to the animal in captivity. This need for movement has been closely investigated by J. S. Szymanski (1920). He describes it as the principle of activity from internal necessity, showing itself in an insistent need for activity until the discharge of the accumulated motor energy occurs. A period of rest then follows such a period of activity. The principle of internally compelled activity, however, does not attempt to show that each action is entirely motivated by internal impulses. It expressly states that external stimuli can activate the organism, even during the periods of maximum rest. We must therefore distinguish between:

1. activity from internal necessity
2. activity from external cause.

In freedom every animal performs the amount of activity of advantage to it, whether from internal necessity or external cause. The activity shown is always several times greater than the amount necessary in freedom, and it is over this amount that the greatest misconceptions exist.

We often find that the amount from internal necessity is surprisingly small among those very animals which, according to customary ideas, must have a particularly strong urge to be active, for example, lions, eagles and others. The activity of these animals in freedom is almost entirely conditioned by external causes, especially escape from enemies; also by the search for food, which has internal causes, but not in Szymanski's sense of inner urge.

In other animals, especially those which get a constant and adequate food supply in the warm tropical forests without much trouble, the ratels (Mellivora) for instance, a considerable amount of activity caused solely by internal necessity can be seen. In extreme cases such animals develop 'motor-extravagances', as mentioned by H. Krieg (1937). Apparently aimless movements occur, but these are followed by relief of tension or the loss of energy physiologically necessary. Krieg quotes examples of similar exuberant muscular activity. These include the play activities among many species of monkeys, the jumping spasms of many antelopes, and the howling orgies of howler monkeys with much expenditure of muscular energy, the screeching parties of many parrots, cuckoos, Dendrocolaptidae, rails etc. He adds that these extravagances, accompanied apparently by feelings of pleasure (relief feelings), cease immediately if their living conditions (balance of food) substantially deteriorate.

The Indian ratel (Mellivora) also shows exaggerated reflex actions. It is perhaps the only mammal, with the exception of the sea otter, that spontaneously turns somersaults in freedom, as F. W. Champion observes (1934).

The family of Mustelidae (weasel group) seems to possess numerous
members with superabundant energy. We have only to think of the continuous activity of two of the Mustelidae, the common marten and the pine marten, or of the otter.

In captivity, where the animal is safe from enemies, largely protected from dangerous rivals of the same species and freed from the necessity to seek its food or a mate, activity from external causes often plays quite a limited part, or none at all; the animal is only driven to activity by internal necessity. In individual instances e.g. the greater birds of prey, this sort of activity is sufficient, as experience teaches us. On the other hand, in some species, including the lion, lack of activity from external causes may have disastrous results. At the very least there will be a hypotrophy in the sense of a physical inferiority in comparison with members of their species at liberty which have been far more intensively 'trained'.

Perhaps O. Antonius (1933) goes too far when he says that the lion, with its remarkably little need for activity, as any zoo keeper knows, refuses to take a step on his own if his daily food is provided for him. At any rate there are plenty of animals that do not use up all the space provided them in captivity, or anything like it, or that, through lack of external stimulus, move about far less than is good for them, so that they eventually suffer from serious metabolic and other disturbances. It is often found of great benefit in captivity to replace the normal external activity-urge of freedom by regular training exercises of a biologically suitable nature. Up till now, training in zoological gardens has been confined to elephants, a few large carnivores, and the anthropoid apes; but there seems to be no reason why certain ungulates (Equidae, Bovidae, Cervidae etc) should not have the benefit of this treatment, to raise the tone of their constitution and efficiency to that of their free-roaming relatives by deliberate increase in their activity. Among captive ungulates (bison, moose, red deer, fallow deer, wild boar, antelopes etc) spontaneous outbreaks of activity, consisting of an infectious rushing around together, are sometimes noticed.

If individuals of the same species of wild animals are compared, the one born wild, the other in captivity, the wild ones usually appear stronger and better developed. F. J. J. Butendijk (1938) quotes a remark of W. Long, that the animal at liberty lives at high pressure. In comparison with this, life in captivity means a sort of low pressure existence. The captive wild animal is, as a rule, under occupied, under exercised and over cared for. Without doubt a certain amount of this can be remedied by training exercises.

A fundamental problem of animal biology is how to neutralize as far as possible all modifying (non-hereditary, externally conditioned) and mutative (hereditary) changes and degeneration phenomena in captivity. To start with, though, we do not yet know enough to identify
ACTIVITY FROM INTERNAL MOTIVE AND EXTERNAL CAUSE

these various phenomena correctly in the morphological, physiological
and psychological fields. Meanwhile the essential for a successful solu-
tion is to aim at a thorough knowledge of them.

In connection with the fox, B. Klatt (1932) has pointed out some
of the most striking results of captivity; under development of
muscles, diminution of brain weight, swelling of the thyroid, shorten-
ing of the facial cranium, increase in breadth of the skull etc. M. Hitz-
heimer (1937) observed very curious and quite unpredictable changes
through captivity and domestication in Bobby, the gorilla brought up
in the Berlin Zoo. H. Nachtshelm (1936) asserts that the carnivore
undergoes more modification of the skull through captivity than
the herbivore; the food of the latter in captivity is more like that of
free herbivores. A comparison between the skulls of carnivores that
have grown up in zoological gardens and those living in freedom shows
considerable differences. Thanks to the capable late assistant of the
Basle Natural History Museum, J. Huber, attention was drawn to the
fact that the skull of an animal from the zoo very often shows asymmetry
both in quality and in difference of proportions compared with wild
animals’ skulls. Most frequently a curvature of the longitudinal axis of
the skull appears.

It has long been known that a curious connection exists between
amount of space and body growth. Experiments have shown that mem-
gers of the same species grow to different sizes according to the amount
of space available (R. Hesse (1934) 136). But these experiments were
usually made on invertebrates or fish, at most on tadpoles, and even
here considerable sources of error were discovered. The position of
warm blooded creatures in this matter has not been clearly discovered.
In this connection, J. Beninde ((1937) 179) reports on his experiments
with rats, in which a ‘disturbance-factor’ was held responsible for the
close connection between density of population (amount of space) and
size of body. He also noticed this strange connection between herds
of wild red deer. The occurrence of dwarf island species should not be
connected with the diminished body size of captive wild animals, as
gigantic growth has also occasionally been observed on islands.

Only careful analysis of a large number of facts will shed light on one
important question. Does captivity in the modern sense i.e. on a
biological basis, produce regularly and in all species, individuals that
are inferior to those living in freedom? There is no lack of evidence
nowadays to the contrary. It is at all events likely that in captivity
regular and abundant food permits a physical development such as is
not always seen in freedom. On the other hand, a rigid selection is at
work in freedom, weeding out all inferior individuals, which in cap-
tivity are often kept alive with difficulty. Hasty generalizations are very
dangerous here. The expert on nutritional physiology, F. G. Benedict
((1936) 17 et seq), quotes observations of P. Matschie, a specialist on

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Gauhati University.
mammals, from which it appears that the shoulder blades of lions and
tigers born and raised in parks are actually longer, wider and stronger
than those of free-living animals. The same superiority of growth
and breeding of park animals has likewise been observed with lions
and zebras (*D. indicus major*). L. Zukowsky points out that a bull gnu
(*Gorgon albojubatus*) born in Berlin was a hand's breadth higher at
the withers than the same kind of adult animals coming from the
wild. It has been noticed that Indian elephants born in European
zoos are on the average larger than those imported from India. In com­
parisons of this sort we must be on our guard against grave sources of
error, especially the idea that there are races of lion, tiger, zebu,
gnu or elephant of different sizes. In the zoological garden there is an
understandable tendency to show the most impressive specimens. A
broad and attractive field of work lies open here.
The Problem of Confined Space

IN CONTRAST with the so-called free-living animals, those in captivity are 'under lock and key'.

To a great number of the people who visit zoological gardens, the animals seem like innocent convicts and the director of the zoo therefore a kind of prison governor. This anthropomorphic conception finds literary expression in countless novels about zoological gardens. Other visitors on the other hand find nothing unusual in keeping certain large carnivores (beasts) behind locks and bars. In the chapter on the animal-man relationship it will be shown that it is the duty of the zoo to protect the public from the animals, and also to protect the animals at least as much from the public.

Biological and Psychological

In this book, which it is hoped may have some share in making the treatment of wild animals biologically more sound, an attempt will be made to abandon as out of date and anthropomorphic the attitude to captive animals usual hitherto, and to replace it by a biologically correct one, through an analysis of the situation of the animal in captivity. We must therefore ask ourselves: What does limitation of space (iron bars, cages etc) mean to the animal? In the main its significance will be one of the following:

1. Prevention of the flight reaction
2. Prevention of encounters
   a. with animals of its own species
   b. with other animals
3. Limitation of territory
4. Protection against encounters
   a. with animals of its own species
   b. with other animals.

Prevention of flight reaction—The popular idea is that the bars prevent the caged animal from regaining the precious liberty it pines for. The real truth about this precious liberty has been hinted at in the section on freedom. In all animals born in captivity, or taken very young, this assumed longing for freedom cannot exist, as they have
THE PROBLEM OF CONFINED SPACE

never known it. For that reason they cannot feel that their cage is an obstacle to regaining freedom. The word cage is used here for convenience and is to be taken as indicating the various ways of confining and fencing in. Contrary to the idea mentioned above, experience with all sorts of animals in zoos shows that animals that are set free often voluntarily return to their cages. At Berne, on one occasion in the Dählhölzl Zoological Gardens, for example, a number of roe deer got out because the gates, several yards wide, had accidentally been left open. Because of passing visitors the animals were driven deep into Dählhölzl Forest, which is scarcely a hundred yards from the enclosure, and has a herd of wild roe deer in it. Shortly after, the whole pack of deer were back again, in spite of having found 'ideal' living conditions in the woods. In this case it is impossible to suppose that hunger drove them back. Finally there is a reason, based on animal psychology, why animals should not regard their cage as an obstacle to regaining their freedom. According to this theory, these animals possess a differentiated memory image of freedom, or the territory they formerly occupied. But even in the case of the highest mammals we should be chary of assuming such a thorough-going 'free memory', in Fischel's sense. The cage is a restriction upon the captive wild animal and upon the tamed wild animal as well, not upon its attempts to get away to somewhere (liberty, or home) but from something, namely from its chief enemy, man—away from surroundings reminiscent of man which are perhaps biologically unsuitable.

In the section on the transition from freedom to captivity we have shown that man has enemy significance for the animal chiefly, his appearance causing escape reaction, even when he is a long way off. The captive animal does not cease to regard man as an enemy immediately after capture; this decisive change of significance only happens in the course of getting used to the new situation or of becoming tame (H. Hediger (1935)). Man, and all human accessories, cage etc are therefore still of sinister significance to the animal, and it tries to escape from them all. Thus it wants to get away from something; that is why it tries to get through the bars that obstruct the normal path of flight.

Often during attempts to escape caused in this way the cage is not regarded as a solid physical hindrance by the animal, but as a penetrable fabric, or, in cases of panic, is altogether ignored. It is possible for an animal to dash itself with all its strength against the cage, thus injuring itself seriously. In this way fractures of the skull or broken necks often result, especially among ungulates, less often in the case of carnivores, primates etc. The wild hare is well known for its attempts to escape in this fatal way.

No zoological gardens have been spared losses of this nature. Naturally the risk is greater the less an animal has got used to things
before it has got adapted to its new surroundings. A practical step to avoid this is to keep such animals in cages so small that they are quite unable to develop sufficient dynamic energy for fatal fractures. Opportunities for dashing against the bars are simply removed until adaptation has gone as far as necessary. In individual instances, perhaps also with the smaller species of birds, padded cages may be used with advantage.

Prevention of encounters—Attempts at encounters between members of the same species separated by their cages are so common in zoos that they are merely mentioned here for the sake of completeness. They may be either aggressive, as with rivals for example, or perhaps sexual, when the two sexes are separated for particular reasons. In the Zürich Zoo a male polar bear broke through the bars separating him from the female and killed the young cub. At the beginning of the rutting season, two strong red deer in Bern Zoo very nearly demolished the railings of their two enclosures, which had only a path's breadth between them. For a moment it looked as though demolition of the tough steel wire netting could only be prevented by letting the two stags, which until then had lived in peace together, get at each other. By this means their great strength would be diverted from the fence to their antlers. A similar instance was observed between strong ibex.

The cage can also prevent encounters between animals of different species. In the Basle Zoo the author once watched a runaway pony galloping past the lion's cage. The lion crouched for a jump, only the bars preventing him from carrying out his intention of leaping upon his prey. In the Bern Zoo the railings around the large deer enclosure never had to be repaired anywhere except where it formed the boundary of two adjacent enclosures. In one of these were Sika deer, in the other fallow deer. The bucks kept on trying to fight each other through the wire, and in this way damaged it; but in those places where destruction of the railings would have opened the way to freedom it was never touched. The same sort of thing has repeatedly been observed in the Basle Zoo.

Limits of territory—When the limits of the cage simply mean a distinct demarcation of territory for the animal, ideal conditions for captivity have been achieved, as far as space limitations are concerned. This ideal often is achieved. The space given to the caged animal is frequently defended against new arrivals as though it was its own property. That is one reason why it is often considered risky to put fresh arrivals among animals that have already settled down. It is often easier to get strange animals used to each other by putting them into their new home all together, rather than one after the other. This fact is important not only for zoo curators; animal trainers in menageries must also be careful to observe it. It has been shown experimentally for various species e.g. for birds D. Katz (1937) 24; for fish, W. Wunder (1931) 147) that domiciliation strongly increases the prospects of
victorious encounters with newcomers, whereas unfamiliarity with a place greatly diminishes them. As a rule, we may sum up thus: familiarity with surroundings stimulates; unfamiliarity depresses.

The circus trainer must make use of this knowledge in his dealings with difficult large carnivores. He must be the first to enter the empty training cage and ostentatiously stake his claim to the cage as his territory. Only then should the animals be let in to him. In this way the trainer has a considerable advantage over the animals in his dealings with them (H. Hediger (1938b)). In quite a different connection, J. von Uexküll and E. G. Sarris (1931) have shown that the dog, a domestic animal, considers everything his property within his range of smell. They say that where the dog shares house and home with a man, the dog's territory coincides with the man's. It is obviously this fact which has created the basis for a symbiosis of dog and man. For each partner protects the other's property when he defends his own. According to K. Lorenz (1940), the celebrated story of the watchfulness of geese is of a similar nature.

C. Stemmler (1933), one of our head keepers, noticed some remarkable behaviour in a couple of chimpanzees in Basle Zoo, when they were let out of their cage on to their playing field, which was surrounded only by a ring of low stones. Both betrayed the typical bearing of owners by right. No one, man or animal, dared set foot on the grass. Peacocks often strutting on the turf. As soon as the chimpanzees spotted them, off they dashed after the ungainly birds, which flew up screeching and disappeared over the heads of the onlookers. On one occasion some scouts walked on to the grass. Max, one of the chimps., spotted them even before the keeper did. Up he dashed, howling mad, and bowled over the three thunderstruck lads. Naturally the keeper, as an accepted fellow species, was allowed on to the chimpanzees' territory.

Contrary to the accepted notion, the space allotted to the animal in captivity, once it gets used to it, is not always a place from which it does its best to escape. Rather, it considers it as its own personal property, and will, if need be, defend it stubbornly. It often happens that animals that have properly settled down not only refuse to escape when they have the chance, but in an emergency, they can only be got out of their cage and into another by force. A slow loris (Nycticebus coucang), looked after by the author for seven years, would never leave his cage of his own free will. The volume of the cage was only one cubic yard. The animal was quite tame; if it was ever taken out for a time, it immediately showed a marked desire to get back to its own territory again, which was liberally sprinkled, that is demarcated, by its own urine.

Many more examples of a similar type might be given. It is a fact that the well cared for tame animal considers his cage or his enclosure
as his territory. In many cases the proof is clear because in this artificial section of space it behaves just as it would in its territory in freedom, by typical marking and by defence. During the summer term demonstrations are usually given in animal psychology in the Basle Zoological Gardens. Both demarcation and defence are easy to show. The most striking is, of course, the provocative marking of the dwarf hippopotamus (*Choeropsis liberiensis*). If the male is given a bundle of hay that has not been impregnated with his individual scent, the bull turns its hindquarters to it and plentifully sprinkles it with both its specific scents (urine and dung) simultaneously. Among the big cats, too, it is easy to produce a sprinkling of urine with the aid of strange scent marks. The most striking example, however, is that of two East African mongooses which were always in the habit of leaving their scent marks on the underside of the bough of a tree. This only had to be wiped with a wet sponge, when the two animals at once approached, sniffed the spot where the smell had changed and performed a regular handstand (H. HEDIGER (1949)), stretching their bodies up vertically in order to get their anal glands in contact with the marking spot to lay a fresh scent.

Two Stanley cranes at Basle are particularly good at provocative defence of their territory. Every year, at the breeding season, they mark out their territory at the same spot in a field where many other animals live (goats, sheep, capybaras, cranes, emus etc). Its centre is formed by the nest, or nesting place, where the two eggs are. Everything that comes within ten yards of these is attacked by the pugnacious owners, and effectively driven off, especially human beings in which both birds obviously recognize rivals of their own species. This is not so with the storks. During the breeding season, only members of the same species are driven off, and even herons and cranes are allowed to stay by the nest without question.

Visitors often ask why the keepers are not allowed to go into the cages of the big predatory animals. The reason certainly is not because the lions or tigers would eat them up because they considered them as prey. In most cases the keeper would be attacked for having entered the predator's territory, just as in the case of the Stanley cranes. The keeper is only allowed to enter cages where the inmates recognize him as a socially superior member of the same species. With freshly caught predators, by the way, the critical reaction would have been released by the keeper as long as the diameter of their cage was not considerably greater than the critical distance of the animal in question.

**Protection against encounters**—Finally, the cage may mean to the animal a protection against unwanted contacts with animals of the same or different species. In the Berne Zoo, a cow moose was separated from the bull, as he was too rough with her during mating, and the cow could not even eat. Scarcely had the trembling cow been let
into the adjoining enclosure when she turned and shut the gate herself. This animal, by the way, often opened the paddock gates when they were not firmly locked by raising the handle of the catch. In a mixed group of performing lions and bears, the lions sat on the left of the entrance to the cage, with the bears on the right. The lion sitting nearest to the bears could not settle down on his perch until a short piece of railing had been stuck through the side of the cage near him, so that he could see the neighbouring bears through bars. In mixed groups, symbolic bars must occasionally be put up between the animals. R. M. YERKES and A. W. YERKES (1934) quote a delightful observation made by SHEAK of a tame chimpanzee, standing outside its cage, that became so frightened at the roaring of a leopard that it fled straight back into its cage and slammed the door to from inside. Thus for the chimpanzee its cage meant a place of safety.

Technical Aspects

General—Basically there are two technical possibilities in the keeping of animals:

1. Adaptation of the confined space to the animal’s capacity for locomotion
2. Adaptation of the locomotion capacity to the type of confinement.

The second possibility will be dealt with first. With inadequate enclosures, escape can be prevented by partially curtailing locomotion capacity (hobbling or tethering). This practice applies solely to domestic animals, which we are not concerned with at the moment, but may be suitable for elephants. With domestic cattle, iron nose rings are sometimes used. With the domestic fowl, wing clipping is often resorted to. In addition to these mechanical methods there is an operation often performed on the wings, and aimed at restricting activity, namely pinioning.

Furthermore, we may recall an attempt that was made to breed from certain mutations in domestic animals with little locomotive capacity. The ‘dachshund’ or short legged sheep is an example of this. According to H. NACHTSHEIM (1936), it was considered particularly successful because thanks to their short legs, the animals are unable to jump over hurdles, and so need less watching. This method has not stood the test with domestic animals, and in principle is not practical for wild ones.

Recently M. HÜRLIMANN (1939) has described most vividly the mistaken ideas that exist about pinioning, even among veterinary surgeons. Putting birds’ wings out of action does not form part of the routine work of the average veterinarian, so it is often performed by amateurs.
without the necessary anatomical knowledge. Strangely enough, there is very little information on the subject. The author knows only of C. B. Moore's short article (1937). Pinioning means amputation, that is a partial incision made through the metacarpals, as close as possible below the thumb, which must be left intact. The purpose of this amputation is not, as has often been mistakenly supposed, to reduce the bird's wing surface, but to make it asymmetrical. It should therefore be cut through only on one side. A bird that has had both wings done is usually capable of a certain amount of flight, but when one side only has been done it cannot keep up in the air, but topples over at once. Birds of many different species (cormorants for example) give up all attempts at flight soon after the operation, and rely only on walking, swimming or diving for getting about. On the other hand, there are some birds that never seem to realize that their wings no longer function properly. For instance, many of the smaller ducks, teal, mandarins and the like, try to fly away even when only slightly alarmed. Hardly have they left the ground before they tumble head over heels. Both these types of behaviour would seem to be a criterion for ability to profit by experience, or capacity to learn.

The following method is used by the author to perform the operation. The place to be cut is found, not by counting the number of primary feathers, as these vary according to the species, but by feeling for the carpal bones of the bird. This has been fastened down on its back with its wings slightly spread. At the same time, with the aid of an assistant, the humerus must be firmly secured, otherwise the ulna might easily fracture if, with a more peripheral method of securing the bird, it struggles to free itself. When the spot below the thumb (pollex) is found where the metacarpals 3 and 4, joining at the carpometacarpus, lie closest, or at any rate very close together, the surrounding area must be exposed by plucking out the large feathers that are in the way. To do this it is necessary to remove those feathers the shafts of which are inserted into the small area of the metacarpals that lies nearest to the body. This usually means two or three primaries, the same number of tectrices, and a few of the underlying feathers as well. A pair of flattened tweezers is often useful for pulling out these small feathers.

When the bones of the wing at the end nearer the body can be felt easily, a ligature is applied, leaving the thumb free, of course. Stout pack-thread is used for the ligature; it must be strong enough not to break when the knot is tied, but fine enough to fit closely at the place where it is tied. The most painful part of the operation for the bird, the only painful part in fact, is when the ligature is tied; then it usually winces and makes a sudden jerk. The danger of fracture of the forearm is now particularly acute if the bird has not been tied securely down. Immediately after applying the ligature, the wing is spread out flat on
a soft wood (pine) board. A wood chisel of suitable width is applied
distal to the ligature, the pollex of the wing gently raised, and then
with a sharp blow from a mallet on the chisel the two metacarpals,
together with the muscles and skin, are severed. The birds show hardly
any noticeable reaction to this operation, which might be thought the
most painful part. The wound is then dusted with iodoform or some­
thing of the sort, and the bird at once released. No visible loss of
blood occurs during this procedure. Even with the larger geese and
cranes scarcely a drop of blood can be seen. The ligature is left on
(Figure 9).

Not a single failure has been recorded yet among the large number
of birds of all sorts that have had this treatment. The greatest surprise
is the behaviour of the bird that has just been treated. The layman may
be surprised that no local anaesthetic is administered for such an opera­
tion. It is quite unnecessary, as the pain felt at the operation is appar­
etly negligible. No indications of post-operative pain can be
detected either. Only at the moment of tying the ligature is any reac­
tion noticed, as we have said. The bird that has just been treated
naturally wants to preen its feathers, and that is when the ligature may
be pulled off. For this reason we usually distract the bird’s attention
immediately after the operation by offering it food. In most cases the
patient, although properly fed beforehand, takes food immediately. In
this way it shows that its health has not suffered noticeably from shock,
for the first symptom of disturbance in a wild animal is its refusal to
take food.

K. Lorenz ((1940) 45) noticed the peculiar behaviour of a grey
geese after it had had one wing clipped. It reacted to this interference
with its liberty by symptoms of severe depression, that is, with curtail­
ment of all activity and complete loss of appetite. As a result, it went
so much off condition that in the following spring it showed no signs
of breeding activity, the usual bright red of beak and legs did not appear,
nor was there any evidence of desire for mating. Immersion of the neck
was never once observed, still less copulation. It was clearly at a dis­
advantage too in the rough and tumble of life in the flock. It will be
obvious that all these phenomena were actually a consequence of
pinioning, since H. Siewert had the same undesirable result the same
spring with his best pair of geese, after the same treatment undertaken
for similar reasons. On the other hand we must avoid making sweeping
generalizations on these observations. In his private zoo a friend of the
author, Werner Krebsen, on the Lake of Thun, bred repeatedly from
pinioned grey geese. It is quite certain that many other Anatidae show
nothing like this reaction after the operation, and are quite unaffected
by it in their mating behaviour (Figure 10). It stands to reason that
this operation should not be performed on birds that are seriously
affected by feather-clipping or pinioning; that would be biologically
Figure 9

a Unwound

b Clipped wing of Nile goose (Alopochen aegyptiacus) a few weeks after amputation
Figure 10. Pair of Nile geese with clipped right wings defending their nesting hole. Typical powerful blows are delivered by the feet and wing.
unsound. Such birds should be kept in large aviaries under conditions that allow them to mate.

Pinioning birds has the disadvantage that they are mutilated by it, even though only slightly. Recently B. Grzimek (1943) recommended a completely new method that had been worked out and published by L. Bodrogy and St. Dozsa in 1939. This is radial-neurectomy, i.e., removal by operation of a portion of the nervus radialis supplying the wing. According to the data given by the writers, it is enough to remove 8–10 mm of this nerve. The operation takes place under a local anaesthetic. Theoretically, this new method appears extremely attractive and gives the impression of a perfect solution of the problem. The bird’s skeleton remains completely intact, so does its normal appearance. The operation is intended only to prevent the bird from stretching out its wing to the full, so that it can no longer fly as a result of this asymmetry. We have tried this experiment in Basle Zoological Gardens on various birds such as pheasants, ducks, gulls etc. but unfortunately without the slightest success. Their powers of flight were in no way affected by this neurectomy.

Not all zoo birds are pinioned. It is a moot point which birds should be treated. To begin with, all the smaller ones living in cages and aviaries are usually left alone. Among the medium and larger kinds, it is usually the Anatidae (geese and ducks), the Laridae (gulls), the flamingoes, the Gressores (waders) and the Steganopodae (web-footed birds); less often, the Phasianidae (pheasants etc). In many zoos untreated pheasants and guinea fowl run free, and it would never enter anyone's head to operate on peacocks. Thus the birds which need to be treated are the obvious migrants and birds of passage. It is a simple matter to induce the Phasianidae to settle in a particular place, thanks to their marked sedentary nature (G. Steinbacher 1941). This is especially true of the peacock, said by W. Beebe (1936) to be the most sedentary of all birds within definite bounds. Because of the domestic pigeon's homing instinct, it does not require treatment either; nor do certain free flying parakeets, just as faithful to their homes. In estimating the need for pinioning a definite biological characteristic, attachment to a locality, must be taken into account.

The fact that birds of prey have never yet been treated is of human psychological interest, rather than biological. Man's anthropocentric attitude with the eagle for instance is once more to blame. Strangely enough, nobody bothers much when the stork, which covers some 8,000 miles on its twice-yearly migration, is pinioned. Yet, thanks to anthropocentric prejudice, no one dares to interfere with the King of the Air. No biological arguments against the operation have yet been heard, only human-psychological ones. Doctored eagles would be no less happy than doctored storks or ducks, since it is a mistake to imagine that the eagle has to fly up towards the sun and into the
glorious aery spaces; these are human aspirations; those of the eagle are
directed towards the ground. He only circles up aloft in order to find
as quickly as possible something to eat (G. Brandes (1939) 78). It
would be better to be able to watch a flock of doctored eagles at
liberty in some broad leafy glen, than eagles capable of flight in their
present wire cages; it would perhaps also be better for the zoos, bio-
logically speaking. It is impossible for every zoo to build the large
aviary of the San Diego Zoo, for instance. Besides, experience shows
that such aviaries are very often not fully utilized by their inmates.

As well as preventing flight altogether by pinioning, there is a way
of stopping it temporarily by clipping the wings. Since these feathers
grow again after the moult, the process must be repeated once a year,
or every two years, according to the species. For this purpose the
bird must be caught again, with all the accompanying disturbance and
risk of injury. Since pinioning means a single permanent operation, as
has been shown, and is no more upsetting for the bird, it is in most
cases preferable to periodic clipping. Compared with mammals, or
even man, the great difference in sensitivity to pain in the region of
the metacarpals in birds is most striking.

If we leave out birds, it is a rule in keeping wild animals that the cage
should suit their capacity for movement, and not the other way round.
We must also remember that every species of animal has its specific
type of locomotion; in addition, each has its own maximum locomotive
capacity for overcoming obstacles in horizontal and vertical directions.
This is of fundamental importance for zoo keepers, as it means the
animal must be kept within barriers which are beyond its maximum
capacity to overcome. Basically, there are two ways of overcoming
obstacles; by getting round them or by destroying them.

Recently, that is, since the time of open cages, it has been the fashion
to make the cage dimensions too close to the maximum capacity of the
animals, or even to underestimate it. Construction has been at the
expense of safety, leading to a series of deplorable accidents. Errors of
judgement or calculation are often to blame, since the critical maximum
capacity of each species is not easy to determine. Fundamentally, the only
sound method is to work out the capacity for overcoming the obstacles
in question for as many individuals of a species as possible, using obser-
vations taken from wild life as an additional check. Altogether this
amounts to only a very small amount of material, based on compara-
tively few specimens, even in the most experienced zoos. General-
izations are thus very risky, apart from the fact that we cannot be sure
that the behaviour of the animals observed, on which the conclusions
are based, really did show maximum capacity. In view of all this, the
greatest care should be taken in the construction of barriers, especially
with dangerous animals. Here, safety comes before architectural and
structural fashions. In dealing with wild animals, safety must always be
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considered from more than one point of view, and even then experience shows that plenty of unforeseen accidents can still happen. Later we shall return to accidents with wild animals.

In dealing with defences we must remember that the capacity of maximum movement of animals in a balanced mental state is far less than that which occurs under conditions of extreme excitement, and in exceptional instances. Animals are like men; unusual situations increase mechanical efficiency beyond belief. The greatest attention should be paid to the excitement factor. Cheetahs have been kept in an open cage less than six feet high. In normal conditions this is quite sufficient, but it must be assumed that under the stress of great excitement this fence could easily be cleared by these animals. Capacity may be stimulated to a surprising degree by over excitement. A five foot fence is high enough for bison under normal conditions of quiet, but will be cleared by them when they are over excited.

Let us quote one example. On 18 May 1926, as mentioned by F. A. VOLMAR (1940), two boys fell into the bears’ enclosure at Berne, the left hand part of the so-called Great Pit. The bears in the right hand portion, though unable to see what was going on next door, owing to a dividing wall, became greatly excited under the stress of escape to safety reaction. A two and a half year old she bear suddenly climbed up the wall of her pit and escaped. The defences (pit walls) which had seemed quite safe for decades turned out to be quite inadequate for this crisis. One might adopt the slogan ‘over excitement weakens all barriers’ in order to draw attention to the importance of the excitement factor. It would be better to say that the maximum performance capacity of the animal is increased by excitement, for example, the climbing power of the she bear. In any event, the rule applies that the effectiveness of a barrier is inversely proportional to the strength of the animal’s degree of excitement (Figure 11).

Figure 11. Effect of the excitement factor; subjective height of wire fence a in normal b in excited condition of animal

The means of confinement—Practical methods of confinement may be classified thus:

1. Imaginary, psychological; effective only through training—the circus ring

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The problem of confined space

1. Real:
   - Biological: ditches, pits, land-water barriers
   - Semi-biological: fences, bars, wire netting
   - Unbiological: glass, electricity.

2. The circus ring, low wooden blocks surrounding the circus arena, does not form a real barrier, but one which becomes effective by special training. Even domestic animals, horses, camels etc. often have to undergo protracted training in order to respect the ring and so become fit for circus performance. At first they go off the track, especially under stress of excitement; it often takes them a long time to realize that they must not break out of the ring under any circumstances. Thus to a certain extent the ring presents a psychological barrier; it is merely the demarcation of a limit. Curiously enough, the police regulations of most countries distinguish between two kinds of circus animals. One kind may perform in the open ring. The others, all the big cat tribe, only in a circular cage. The first category, besides domestic animals and elephants, includes sea lions, anthropoid apes and, strange to relate, bears; as if a bear was not as dangerous during its performance as a lion! Only the layman considers the bear less dangerous than the lion. Malayan bears, as is well known, have a most harmless, even comic, appearance. Yet they ought to be treated as the most dangerous of all bears. That is why they seldom appear in circuses. Here we see one more instance of an animal's character being judged anthropomorphically, instead of biologically. Whether an animal is fit to perform in the open ring or not depends not so much on its belonging to a particular species as on the qualifications and training methods of its tamer.

Among real means of confinement we must next consider those that may be called biological, because they are more or less like natural obstacles found in freedom (pits, ditches, land-water barriers). The pit is the most primitive method of confining animals, literally and historically: hollows in the ground were used, from which the animals could neither jump nor climb. Palaeolithic man made use of this method for his pit traps, at least as a temporary place of imprisonment for wild animals prior to killing them for food. There is evidence that he kept cave bears in such pits for a considerable time in captivity, and perhaps even the mammoth as well (G. Jennison (1928) 11). Natural pitfalls, familiar to palaeontologists, are those pits formed without man's help into which wild animals can fall. Ditches for wolves, lions and bears were very common everywhere until recent times. The bear enclosures in Berne in principle still represent the old type of ditch, divided into three compartments.

We must include among cages for deer, lion and bear those long ditches, often sections of old city moats, usually closed at one end or
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both by masonry or railings. In the older zoos there still are such enclosures, usually for large carnivores or bears. These genuine animal pits at the bottom of which the animals live are not the same thing as the moats which surround modern free enclosures. With the latter the difference lies in the fact that the animals do not live in the moat, but on the level ground enclosed within it. These moats can either be dry or wet, when they serve on occasion as bathing pools. This type of confinement must also be considered a biological one, since similar obstacles may be met with in nature (cliffs, streams etc).

The pit is a vertical barrier, but the ditch mainly a horizontal one. It is true that the side from which the animal might jump out is made lower, so that it would have to clear a good height to land on the opposite side. In addition, the inside edge is made so that the animal cannot take off easily, or else finds so uncertain a foothold that it keeps away from the edge. Elephants' enclosures often have iron spikes along the margin, but even this precaution has proved dangerous, individual animals having been pushed on to the spikes by their companions, and suffering injuries. We must always remember that these devices, thanks to their special construction, may do much to stop the animal from actively surmounting them (always with the risk of the excitement factor), but that no ditch made without a high enough fence can stop an animal from being passively pushed into it, or from falling in.

The water-filled ditch may act only as a relatively effective boundary for animals that dislike water. The excitement factor must also be taken into account here as well as freezing in winter. On the other hand, aquatic animals can be kept within bounds comparatively easily by a land-barrier. It has always been assumed that seals (sea elephants) could not get over the edge of their pond when it was low and steep, but only at flat places with sloping banks. Here too, surprises were in store; for example, at Hagenbeck's zoo. Many accidents as well as losses have occurred through the assumption, biologically unsound, that certain land animals (many monkeys, for instance) will on no account go into water, but that others (e.g., bears) are fond of it, and can swim. Most aquatic animals (primates and others), and land animals that occasionally take to the water, not only can swim but often dive as well, and leap out of the water to a considerable height. The otter, for example, can do this just as well as the polar bear. Thus the height of the wall for water-filled ditches must be calculated not only for the swimming animal, but for one leaping clear of the water as well. A child was seriously injured at Basle Zoo through a polar bear leaping out of the water; in consequence, special safety measures have had to be adopted.

Many wrong ideas exist about the value of water barriers for land animals and land barriers for aquatic ones. In many zoos the arrangements do not fulfil the minimum conditions for safety. The fact that
they have satisfied requirements for years, even scores of years, is n proof to the contrary. A crisis may not occur until a fresh animal introduced, or until the excitement factor or spontaneous change is mood suddenly comes into play.

One would think that fish are bound to respect the land barrier simply because they cannot breathe on land. Quite apart from specially adapted ones, like climbing fish (Anabas), mud-hoppers (Periophthalmus), lung-fish (Protopterus) etc this barrier does not work even for the most obvious water breathers. For safety's sake, every aquarium keeper covers his tanks over, usually with glass. In large aquaria, where glass is not practical, wire netting is often used instead. But fish are apt to make sudden leaps and can do themselves serious damage. That is why large tanks should be covered with a loose net, a foot above the surface of the water. Jumping pike and others are caught harmlessly and slip back again into the water. We used to leave fish that obviously live at the bottom, such as the Scorpaena (bull-head) uncovered, until one night one of them jumped into the adjoining fresh water tank and perished. Sometimes fish, living quietly in their aquarium for years, suddenly start jumping out for no apparent reason.

Among semi-biological methods of confinement we may include wooden fences, iron railings, wire netting, and the like. True, there is nothing exactly like these in nature. Still they have some sort of resemblance to a close network of branches and creepers, and are usually treated as such by the animals. They usually refrain from injuring themselves against them, although the excitement factor must always be allowed for. In a sudden fit of excitement, when fighting or under the impulse to escape, the animal acts as though it could force its way through this impenetrable network, and then dashes at top speed into the barrier. This often results in serious injury, even fracture of the skull or a broken neck. To prevent this, stout wire netting is best, as the animal simply rebounds unhurt. Historically, rigid wooden posts and thick iron posts are the oldest material; in recent times finer and finer wire netting has been used, and latterly wide meshed springy steel netting. These obstruct the view less than a fence or heavy iron bars.

Non-biological methods of confinement such as glass and electricity are not found in nature, nor anything resembling them. Neither exists in the animals' world, if we except the few electric fish that use their electricity partly to avoid enemies and partly to help them to catch food. For many smaller creatures, especially fish as well as reptiles and amphibians, glass is almost the ideal material on account of its transparency. Any type of climate desired can be reproduced in a glass cage, and with no other material except possibly plastics is this so. In addition, a glass pane is the best remedy for undesirable feeding, or infection by members of the public. Recently new plastic materials have been used instead of glass.
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Yet there is one drawback that becomes more serious the more highly organized the animals kept under glass. It concerns their sense organization. The widest use made of glass is for fish, but the disadvantage for them is minimized, as most fish possess long distance detectors in their lateral-line system warning them of the presence of the glass. But neither amphibians, reptiles, nor birds or mammals have any visual means of detecting glass or plastic panes. Occasionally, too, we get reflections, undesirable both for the animal, and for the human observer. A sea turtle constantly snapped at the reflections of fish in the glass sides of its tank. In the Berne Aquarium, the glass sides were slanted inwards to prevent reflection; but in spite of the slight degree of the slant, an extraordinary amount of dirt collected on the sides in most tanks.

Recently birds have been kept behind glass. The onlooker has the pleasure of an uninterrupted view; shape and colours suffer no interference through fences or wire netting and thus their beauty is seen at its best. On the other hand, glass is so transparent that it cannot be visually detected by the birds. Until the bird has learnt by experience there is danger in this; even then it sees the glass no better than the fly sees the spider's web, but discovers the exact dimensions of its flying space by bumping into it. Normally, the experienced bird turns smartly away close to the glass. The excitement factor enters here too. Under such conditions of stress as chasing during the breeding season, it may lead to disregard of the space barriers, otherwise faithfully observed. Under certain circumstances a bird may dash at full speed against the glass, often suffering as a result from concussion, or even fracture of the skull. This danger is increased by the amount of space the bird has already covered i.e. by the speed it has reached.

The bird doesn't get injured every time, however. A peacock that had got on the staircase of a zoo restaurant was chased away by some visitors, and flew through a closed window as if it had not been there. Landing on the lawn, it at once started looking for food, although strange to relate, it had left a hole behind it in the glass, so small that it was exactly the bird's diameter with its wings folded close. The same thing happened later on to another peacock.

Birds get so accustomed to cages with glass walls that, although they cannot see the glass, often bumping into it at first, they become so familiar with their flying space that, after a time, they completely avoid the invisible barrier. This fact may be of use, biologically speaking, in the solution of the problem of confinement. With birds thoroughly accustomed to flying in glass cages it is possible to remove the glass panes, at least for a time, without the birds flying away. This method of an open flying space i.e. aviaries without glass or wire netting, has already been described at length (H. Hediger (1943a)), and has since been developed further. The problem was to reinforce
this psychological barrier by the action of light so that the inside of the cage should be kept bright but the space outside, for the spectators, dark. This has long been the custom in aquaria. Following the conference of zoo directors in Rotterdam in 1946, the author had a conversation with the new director of the Antwerp Zoo about this improved type of cage. That same year he constructed a similar experimental cage in the Basle Gardens. This was officially visited in 1947 when the conference of zoo directors met in Basle. In 1948 cages of this sort were opened to the public for the first time in the modernized aviary in the zoological gardens at Antwerp and claimed as an Antwerp discovery. It was soon adopted in North America too, where to the best of the author’s knowledge it first appeared in the renovated aviaries of the Philadelphia Zoo (Parks and Recreation, 32 (1949) 51).

The experimental cage at Basle, which was first shown to the public on the occasion of the seventy-fifth anniversary of the Gardens, is a three foot cube, the front consisting of a glass window that can be lowered. A lighting installation consisting of four Philora tubes lights only the inside of the cage. This is fitted up with branches and nesting boxes and is completely darkened on the outside. As soon as this four-part lighting unit is switched on by four switches, or by the master switch, everything outside their cage looks black to the birds. That is why the glass window can be lowered as long as the light barrier works. We only raise it again at night when the light is switched off so that the birds can sleep undisturbed.

Naturally this type of cage cannot be used for all birds, especially for nocturnal ones, but only for true day birds. These do not all react in the same way, even those that belong to closely related species. Budgerigars (Melopsittacus undulatus) for example, can be caged as safely by this light barrier as by solid wire netting, while love birds (Agapornis fischeri) occasionally break through the light barrier. The author was naturally curious to discover whether the artificial daylight contained all the necessary components, that is, whether it was a satisfactory substitute for daylight. To test this he has been rearing budgerigars since March 1947 in such a cage, and with complete success. Of the dozens of young birds that have grown up entirely in this artificial light, all have without exception developed perfectly normally.

Cages of this sort have the added attraction of novelties to the public. The walls are suitably painted and they show up the birds' colours most effectively without the least visual discomfort for the onlooker. The principal drawback is that the place for the public must be kept dark and the birds are at the mercy of the public. In spite of a barrier placed a certain distance away from the cage we find there are always visitors who want to test whether there really is glass there, either with umbrellas, sticks, or by throwing odds and ends.

It really is surprising how little imagination has been shown up till
now in research into methods of confinement. It is possible to confine poikilothermous animals by using thermal barriers in the same way as by using light barriers for birds as we have described. We must not imitate, however, the efforts of the individual, who, misunderstanding the facts, made a kind of hot plate surrounded by three walls and barred it with a refrigerated plate set in front. He then expected the snakes that he put into the completely bare warm part to behave themselves and stay there.

Thermal barriers can only be successful with reptiles if they are given a biologically equipped terrarium acceptable as their territory. In this way the reptile will be firmly attached to its cage, and this is, of course, the aim with every animal. Then it will have no need to break loose. In order to prevent any possible roaming—there are reptiles with marked periodic increase in activity and tendency to change of place—we can substitute for the usual glass a decrease in floor and air temperature. This double thermal barrier must be supplemented by a considerable slope in the ground level, to act as a powerful mechanical brake on the animal. Then the effect of the thermal difference i.e. the negative stimulus of cold temperature, will be all the stronger, and will generally turn the animal back. Reptiles show very different reactions to high or low temperature stimuli. It is thus a help to use an auxiliary electrical barrier along with the temperature and mechanical barrier, so as to have the advantage of a combination of different negative stimuli. Absolute safety cannot be guaranteed by this method and it would be irresponsible to keep poisonous snakes for instance in this way.

A great deal has been heard lately about another non-biological means of confinement, the electrical barrier. It was first used on wild animals in the Anthropoid Ape house in Düsseldorf. G. AULMANN (1933) reports that there for the first time anthropoid apes were exposed to the public gaze without bars or any intervening partition. The barrier consisted of an electric current. At first, this arrangement worked wonderfully. In a very short time the animals grew so accustomed to the barrier that they no longer tried to touch the brass rods, so that the current could be kept off. This original and up to date idea had only a short life, and a promising device had to be abandoned. The orangs soon got so used to the weak current that they climbed down into the service quarter below with the help of the rods, while the chimpanzees jumped over without touching them, and gained their freedom that way. So this attempt at confinement, not known to have been tried at any other zoo, failed (personal communication, 1938).

Although electrical devices are often used with success to fence in domestic animals, this method does not seem practical with wild animals. Perhaps this is because of their different escape tendencies, and also the different intensity in their urge to escape. Both are far
greater in the wild animal than in the domestic one (HEDIGER (1938) 39). Owing to increased danger of foot and mouth disease in the Basle Zoo it was decided in 1949 to fit an extra fence inside the enclosure wall and prevent direct contact between the public and certain ruminants. This fence consisted of solid planks. Purely as an experiment, the yak's enclosure was fitted with an electric fence consisting of two plain galvanized wires 18 in and 3 ft above the ground and 5 ft within the wall of the paddock. These wires, fixed on light wood or iron stakes, carried a current of 12-14,000 volts (induction current) [system Lanker, Speicher and Kt. Appenzell], flashed on at short intervals i.e. at approximately once a second. This electric fence worked perfectly with the yaks so it was also tried on American and European bison. Here too it was so successful that the idea of using a heavy wooden paling was given up. Two six volt batteries are used, one in use while the other is being charged. Transforming to 12-14,000 volts takes place in an induction coil. Of course the author would never run the risk of using this electric fence by itself but only as an extra protection inside the paddock wall. Under conditions of excitement the animals might not take sufficient notice of the thin wires. Recently experiments with electric fences have been made in Texas, as J. G. BURR reports (1940), not in order to confine wild animals, but to stop them from breaking into plantations. This is a far simpler problem to solve, as it is much easier to touch off the escape reaction than to inhibit it. With this kind of barrier, to some extent represented in the zoo by the reflected image, striking differences appeared among wild animals. Cattle and horses could be kept out by a simple live wire, but not deer. During a three month experimental period the following device was used with these. About 4 ft 6 in in front of the existing fence, not in itself sufficiently high, a live wire was stretched parallel to the ground at a height of about 18 in. The deer do not step over both obstacles, but test the situation. In doing this their muzzles touch the wire and away they run. They would have cleared the single obstacle without further inspection. The advantage of this double barrier is relatively small and depends on the fact that the usual fence need not be very high, nor does it much matter if it gets a bit out of repair. Too much must not be expected of the electric fence, at any rate from the scanty data available. In isolated North American Reserves, for example in Estes Park (Colorado), the attempt has been made to stop black bears (Ursus americanus) that were becoming a nuisance from getting into food stores by using electric wires when the barred windows and doors had been repeatedly broken in by them.
Cage Breakers include animals that break out of their cages, paddocks etc often in the absence of man; by runaways we mean those that have already got out of their usual place of confinement, and for some reason or other run away out of control from the man or men responsible for them.

First the cage breakers. Apart from their interest for the animal psychologist, they are important for two reasons. In the first place they may be dangerous to man, though this danger is usually greatly exaggerated. Secondly, they may cause material damage in escaping. In addition, cage breakers may be an indirect cause of loss to the zoo. Poisonous snakes that escape may cause a temporary closing of the gates of the zoo as a safety precaution, and thus be responsible for a considerable drop in the takings, as once happened at HAGENBECK’S Zoo.

Individual species have a reputation for breaking out, the badger being an example among native animals (G. RAAM (1940)), and among exotics, the Tasmanian devil (Sarcophilus ursinus). The latter’s escape from its cage has been told in words and pictures by O. ANTONIUS (1933). The giant armadillo (Priodontes giganteus), aardvark (Orycteropus) and others are formidable cage breakers. A survey over a wider field of cage breakers shows that two things need closer practical attention. First, the strength of the materials used (walls, floors, ceilings) and secondly, movable parts such as doors, locks, ventilators, covers over gutters etc. Before new inmates are put in, every cage should be closely examined inside and out, and tested by all possible physical means. It must not be forgotten, first, that the animal possesses extremely efficient tools in the shape of teeth, claws, and horns; secondly, it has plenty of spare time in which to find suitable opportunities for using these tools; thirdly, it possesses sense organs which are far superior to man’s, and which can help it to discover weak spots in the materials or the most suitable places for breaking out.

For these reasons, the Principle of Double Security should always apply in the caging of wild animals, especially for dangerous species, so that once an animal escapes, it should find itself in a safety zone, from which it will have to break out a second time in order to get right
It always means a serious handicap when there is no outer zone which can be closed in an emergency. The various animal houses, or the main blocks of them, should be constructed on this principle of double security. It should be possible for a poisonous snake that has got loose to be confined to its own building, or a lion to the block for beasts of prey. Heating ducts, ventilators, drainpipes and the like are centres of special attraction (home effect) for escaping animals.

Specific methods of escaping occur in different groups of animals, and might lead one to a biologically tempting classification of escape types. Below will be found a rough guide to the chief categories, with examples. We must also recognize the difference between escapers and those animals which just as characteristically never escape at all, or else which return to their quarters after they have been driven out by flight, or some unusual incident: e.g. the deer mentioned on p 44; or Yerkes's chimpanzees, or peacocks. Possible motives for non-escape are: pronounced attachment to territory, marked sedentariness, attachment to a particular home (nest, eggs), to comrades (socially conditioned), to young, or to food. Hungarian Zackel sheep are not easy to catch in an enclosure, being partially domesticated animals in which the flight tendency is still strong. Yet they follow at the keeper's heels if he is carrying their lambs in his arms. Domestic animals have been known to go back into their blazing stalls.

Cage breakers may also be classified biologically by the tactics they adopt to escape, which are intimately connected with their physical make-up and way of life.

1 Escape through demolition of the cage (floor, roof, bars). To this group belong first and foremost beasts of prey, ungulates, rodents, in fact all that possess stout tools in the shape of teeth, horns, claws and hoofs. Among birds we might include parrots with their chisel-like beaks.

2 Escape by opening doors or undoing catches. This method is largely a speciality of elephants and monkeys. The trunk obviously acts as a hand. Thanks to their trunk-like snouts, moose are able to lift gate fastenings and are the only species of Cervidae that can do so. A moose that was particularly good at this kept getting into another paddock so that the fastenings had to be specially secured. Wild pigs too are often very good at opening catches with their snouts. These breaking-out tactics, by the way, are widely used for experimental animal psychology in the well known experiments with puzzle boxes.

3 Escape under stress of abnormal activity (excitement factor), and overcoming defences which would normally be adequate to resist attempts. Here, according to opportunities for locomotion, we must differentiate between swarming over (sheep), climbing out (bears, foxes, cat tribe), jumping (guanacos, goats, antelopes, chamois, fishes) and burrowing (foxes, aardvarks, armadillos).
CAGE BREAKERS

4 Escape by suddenly squeezing through gaps between bars, netting, ventilators etc as snakes do. Hedgehogs and badgers can get through incredibly narrow spaces. Young red-billed ducks pushed their way through gaps 19 mm (0.76 in) wide; adult house mice through wire netting of 10 mm mesh (0.39 in). Mice sometimes get stuck in this sort of netting.

Motives and Situation

Motives for escape are also classifiable. It has already been shown that it is not a question of hunger for freedom, an attempt to get away to somewhere, but rather from something. With untamed animals, the chief impulse is doubtless flight driving the animal away from man, and from man-made surroundings (captivity). In other instances it is not so much man as biologically bad conditions that cause the outbreak, for example, too much light, too little cover, too much disturbance etc. We often notice in outbreaks of this kind that the animals do not go far, but slip away to the nearest suitable place. By providing more suitable quarters for them it is surprisingly easy to get such animals to give up trying to escape. A third important motive is caused by the presence of other animals, of the same or different species. If two red stags are in an enclosure at the rutting season, the defeated one tries to find a way out so as to get beyond range of the victor. Finally, among animals that have a periodic cycle of migration there is a restlessness of biological origin, usually driving them to stubborn, abortive attempts to break loose, thus possibly leading to injury. This migratory disturbance is very marked with caged birds of passage: attempts to escape, often violent, may be curbed to some extent at least by appropriate technical measures e.g. padding, or even so deadened as to cause no noticeable damage. Migratory disturbances in birds have been analysed in detail by H. Wagner (quoted in W. Fischel (1938) 22 and F. W. Merkel (1940) 167).

Recently, P. Palmgren (1944) has published some very careful observations on the daily activity of caged birds of passage. Among other things, Palmgren puts forward the idea that migratory activity and normal daily activity of a migratory bird may be two quite different, even differently localized, kinds of activity. Incidentally, this fits in well with the greater and lesser space and time systems. This investigator, and it is of great interest in our connection, established that the migrant often keeps to its normal times of activity and sleep with surprising tenacity, even being wakened again by the migratory restlessness immediately after falling asleep. In other words, the activities of the lesser space and time system assume their normal course until the inexorable intervention of the larger space and time system. If it were true that there really was a different localization of both types of
activity in the central nervous system, a question would arise for the biologist of the zoological garden. Would it not be possible to affect one centre, that responsible for migratory restlessness, by a specific sedative so that senseless and fatal restlessness in the cage might be suppressed or completely eliminated? If this troublesome migratory restlessness could be removed at the critical time it would mean an encouraging step forward in the care of birds. But from communications received from Professor Palmgren and various pharmacologists it seems that at any rate for the present such prospects are not very hopeful.

Motives for escaping are seldom of a pathological nature. So far, the author has had experience of only one such case, and that was with a wild boar in the Basle Gardens that had lived with another female and a male for years and had brought up young every year. In the spring of 1946, this animal, which had again produced a litter two months before, suddenly jumped over the low wall round the wild boars' enclosure and was found in the neighbouring yaks' enclosure. It was assumed that this unusual behaviour had been caused by some fright or other and the pig was caught in the yaks' enclosure and put back into its own, expecting that it would soon settle down there. And so it seemed to do. As a precaution, however, a keeper was put on guard. Suddenly, just when two elderly ladies were expressing their pleasure at the prettily striped young pigs, the sow jumped over the wall again between the two ladies and dashed off, luckily into that part of the gardens which can easily be shut off from the rest. All the keepers brought to the spot by the alarm were of the opinion that the wild pig had gone mad. It now attacked every man who tried to get near it. The author was certain that the sudden change of behaviour in an animal normally so reliable and quiet must have been from a pathological cause and felt compelled in view of its completely incalculable nature to have it shot on the spot to avoid all risk. The pathological anatomical examination of the brain showed a recognisable change which, however, did not admit of a clear diagnosis. A wild pig of normal behaviour would have been comparatively easy to recapture.

The position of escaped animals, if we may return to this subject, is usually completely misunderstood by the public, and, thanks to this, the most absurd measures are often taken, resulting in marked increase in the gravity of the situation. In view of the importance, practical and legal, of escapes by large animals, and also because of its value in the study of animal psychology, two classic examples, so to speak, will be given in detail and analysed. They are the Leipzig lion hunt of 1923 and the escape of the black panther from Zürich Zoo in 1933.

The Leipzig lion hunt happened under the following circumstances according to J. Gebbing (1928) 35). Some animals escaped in the night from Barnum's Circus. One group was captured alive in Blücher-

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strasse by the zoo staff; a second group (six in all) was shot by the police. The bodies of the victims of the now world-famous Leipzig lion hunt were put on show at the zoo, and next day enormous crowds flocked to see them. (Note, in passing, the great interest in the slaughtered lions by the public; this shows that the public need enlightenment about their interests and taste.) This example, one of many, confirms the fact that in such situations the police usually shoot far too soon and generally without need. Naturally, they act on the firm conviction that the sacrifice of human lives must be prevented by making the dangerous carnivores harmless as quickly as possible. It is not easy to convince the police that danger hardly exists. To show the truth of this bold assertion, so contrary to popular opinion, let us quote two arguments. In the above instance, the zoo staff caught several of the escaped lions without being eaten up by them; practical proof that they should not be shot at sight. Secondly, it is impossible, psychologically speaking, to call these lions man-eaters. Unfortunately full details of the escape are not known, but it is safe to assume that the lions were not in a condition of extreme hunger.

To begin with, the lions can have had no other impulse than to seek cover. Escaped beasts of prey are not dangerous absconding criminals, but just wild animals undergoing flight reaction. As such, they try first and foremost to put a safe distance between themselves and man, to find a home. An escaped lion is obeying the law of flight and must do so from biological compulsion. Even a completely tame lion with no urge to run away from man will, in this situation, be subject to the law of flight. Every escape of this sort is associated with conditions of excitement; and panic, even in tame animals, causes their innate savageness to flare up again. But savageness does not imply blood lust, merely tendency to flight. This cannot be over-emphasized, particularly in any critical analysis of accidents among large animals.

From this analysis, the situation of the escaped lion is clear: its efforts are aimed at the unhindered course of flight reaction and never at devouring the first human being it meets! Now there are two real dangers; the release in the lion, both of the defence reaction and of the critical reaction by the men who are chasing it. In other words, the change from flight to attack, or defence (in the situation of self-defence). But these dangers can be avoided so easily by anyone with the least experience of animals that the risk is reduced to a minimum. Indeed, the defence and the critical reaction may both be of great use in recapturing such animals; by skilfully foreseeing their biological reactions, the animals can be got into a travelling cage, brought for the purpose, with just as much certainty as the lion tamer who coaxes his lion to sit down on its pedestal. Hence in practice it follows that shouting should never be tolerated in such instances. The initiative and organization should be handed over to the zoo or circus authorities.
The police have the extremely important task of preventing the public from interfering with the measures taken by the animal experts. Disastrous results may follow through allowing inquisitive people to get too close, and thus overstep the critical distance for flight, defence or attack.

Of special biological interest is the escape of the black panther from Zürich Zoo described by R. Wenng (1934), as in this case all the essential details, including previous history, are accurately known. It concerned a female black panther, bought as a wild animal. According to the report, the animal was of extremely timid behaviour; she never took the opportunity of investigating the passage leading to the open air, although the communicating doors were left open daily. She seemed to get on all right with the male panther, as black as herself, but when an injury on her forepaw was noticed after a week, the couple were separated, a matrimonial quarrel being suspected. After another week or so a second injury was seen on her right hind leg. On the morning of the eleventh of October the panther’s cage was empty.

According to the investigation, the animal had squeezed herself through a break in the roof bars and reached freedom by means of a partly open slatted ventilator. Not a trace of her could be found. In the traps set for her, a few half-wild dogs were caught. Nearly ten weeks after the escape, that is not until the middle of December, a casual labourer on the boundary between the Zürich Oberland and St. Gallen discovered the panther under a barn, and killed it for food. Before that, information was often received that the panther had been seen here, there and everywhere, yet the whereabouts of the great cat could never be pointed out with certainty, suspicious tracks always turning out to be those of dogs. The most incredible suggestions were made by the public to the zoo authorities; for example, the help of a clairvoyant should be sought to search for the escaped animal, or that it should be exorcized by the representative of a certain religious sect. In the Swiss press alone, about eight hundred articles on the ‘panther case’ appeared. At all events, the Zürich Zoo, then in its early days, sprang to fame overnight thanks to this incident. The propaganda value of the escape was incalculable.

Psychological analysis of the animal’s behaviour showed this: it was an untamed animal, still in the characteristic state of continuous excitement and mental tension and had not yet reached the stage of settling down. Significantly enough, the panther had never taken advantage of the open air cage at its disposal. It was thus clearly not an example of escape from close confinement. The motive for escape is obvious—escape from man, from human surroundings, perhaps too from a hostile mate by whom it had more than once been injured. The escaped beast never attacked men, but sought refuge in a wooded district. The fact that this big tropical cat was able to fend for itself
for more than two months in the middle of a Swiss winter is of some biological significance. Very likely a few roe deer, the remains of which were found in the vicinity, were pulled down by the panther. In its place of refuge the animal could easily have been recaptured.

Runaways

Runaways have already been defined as animals that suddenly escape from their human escorts when, in the usual way, they are being walked about outside their quarters. In a condition of excitement, they dash off out of control. Elephants are prominent among these, then apes, bears and zebras; other large species of wild animals are only paraded free, that is outside a safe fence, by way of exception. We must also take into consideration all those animals that perform in the open circus ring, confined to it merely by the ring wall. This is a psychological barrier which they have been trained to respect and from which they may escape under the influence of the excitement factor (disturbance).

Running away is almost always caused through panic, less often by strong sexual emotion, as in apes or stallions. In domestic animals this corresponds to breaking loose, and is chiefly found among horses. It is a fundamental point in dealing with wild animals that all excitement should be avoided. Even in the perfectly tamed wild animal, wildness i.e. flight tendency, flares up in conditions of disturbance, as previously pointed out. There is a classical example of a runaway in the Munich elephant panic of 31 July 1888. It has been described in detail by C. Hagenbeck (1909) 232.

The elephants taking part in the Hagenbeck Circus street procession grew restless during the long walk and shied. Their drivers at once took them energetically in hand, but the elephants, now grown wild, were driven back by the Light Horse Dragoons. They turned into a narrow side street, broke through the crowd, and a frightful panic ensued. Everybody fled screaming in a mad dash to get away. Horses bolted, even the police and the military broke their ranks. Some of the elephants scattered in the colonnade of the Residence Theatre and then stormed the portico of the Court Theatre where they trampled a party of girls from the mountains. This unparalleled panic was caused by a traction engine, disguised as a dragon, that suddenly blew off steam just as eight elephants were passing. In a flash hundreds of spectators were pushed over, the rest fell over them as they ran away, and countless broken bones were the result. Passers-by who had been driven against the walls of the Residence Square waved their umbrellas about in the faces of the elephants and thus made them still wilder. Fifteen casualties lay in the Luitpold Palace, and countless seriously injured in the Odeon. The commotion in the city was indescribable. The police received a report that a woman had been killed.
The press report caused Hagenbeck to make investigations on his own and among others he reached the following conclusions. In certain narrow streets, where the procession kept stopping, the animals were deliberately bombarded with bread and fruit. Their behaviour was exemplary until they came to the dragon in the procession on its way back. The dragon, at that moment standing still, suddenly started to move, spurted steam at the hindmost elephants and so terrified them that they plunged forward. Hagenbeck at once dashed up to the last four elephants to bring them to a standstill. This he would have succeeded in doing, with the help of his men, if the public had behaved calmly, but the shouting made the animals worse and they dashed ahead. He had brought his four elephants to a stop once, but the swarming mass of onlookers, attacking them with sticks, umbrellas, knives and the like, drove the animals steadily down the street. After the elephants had come out of the theatre again, he jumped in between them. He managed to keep his feet, brought them to a standstill and rushed to the front of them. A few moments later, however, the mob set the animals off again with their shouts. Hagenbeck followed them as far as the Tal, where he collapsed.

This incident seems clear proof that the motive for running away was shock. The animals fled in a state of terror. In all examples of this sort the only appropriate treatment is to calm the animals. With elephants, and many other animals, too, a word from the keeper they trust can often restore them to a state of calm. This, in fact, happened in the case we have quoted. But as the public stupidly continued to shout and hit the animals they were put into such a state of excitement that they ran away. Any movement from behind, or running after them, must be avoided in such cases for a quick move from the rear must inevitably increase their flight panic. There must be no chasing; the right move is to get ahead of the animal, to cut it off. The reason that the sudden appearance of the trusted person in front of the animal has the effect of a brake is as follows: the person who suddenly appears in the line of flight does not need to be recognized as the trusted keeper. He will probably be taken for a fresh enemy whose appearance will have the effect of releasing flight reaction again. For this reason the previous course of flight is checked. This slowing down gives a better chance for proper recognition of the familiar human being, or of the sound of his voice, than headlong flight. The trusted person, once he is recognized, has a particularly strong effect like a magnetic pole. This effect is immediately spoilt, however, if the attention of the animal, till now fixed upon him, is distracted by fresh signs of the enemy from behind.

The excitement of men or animals e.g. horses, that are running away is caught by the animal that has broken loose; this causes intensification of its feelings, culminating in actual panic, when the animal no
longer responds to attempts to calm it down. The more the animal's condition departs from the normal, the greater the risk of its breaking loose. Processions with their moving crowds, costumes, decorations, strange wagons, flags, bands and noise are especially dangerous. Only a few animals, mostly circus ones, are used to such situations. With them, the constant change of surroundings, the unreliability of appearances is, as it were, normal. Two facts should not be overlooked here. On all occasions of this sort some risk is unavoidable, for there can be no double safety, no real safety at all. In addition, the behaviour of the public is usually far less predictable than that of the animals. Even with an animal that is completely familiar, one the behaviour of which can be foreseen in all imaginable circumstances (the ideal case), there is still one unknown factor and a big one at that—the public. Experience tells us that in awkward situations of this sort the public will always do the wrong thing. Anything that excites the animal is wrong; but at the critical moment this fact is ignored.

Accidents with wild animals, as well as breaking out and running away, are of great interest to the animal psychologist, as they often indicate miscalculations in the prediction of animal behaviour. The animal psychologist must do his best to predict the behaviour of the animal accurately in any given situation; only when his forecasts are regularly correct can he assume that he understands the animal to some extent. The checking of behaviour forecasts is of great importance in practice as well as in theory. In this respect theory and practice are intimately related; one has much to gain from the other.

Because of the value of these behaviour forecasts, one point in the example quoted will be examined rather more closely. Hagenbeck made sure that his elephants were as quiet as lambs and thought this excluded any risks. Confidence in the animals, however, is only one factor in the calculation: by itself it is no criterion for the total situation—in this instance a public procession: it is not constant, but is liable to the powerful effects of the excitement factor. In taking an elephant through a busy part of a town, one is not justified in considering an accident out of the question because the elephant is easy to lead. One must also take into account related factors: for example, yapping dogs that do not usually frighten the elephant but may perhaps cause it to swerve a little. In this way the creature may move too close to the spectators and these grow restless, shout and wave handbags, sticks and umbrellas. Or a horse may shy and thus upset the elephant; a horse in the procession may break loose at the unexpected appearance of the elephant and thus cause accidents. Many accidents with large animals might have been avoided with proper foresight. Even the quietest wild animals that may be led round outside a safe enclosure are potential runaways. One safety measure in particular should be aimed at. The animal being led should be escorted by other men at a certain distance
so that they can remove disturbing elements if necessary, or help to calm it down. R. J. MüLLER (1921) has given complete details of a difficult instance of transporting elephants.

The elephant has been quoted as an example of the runaway. Now the danger arises of confusing animals that break loose in terror with the so-called rogue elephants of Indian and African literature. Rogues are nearly always bulls. In exceptional conditions, and with all the symptoms of a fit, they destroy everything they come across in a kind of frenzy. Thus they are not elephants seeking safety by flight. Rogues are far more dangerous than runaways: the analysis of their condition can be of no interest to us, but belongs to the special biology of elephants.
Quality of the Environment

The lack of freedom of movement of captive animals compared with wild animals has long been considered the critical mark of life in captivity. Far too little attention has thus been paid up to now to the quality of the animal's living quarters. In reality the quality of the space at the disposal of the animal is of the greatest importance for its welfare. The captive animal no more lives in a homogeneous space than a wild one, but rather in a highly differentiated one. For these qualitative details the animal needs materials, often quite definite materials. In providing these, we must put ourselves into the animal's position as far as possible and foresee its needs. Anthropomorphic conceptions must be abandoned, and we must act as zoocentrically as possible. Highly ornamental salon aquaria, with fish gasping for air among their over-ornamented surroundings, still exist in many a zoo. Many aviaries, many mammals' cages are constructed, less obviously perhaps, in an anthropocentric way, none the less fatal for the animal. A painfully clean feeding trough may be of far less importance than a home; a beautifully fitted up nesting box than a branch to climb up, or a couple of spadefuls of sand for scratching in. It is true that in the last few decades the idea has gained ground that the animal's space should, as far as possible, be arranged 'naturally'; but mistaken opinions about this naturalness have been common. Intended naturalness more often than not appears as pseudo-naturalness. The best guarantee of complete naturalness is assumed to be a faithful copy of a piece of natural scenery. This apparently logical conclusion is based on a false ecological estimate that may have serious results. Even an untouched section of it natural ground, enclosed within six sides (i.e., the closest possible imitation of a section of the biotope) is likely to be unnatural. A cube of fifty gallons of water containing a pike removed from a lake and put into an aquarium would not reproduce natural conditions, in spite of it appearing at first glance that it would be utterly impossible to improve on the naturalness of the quality of space provided. In this exposed cube of water, the pike searches in vain for a home, or else it soon feels the lack of oxygen. Mistakes of this kind, resulting in a pseudo-natural arrangement of space, are due to ignorance of the following elementary fact: a cross section of nature is not an equivalent part of the whole, but merely a piece which, on being completely isolated, alters its
QUALITY OF THE ENVIRONMENT

quality. In other words: Nature means more than the sum of an infinite number of containers of space (cages), however natural.

The essential thing about the isolated section of nature is that it is cut off from the main cycle of life. There is nothing to be done except to replace this cycle artificially in captivity. Naturalness in the treatment of wild animals does not consist, therefore, of a pedantic imitation of one model section of nature. It means that a substitute for it must be found suitable for animals, taking into account the new conditions of life in captivity. Naturalness, in the sense of biologically correct type of space, is not the result of an attempt at imitation, but of an adequate transposition of natural conditions.

What cannot be avoided in keeping animals in captivity, as we have said, is isolation from the cycle of life; therefore a fresh artificial cycle must be created. This substitute for the life cycle consists not only of the artificial provision of food and removal of excreta—perhaps its most obvious part—but of many other factors, including psychical ones. The whole psychical apparatus of the captive animal, so to speak, must be scaled down from the larger life cycle (in which avoidance of the enemy plays the chief part) to the small artificial cycle of life in captivity. It must be kept working by suitable new stimuli, and the more differentiated the apparatus is, and the higher the particular animal’s standard of development, the greater the urgency. In the chapter on the animal-man relationship we shall return to psychical substitutes for filling the gap left by interruption of the natural cycle and isolation through captivity.

The importance of the quality of space is particularly marked with marine organisms (fish, sea anemones), for these live in a medium of great constancy. Even slight changes in the usual surroundings, such as composition of the water, oxygen content, temperature, have serious consequences and often result in the sudden death of these animals. In keeping such marine animals in the aquarium, the need for an artificial cycle is evident in the most commonplace details of quality of space; e.g., the filtration plant necessary for any sea water aquarium, to some extent replacing the sea currents, waves etc. Aquarium and filter tanks are literally part of the same unbroken cycle through which the little section of water is constantly moved, purified and oxygenated.

It is well known that most large sea water aquaria inland do not use natural but artificially reconstituted sea water, significantly enough, because this is better than the natural water, or at least as good (O. Heinroth (1937) 179). It is made from fresh water to which eight or ten different salts are added in correct proportions. This artificial substitute for natural sea water is almost perfect, as proved by the length of life and the breeding of many marine animals in the aquarium.

Whilst the quality of space for marine animals in the aquarium is determined by man, at least as far as the composition of the water is
Endogenous Factors

In the following two chapters those factors of space quality will be dealt with that are influenced by man and the surroundings made by him. But the animal too has a definite share in differentiation of space; it elaborates and makes use of the material provided for it to suit itself.

Often it is difficult to get the material needed by the animal for its endogenous space-formation. In this matter any anthropocentric action, the imposition of human requirements, must be considered harmful. The important thing is to give up the last remnants of anthropomorphism and to behave as zoocentrically as possible. It must, for instance, be clearly understood that metal and glass, important constituents of many cages and enclosures, are completely unbiological material as are to a certain extent, concrete, artificial stone etc. The prime necessity for the animal’s space conditions is vegetable matter (p 99) and earth of varying qualities. These elements should not be denied the animal altogether nor withheld more than absolutely necessary.

Habitability and comfort for man and animal are sometimes fundamentally different. A fresh clean layer of peat on the cage floor is suitable enough in many instances, but for a loris (Nycticebus coucang) it only becomes habitable when it is thoroughly soaked with its urine, and thus provided with its scent marks. Every time its cage is cleaned out this animal has to drink incredible quantities of water straight away and sprinkle the nice clean floor systematically just like a watering-cart. This shows that habitability must be treated subjectively.

As has been said in the chapter on life in nature about the characteristics of the animal’s living space, the captive animal also tends to regard the space assigned to him as his own territory, and to set up his subjective space-time pattern in it. In his efforts to do so the animal must have as much assistance as possible. The surroundings of the captive animal then lose their significance as a place to escape from at all costs, but gain on the contrary the significance of an individual living space (territory), to be defended against all, and only to be forsaken under compulsion. One of the most important qualitative differentiations of the space is the home, the place of maximum security. In accordance with its function this place must, as far as possible, be safe from all disturbances. It must not be exposed, and often needs subdued light. In building its home the animal must be helped a great deal. Often the home is the only place in which harmful states of tension due to captivity can, to some extent, die down and change into a
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harmonious mood, necessary for the animal’s health. Often, too, many concessions are made to the visiting public of the zoological gardens, at the expense of the home. During its life in the home, the animal sometimes withdraws from the public gaze. This cannot be helped, for many animals need periodic isolation.

As a rule, the animal living in captivity builds its secondary space from the starting point of the home (J. von Uexküll (1937)), which forms, as it were, the zero point of a system of coordinates. In this the animal orientates itself, laying down its beaten tracks (Figures 5, 12) and in particular, establishing its space and time pattern in which the home forms one of the essential points. Other biologically important components of the pattern may, for example, be: shelter, refuge, places for defaecation (Figure 13) and urination, bathing places, such as the wallow (Figure 14), sand bath etc storing places, feeding places, look-outs, demarcation places, and so on. For many fish, too, the home forms to some extent the foundation for the construction of the subjective space. G. Lederer, for instance (1939) states, that if some coral fish, such as premnas that live alone, are put into a suitably equipped tank, they at once swim round the tank and find a promising hiding place. They keep to these places once they have chosen them; they rarely change them, and make excursions into the open water from their stations or homes.

The captive animal’s space and time pattern should have the greatest possible consideration, not only in the preliminary fitting up but during maintenance, cleaning out and especially during any sort of handling. Many animals intensely dislike being disturbed during rest in their homes. On the other hand, for example, an artificially made place for defaecation, deliberately chosen and provided with a sample of the animal’s faeces, may considerably simplify cleaning out for animals with localized excretion and urination, as other parts are left comparatively clean.

Practical use of the home effect is often valuable in the treatment of animals. Animals may easily be got into travelling cages or other narrow containers by providing these with an obviously homelike atmosphere and by gradually decreasing the amount of cover in the cage they are living in. By this means the use of force with its consequent upset can often be avoided. The author has often used this method with success e.g. in handling poisonous snakes. Cobras (Naja) often have difficulty in casting their skin, sometimes failing to cast the watch-glass shaped skin covering their eyes with the rest of the skin. This can happen time and time again so that the animals no longer see properly and even appear blind. If possible, handling poisonous snakes should be avoided. As soon as the skin-casting trouble mentioned begins, a rectangular tin box is put into the terrarium of the snake to be treated. It has two parts; an inner and an outer (Figure 15), the inner box made of wire, the outer of solid tin. Both parts have a
Figure 12. Beaten tracks in fallow deer enclosure

Figure 13. Defaecation point of male llama with single track

Figure 14. Red deer does at wallow hole made by the animals themselves
Figure 15. Practical use made of the homing effect in a reptile

a. Metal cover and wire cage used for eye operations on the cobra
b. The snake's head held by rubber tubing
narrow opening let into the same side. The cobra under treatment regularly creeps into this simple operating cage during the night, regarding it as its home. In the morning, all that has to be done is to shut the opening and remove the outer box. The snake in the wire cage is then ready for the operation. It is a simple matter to secure the snake's head with rubber bands to the wires. The patches of skin causing the trouble can now be removed after being softened from the eyes with tweezers and without any risk at all.

Under the influence of certain conditions of captivity (space-confinement, hypertrophy of valencies, lack of amusement and occupation), peculiar partial hypertrophies of the space-time pattern may occasionally occur, fixed stereotyped movements for instance (H. Hediger (1934b)). It should first be said that stereotyped movements are a sure sign of wrong treatment. We shall refer in detail on p 88 to the stereotyped movements of an armadillo, analysed by Holzapfel, and due to an unbiological floor.

As we have said, a considerable number of such stereotyped movements may be considered more or less serious partial hypertrophies of the space and time pattern. Take the case of a predatory animal, keeping watch for the arrival of his keeper with meat, from a fixed point in his space-time pattern, its look-out. The man keeps him waiting. The animal turns round and follows a fixed path or track which brings it back to its look-out, the smaller the space the sooner, where it keeps watch once again. Waiting for food at the usual time causes definite excitement. Moreover, food, one of the few things in its world worth attention, possesses an extreme valency effect. Thus an originally significant action—watching for food at a fixed time and place—may be performed far too often and for too long, because of a lack of other possible activities and under the influence of the tendency for repetition to which any creature is liable. The action then gets gradually rounded off, or shortened, in the course of frequent repetition, and results in a fixed stereotyping. This may go so far that the animal performs it at other times as well as at feeding time. Eventually, through moving senselessly to and fro, it rubs itself sore. An imaginary example has been chosen here on purpose. There are many kinds of stereotyping to be seen, all of them pointing to this sort of origin and largely reducible to this pattern.

Like many other species of marten, the pine-marten (Martes martes) is characterized by laying scent marks at fixed points in its space-time pattern in nature. To do this it deposits secretions from the anal glands on projecting branches and the like. All scent marks must be renewed from time to time by the laying of fresh secretions. F. Goethe (1938) showed that a branch with secretions of this sort on it kept its characteristic smell after a fortnight's exposure to wind and weather. Thus a periodic renewal of scent marks at long intervals is enough, A
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typical hypertrophy of this behaviour occurred in a captive pine­
marten, observed by Goethe, and we were also able to confirm several
other cases of this type. Goethe states that he counted the visits to
scent marks on a certain day and in the case of the male animal he got
a total of forty six in ten minutes, and in each minute that followed:
5, 5, 6, 5, 5, 7, 5, 5, 2, 1. The uniformity of this scent marking can be
seen from his diagrams. Goethe discovered significantly that the marten
in a small cage visits the scent marks far more frequently than in a big
enclosure or outside. The field of influence of such a scent magnet
grows with the decreasing size of the living space.

This is a striking example of a partial hypertrophy of the space and
time pattern in the sense previously described, under the influence of
confined space and the hypertrophy of valencies thus produced. Peri­
dodic visits to the scent marks are right and proper, but a renewal of
them on an average five times a minute is quite senseless, and has indeed
become a stereotyped action. This stereotyping is not serious, yet it
shows clearly enough that the animal’s surroundings need enrichment
by the introduction of new valencies, for instance, enlargement of the
cage (which led to definite improvement in this case) or by other
amusements or occupation. Lack of occupation of the captive animal
is an urgent problem of animal management, but is capable of solution.

M. HOLZAPFEL, whose thorough investigations are well worth reading,
states ((1939a) 568) that stereotyped movements in wild animals are
practically never due to a single factor. Three main factors enter into
the explanation of the origin of stereotyped movements:

1. Tendency to habit formation
2. Emotion
3. Blockage of this emotion i.e. an external or internal hindrance
to normal emotional outlet

The writer has pointed out that serious biological and psychical needs
of the animal may be inferred from apparently meaningless and sense­
less stereotyped movements. Stereotyped movements are thus not
merely of theoretical interest, but should receive more attention in
practical animal management than hitherto ((1939b) 529). Many stereo­
typed movements may be considered as partial hypertrophies of the space
and time pattern i.e. of the tendency of the animal to perform certain
actions at a certain time and place. We do in fact often find in stereo­
types of this sort a striking connection between space and time. The
stereotyped movements are not performed at random, but usually occur
at a set time and place. M. HOLZAPFEL ((1939a) 573) was able to displace
the stereotyped behaviour of a sloth bear (Melursus ursinus) in time by a
special experimental arrangement. In the path stereotypically followed by
a dingo (Canis dingo) she observed a spatial dependence upon definite ex­
ternal factors, such as the presence or absence of the public ((1938) 51).
'Floor fear' in an arboreal animal. A slow loris (Nycticebus coucang) dare not leave go of the branch and walk on the flat floor.

Figure 19.

A fox on a perch nearly six feet (two metres) above the ground. An extravagant phenomenon conditioned by captivity.

Figure 20.
Figure 21. Overgrowth of hoof ('shoe formation') in a giraffe due to insufficient wear.

Figure 22. 'Shoe formation' in a Sardinian wild sheep (Ovis musimon).
ENDOGENOUS FACTORS

Usually the stereotypes connected with movements from place to place are linked with definite tracks of a geometrical character i.e. the same paths are always followed in the same direction. Figures of very frequent occurrence are the circle, running to and fro in a straight line, the figure of eight etc (H. Hediger (1934b) 349). These various forms have been carefully investigated by M. Holzapfel (1938) 48).

It appears, for example, that the figure of eight derives from the movement to and fro in a straight line. Moving up and down alongside a wall or railing may be caused either by flight to a place i.e. by the animal’s attempts to get away from the public, or by a strong temptation on the part of the animal to get through the wall or railing to an attraction on the other side, to food, a companion or a sexual partner.

At either end of the straight line track the animal is forced to turn round; only in rare cases is the return journey performed backwards, as in the free-swimming cuttlefish (Loligo), in certain polar bears or some pathological horses. Turning usually happens in this way—the animal’s head remains as close as possible to its goal (flight goal) and the hindquarters have to make the movement, which causes the turning away from the goal (perpetual wall-turning). The straight to and fro course with constant turning at a wall may be considered as a very narrow figure of eight with extended middle, according to Holzapfel. Then follows gradually an increasing detachment from the obstacle, the wall or railing, in the course taken by the animal, with corresponding increase on the return journey. Eventually a broad figure of eight may develop from it (Figure 16).

Through hugging close to the wall, a figure of eight along a wall or railing can only be followed in one direction, that is, so that the turning at the top of the loop causes the animal to face towards the wall. Figures of this type are found among various animals; camel, dingo, or brown bear (Figures 17, 18). A figure of eight with unequal loops results when the goal, at which the reaction leading to release from stereotyping is aimed, lies on the other side of the obstacle, as in the example given for bears. It cannot, then, be approached equally from either side owing to the peculiarity of the space available for the animal, here the semi-circular plan of the bear pit.
Exogenous Factors: Physical Environment

Water and Air (Climate)

We classify animals, with R. Hesse (1924), into aquatic and land animals. Among land animals we include not only those that fly (insects, birds, bats) but all the bodies of which are surrounded by air and not water; also those animals that move on the ground, bore into wood or dig the dry earth. Again, among aquatic animals, we may differentiate between those the ancestors of which have always lived in the water (primary aquatic animals) and those which, though descendants of animals living in air, have, in the course of development, changed back to an aquatic way of life (secondary aquatic animals).

The primary aquatic animals take oxygen from the air dissolved in the water. Thus they are water breathers, usually cold blooded, and include the fishes. It has been pointed out in the previous chapter that far more attention is usually paid to the quality of the space arrangements of these primary aquatic animals than of most air animals, which do not immediately die if there are slight deficiencies in the quality of their space. The goldfish bowl almost completely disappeared years ago and considerable care and attention is paid to maintaining a biological balance by most aquarium keepers. Amateurs are careful to provide their charges with a suitable bottom, with plants, in some cases with apparatus for aeration, filtering, lighting and heating.

The quality of space is often not so well adapted for land animals; that is why we should like to emphasize a few essential points here. Whilst every aquarium keeper pays attention to the pH content of the water, it is only recently that the importance of ionization of air for captive land animals has been pointed out for the first time (H. A. Meixner 1939). In order to keep the respiratory organs of his orang-outang in healthy condition, G. Brandes (1939) maintained a high acidity of the air by installing a Kapl's evaporating apparatus. On the other hand some space factors, e.g., climate ventilation, atmospheric moisture etc as well as the use of various rays (ultraviolet) and transparent materials (glass) were discovered comparatively early and have been dealt with by many writers.
WATER AND AIR (CLIMATE)

Of all the climatic factors now under review, the first to get attention was the temperature of the animal's space, often, in fact, more than was necessary for the animal's good. The temperature requirements of many tropical homoiothermic animals were considerably overestimated until Hagenbeck revolutionized ideas on this subject by his bold, sensational experiments (C. HAGENBECK (1909) 330). The same results were reached by the investigations of the Société anonyme des Jardins Zoologiques d'Acclimatation, founded in 1854 at the instigation of Isidore Geoffroy de St. Hilaire. Nowadays, we know that many tropical birds and mammals can stand very low temperatures without harm, and that even extreme winter temperatures only cause indirect harm, for instance, when soft moist food freezes as hard as iron, or through the mechanical effects of snow and ice. Flamingoes, often considered by the outsider as particularly sensitive tropical creatures, will find danger only in the sharp edges of the ice on their ponds because they may injure their legs against it. A most interesting and complete account of the effect of the European winter on captive wild animals in zoological gardens has been published by K. M. SCHNEIDER in a special number (I, 2 (1941) No. 13) of the periodical Der Zoologische Garten, edited by him. Here again we only mention a few fundamental points.

Next we must refer to the secondary effects of confinement of space under captive conditions, namely the impossibility of the animal's choice of an optimum micro-climate at a given time (G. KRAUS (1911)) already mentioned on p 31. The free animal, within its limited space and with its freedom of movement restricted, can choose the optimum part of its terrain at a given time, a breezy or a sheltered spot, a cool or a warm one, a sunny or a shady place, a damp or dry, a bright or dark one. In captivity this is usually impossible because the space offers nothing like this choice, or because certain parts of it are not accessible for all sorts of reasons. That is why special importance attaches to the artificial, optimum climate. Life in captivity often presents extreme conditions which do not occur in freedom, for instance, the abrupt change between internal and external surroundings e.g. cages. It is not always right, therefore, to talk of the softening effect of life in captivity; occasionally it may lead to a considerable hardening. Significantly enough, a far greater number of colds are caught during acclimatization than after it has been successfully accomplished.

It is quite another thing, of course, with cold blooded animals which are unable to generate any body warmth, or none worth mentioning. With them there is no acclimatization; the necessary warmth must be provided for them externally. Misconceptions still arise occasionally about the amount and type of heating to be provided. This is not confined to small exhibitors, though these often carefully wrap their
tortoises and giant snakes in blankets during cold weather and then imagine that the animals must keep nice and warm in them. They do not realize that even the thickest woollen blanket can only help to insulate existing heat, not to generate it.

For many aquatic animals, the temperature of the air above the water in which they live is important, especially for those adapted for breathing atmospheric air, as, for example, the labyrinthodonts, many amphibia and aquatic reptiles such as turtles. Here, optimum temperature control of the water is not enough, as the breathing of air that is appreciably colder than the water may lead to serious chills.

Every species of animal prefers a definite temperature, the favourite temperature, and there is reason to think that this is also the most suitable temperature for the species i.e. the optimum temperature. In several papers K. HERTER (1934) has investigated this ‘thermotactical optimum’ in rodents and examined how far it is consistent for species and race. In 1936 it was shown that with various mice this optimum was transmitted as a dominant hereditary factor on a simple Mendelian pattern. In a more recent work K. HERTER (1940) gives extremely valuable data on the favourite temperatures of twenty five different species of lizards and snakes. He discovered that lizards usually have a higher favourite temperature than snakes, in similar biotopes with similar manner of life. Further, species from ‘cold’ biotopes with a ‘cold’ manner of life have lower favourite temperatures than species from ‘warm’ biotopes with a ‘warm’ manner of life. Thus the favourite temperature of the slow-worm is a little above 25°C, that of Agama stellio on the other hand more than 40°C. Most of the species investigated have favourite temperatures of 36–40°C. According to F. G. BENEDICT (1932) 497) the optimum temperature for most reptiles is about 37°C, for many cold water fish 10–15°C, for tropical sea fish e.g. coral fish, on the other hand, 25–27°C (G. LEDERER (1939) 79). For most tailed amphibia the optimum temperature is about 16°C (W. HERRE (1939) 95).

There are animals like the giant tortoises that are nearly always kept too cold, so that their metabolism is at a minimum instead of an optimum. Under such conditions growth ceases, or nearly so. From this slight annual increase in size wrong conclusions are drawn about the ages of large animals (R. L. DITMARS (1932) 242). C. H. Townsend and E. Heller put young giant tortoises into more favourable temperature conditions and obtained a great increase in growth, in fact their weight rose from 100 to 150 per cent in a year. A twenty nine pound animal weighed 350 pounds after seven years. These results are of fundamental importance. Many other animals live in a similar state of minimum instead of optimum conditions. It now becomes possible to explain why giant tortoises have never so far bred in captivity. The fact that any captive animals have failed to breed is always a sign that something
is wrong with their treatment, often quite a small thing. With giant tortoises it is clearly lack of warmth, especially ground warmth.

For his experiments on preferential temperature among land animals K. Herter (1934) constructed a temperature box, a choice of temperature apparatus. In principle it is an oblong experimental cage with an almost rectilinear temperature gradient accurately measurable. By means of a large number of observations it is possible to chart the temperature range in which the test animals prefer to be. Naturally, this method presupposes that the interior of the test cage is quite homogeneous, except for the temperature, so that the animal really only reacts to temperature. On the assumption that the animal does stay in a temperature in which it feels most comfortable as far as sensations of warmth are concerned, F. Werner (1939) recommends the following ground heating arrangements for the snakes' terrarium. The heating should be arranged eccentrically, and the animals left to find the suitable spots themselves. It would then be noticed that when the animals had got warm enough they found a cooler place in the terrarium, just as they go on to the land after they have been in the water for some time. We must not assume that they always behave like this, either in the temperature box or in the terrarium, but only when there is an undisturbed mental state and in familiar surroundings. Animals are far more complicated things than mere physical reagents and the importance of the mood factor should not be underestimated. Every part of its space is not only a locality of definite temperature for the animal, but may have an attraction or repulsion effect subjectively on the animal for various reasons as well. These effects (e.g. home effect) may be so strong as to make the warmth effect negligible.

In the zoological gardens at Berne a large Python sebae escaped and crept into an opening over the hot pipes nor could it be dislodged by force. It remained for several days in this hiding place, and eventually it became obvious that the pipes were far too hot and had seriously burnt the snake. Later the animal died of its burns. In a similar plight an escaped boa constrictor suffered only slight burns. Another Python sebae appeared so timid at first that for weeks it would not come out of the water tank into which it had at first retreated. On emptying the water, the animal stayed in the tank, although in consequence of a heating defect parts of the tank floor became overheated so that the snake's underside was badly burnt, and it needed protracted treatment for several months. There have often been similar experiences with pythons.

Mammals as well as reptiles have been seen to persist in staying in harmful, even painful, temperature zones when they had the chance to find other spots. One winter an Australian opossum (Pseudo...
EXOGENOUS FACTORS: PHYSICAL ENVIRONMENT

all four paws and on the bare patch on its curly tail as a result. Correct choice of the optimum temperature apparently only happens when the mental state is undisturbed. The mood factor plays an extremely important part here, as always in caged animals. No animal should be treated as a mere physical reagent. The opossum also repeatedly showed marked inhibition. Compared with the perch, the hot pipes clearly had greater cover value; they ran close to the roof and along the wall. The corners in which maximum cover was offered were special favourites. The snakes mentioned behaved in just the same way. Cover or homing even deadens strong pain stimuli in an animal in a state of excitement. This is often confirmed in dealing with animals; hence it is evident that for the animal great importance attaches to the home.

Apart from correct maintenance of warmth or coolness, lighting and irradiation are most important. In fact, much attention has been paid of late to ultraviolet radiation as a substitute for sunlight (G. LEDERER (1927) 163). In the planning of animal houses and enclosures, apart from animals that are definitely fond of the dark or cold, it is a fundamental recommendation to give rather too much than too little sun. Excessive sunlight can be corrected by artificial shade but it is much harder to increase too little to the requisite amount. Many animals which are considered exclusively nocturnal e.g. the field hare, are in fact fond of sunshine, if they have the chance. Apart from the sun being a very efficient source of valuable radiation, warmth and light, it is also a first class source of vitamin D and a powerful disinfectant. Often, on the other hand, many species that might be considered to need plenty of sunshine are really extremely sensitive to the sun’s rays. This even includes tropical animals, especially those that live in virgin tropical forest.

It is often believed that crocodiles grill themselves for hours in the burning tropical sun, and can stand any amount of sunshine. At the same time collectors who want to kill these animals without damaging them use the simple method of laying the captured crocodile out in the sun, when it dies after a short time. The author has known a case from personal observation in the Pacific where a healthy crocodile died after a two hour exposure to the sun in the early morning between seven and nine o’clock at that (H. HEDIGER (1934) 37). A crocodile (Crocodylus acutus) was killed by H. BOKER (1939) 49 after an exposure of only twenty five minutes to strong sunshine in San Domingo. In order to estimate the need for sunshine or tolerance of it, we must think in terms not so much of warm tropical climes and equatorial sunlight as of the actual microclimate. Crocodiles can get rid of considerable quantities of heat in freedom through panting as well as being able, by periodic immersion, to bring about cooling through evaporation. Often the saturated atmosphere of their surroundings is a powerful protection from rays, added to which is the
WATER AND AIR (CLIMATE)

reports that crocodiles sunning themselves are covered with a thin grey film of dried mud, and that many have their wide jaws open. Now and then one of them turns towards the water and slowly pulls himself in; another crawls slowly out. These 'armoured' lizards are thus far more sensitive to strong sunshine than we might at first suppose. The same thing applies to various chelonians, for example, the Greek tortoise (Testudo graeca), often kept by amateurs, and ruthlessly put into the strongest sunlight. In its natural habitat in North Africa this animal is a decided sun hater in summer and creeps into hiding soon after sunrise (H. Hediger (1933) 3). Some of our native snakes, as for instance, Natrix natrix and Natrix tessellata, are known to be so sensitive to sunshine that they can be killed by less than half an hour's exposure. It must also be remembered that in a terrarium, through the small amount or even total lack of ventilation as well as the action of the glass, intolerable conditions may arise far more quickly than even in the closest confinement of the aquarium. R. Mell (1929) put an adult Chinese cobra (Naja naja atra) in a big glass accumulator tank and an immature one, twenty one inches long, in a large preserve jar both in the sun. The young one lay on its back gasping for air with wide opened mouth after three minutes; the old one did the same in five minutes. Only the adult snake completely recovered after the animals had been sprayed with water and put in the shade.

Many animals of the virgin tropical forest avoid direct sunlight. When the natives of the South Sea Islands brought the author snakes (Python amethystinus, Nardoana boa etc), a constant watch had to be kept to see that the snakes, usually tied to stakes, were not left in the sun. Even less than thirty minutes' exposure could kill them. M. Eisenbraut (1933) mentions the Azara capuchin monkey (Cebus azarae) avoiding strong sunlight. A captive animal, the chain of which had got tangled so that it was exposed to the sun for a considerable time, was noticed to be suffering from marked sunstroke. The Pudu deer (Pudu pudu), a typical inhabitant of thickets in virgin forest, avoids the sun and dies after an exposure of two to three hours (C. Junge (1933) 241). Concerning the Caspian tern (Hydroprosne caspia), R. H. Pough (1941) says that the summer sun soon kills its young. Thanks to thoughtless watchers, hundreds of young birds are often killed off, as their presence prevents adult birds from flight tendency from shading their young. A. Rzassnici (1933) observed how a Chapman's zebra mare during a heat wave in summer used to stand in such a position that her shadow fell on her foal resting on the ground. The relations between animals and their shadows are not only of practical but also of considerable theoretical interest, as the author has tried to show recently (1947) in a short paper on the problem of consciousness in animals.
EXOGN MOUS FACTORS: PHYSICAL ENVIRONMENT

There are all sorts of gradations among vertebrates, between desire for and avoidance of sun, hunger for and avoidance of light. For many wild animals light is not only necessary in order to be able to see and get the necessary food e.g. many birds, but important for the infrared and ultraviolet rays beyond the visible light. Much success has already been had with artificial radiation; on the other hand far too little attention has been paid to the importance of daylight for extremely light-shy animals. There are animals which cannot tolerate daylight. J. Vosseler ((1930) 8) first drew attention to the need of light protection for many animals that one would never suspect of being so sensitive. Over the cover bars in the inner cage of his predatorial animals, Vosseler spread a piece of roofing felt several yards wide. He says that this simple device provided a highly desirable resting place in subdued light, for all the inmates, the big cats, hyenas etc and was obviously of physiological importance for the well being of the various inhabitants of the cage. According to his observations and experiments, nearly all tropical predators feel that constant light streaming vertically down on them from above is an uncomfortable stimulus upsetting their psychic state. This applies even when the intensity and duration of our northern light seems to have no effect worth mentioning, according to our human perception. In freedom also many species seek covered resting places, protected if possible by bushes, for complete rest and the relaxing of mind and muscle. Such species, lions and leopards for example, do not at other times shrink from following broad tracks exposed to the full sun’s heat. The feeling of safety that such a partial protection from light induces is not usually appreciated as a biological factor and accordingly hardly ever taken into account in our zoological gardens.

Temporary shade during the first adaptation phase is to be recommended for its calming effect on freshly captured excited ungulates, among which the danger of fracture of the skull or limbs arises. For example, freshly caught chamois have been kept with success in a fairly dark place. Bright colours, even white patches, have an irritating effect on many animals. In its attitude towards a white wall, one of G. Brandes’s orang-outangs ((1939) 6) showed symptoms like those of imprisonment psychosis in man. Brandes learnt from observation to avoid putting white close to the animals, and chose green panels for the wall surface of the newly built day enclosure. The desired result followed. The animal did not take the slightest notice of the wall panels afterwards.

Daylight is quite unbearable for many nocturnal marsupials, such as the American opossum (Didelphys paraguayensis). This animal was considered untamable and stupid. All observers who had anything to do with it could only get defence reactions from it. In an earlier article (1934a) the author showed that this opossum, if suitably
treated, that is by taking into consideration its supersensitivity to light, becomes not only quite tame, but can also be trained. Clearly the Tasmanian devil (Sarcophilus ursinus) is of similar sensitivity and is likewise considered thoroughly stupid. O. ANTONIUS (1933) 247 observed how one of these animals in an unusually bright cage showed increasing excitement and its ears, normally pale, finally turned red. Among pro-simia, the loris (Nycticebus) for example is extremely sensitive to light. To get proper reactions from this markedly nocturnal animal it is necessary to deal with it at night, and protect it from harmful daylight. F. J. GORTER (1935) 95, in his experiments on the loris, took no notice of these considerations and thought this animal the most stupid of all primates, whereas the author has been able to show, in the course of many experiments performed at night without any disturbing illumination, that there is surprising psychic efficiency in this animal. Surely the reason for the short life of the loris in European zoological gardens is partly through keeping the animals in over-intense light, causing a constant state of excitement. One specimen which was looked after for nearly seven years was kept in a darkened room in which it obviously felt happy. During occasional short exposures to sunlight, signs of discomfort and copious watering of the eyes could at once be noticed.

Mammals and birds may be extremely sensitive to light, and so may reptiles. R. MELL (1929) has described instances of a number of Chinese species staring hard at the light (Heliocataplexy). The behaviour of a poisonous nocturnal snake (Bungarus) is very striking. Under the influence of daylight it loses its psychic capacity for biting, or for any sort of activity at all. These snakes remain just where they are caught in the morning by the sun's rays, in the middle of the close-cut turf of a golf course, on the freshly turned bare earth of a clearing in the virgin forest. Fish, too, may be very sensitive to light. An electric cat-fish (Malapterurus electricus) showed great restlessness and by swimming to and fro against the glass side eventually injured its lips. Only when the rear of its tank was provided with a suitable protection from the light did the animal settle down and give up its harmful or stereotyped movement.

E. MERKER (1937) 70 has shown that light can even mean death for certain moist skinned poikilothermous animals. He says that smaller moist skinned animals from the crab, insect or worm groups behave quite differently in light than do adult frogs, lizards or dogs. The smaller animals are extremely stimulated by the light, dashing madly about and only settling down in the shade. During a period of rest through exhaustion they apparently build up fresh strength, for after a short time under continuous irradiation they begin dashing about again. In this way, rushing round alternates with exhaustion until their physical strength is completely used up, and the animals die a horribly
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Slow death. It can be imagined that similar behaviour might occur in more highly developed animals such as Amphioxus, small fish, and amphibia and their larvae. At all events, in some instances an excess of light—or the opposite—can be a decisive factor for life or death.

The humidity of the air, as has been said, presents another climatic factor of the greatest importance, not only for amphibia with moist skins, liable to die of lack of moisture in dry air, but for the higher vertebrates as well. The daily shower bath is a necessity for many reptiles; many snakes and lizards are not used to drinking out of vessels but only from precipitated moisture or other kinds of water drops. Some rattlesnakes prefer to drink drops from the scales on their own bodies; in their universe the bath tub often has no drinking significance.

The scales of many reptiles are very sensitive to changes in air humidity, more than ever during the sloughing period. F. G. BENEDICT (1937) points out that even the shells of tortoises play a part in the water economy of these animals. The horny parts of birds’ bodies too, especially the beak, need a certain amount of humidity, usually got by dipping them in the water. Periodic wetting is often necessary to keep the plumage in a healthy condition.

Even among mammals the large horny parts, especially the hooves, require protection from drying up too much, as do other regions of the epidermis. In the hippopotamus the whole epidermis has to be of a definite humidity, otherwise there is characteristic ‘blood-sweating’, that is, the secretion, in itself harmless, of slimy red fluid of a sweat like character. In connection with his observations on the weasel, I. KRAMMBREGEL (1935) draws attention to the need for moist air of various small mammals.

Whilst care must be taken on the one hand that the air has the right degree of moisture for the captive animal, there are definite dry-air animals for which moist air is unsuitable, and the distribution of which in free life is more or less directly dependent on the humidity of the air. Camels and dromedaries are known to be unable to exist anywhere where the absolute atmospheric humidity exceeds a monthly average of 11-12 mm (E. MARCUS 1933).

Whilst most higher animals can easily tell where they can get shelter from rain there are some notable exceptions. These include some races of the African ostrich, which are apparently unable to understand the effect of a roof as a protection against rain. This faculty also appears to be wanting in some Camelidæ of the New World. Perhaps this peculiarity of the ostrich is connected with the fact that it very seldom rains in its natural biotope, and that as a typical inhabitant of grasslands it has no opportunity for sheltering. Rain does not seem to exist in its world.

In zoological gardens recently, cages have been built with automatic climate control installations for delicate animals. In 1946 a similar
cage was fitted up in Basle for the anthropoid apes, largely for the reason that most of the apes (chimpanzees and orang-outangs) previously exhibited had died of tuberculosis, probably caught from the public. Now these delicate animals, especially the gorilla, are separated from the public by airtight plate glass and are thus protected from infection by tuberculosis. In addition the keepers are periodically x-rayed. We also put a certain amount of ozone into the ventilation system which has automatically regulated air temperature and humidity, and this acts as a mild disinfectant and has a very beneficial effect on the apes. Of course, as has been said, there is no such thing as an absolutely sterile maintenance of large animals, not even for these anthropoid apes, since the keepers can always introduce infectious material on their boots, clothes, or the animals' blankets etc. Epidemics, however, can be prevented by climate control installations of this sort, and so the purpose is achieved.

Whilst valuable aquaria must be properly fitted up with aerating plants, the terrarium is often strangely neglected in this respect. Quite apart from the ecological and hygienic importance, it would seem to be particularly important with reptiles to avoid stagnant air, because most species smell strongly. Thus there seems to be a psychological reason for keeping the air in glass cages moving and adequately renewed, being careful, of course, to avoid draughts. Many terrarium inmates grow more active through this, especially when biologically interesting smells, such as those of predatory animals, are admitted to the air supply from time to time. For this reason the author would like to recommend controlled central ventilation for the terrarium as well as for the aquarium.

The Ground

All aerial creatures without exception are bound to rest for a certain time on a suitable support which they can only leave temporarily. Since many cannot leave the ground at all, details of surroundings are of prime importance for the captive animal. Only with aquatic animals does it happen that certain species are exempt from this permanent or periodic attachment to the ground, at least for certain phases of their life, when they are able to move about freely in the water. From the point of view of the biology of zoological gardens three main groups may be distinguished, namely, animals that live

above the ground; flying or climbing either trees or rocks
on the ground; pacing, hopping, crawling etc
in the ground; permanent or temporary; burrowing or digging.

This broad outline shows that there may be no such thing as a uniform floor or a uniform cage. Most animals are completely adapted for
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a specific floor. Their build and methods of locomotion are modelled on it to such an extent that if they cannot get enough locomotive activity they may often show serious physical and psychical disturbances. Physical damage includes sore paws in soft footed animals or excessive and abnormal growth of hard parts such as claws, hooves etc. The wrong sort of floor can result psychically in a permanent state of excitement with fatal stereotyping of movements. M. Holzapfel (1939) was able, at a stroke, to remove a long standing stereotyped movement in an armadillo (Dasypus villous) kept on a slippery and therefore unbiological floor, by providing a layer of earth ten inches deep. G. Hinsche (1941) observed an extremely close reactive relation between organism and floor in various amphibians; it is, however, very pronounced in many other vertebrates, too.

Life above the ground—The animal chosen as a typical example of living regularly as a treeclimber above the ground is the orang-outang. For this anthropoid ape, that only exceptionally comes down to the ground in freedom, G. Brandes (1939) made an artificial floor that must be described in detail because of its biological value. According to his plan, orangs (and many other primates and arboreal animals as well) should be kept in an environment corresponding to their natural biotope, the upper and lower limits of which consist of a network of tree trunks and branches. For a barrier beneath the tree trunks he chose wire netting about four feet above the ground, so that urine and excreta dropped at once out of reach of the animals. By this means he managed to reduce the risk of coprophagy (the eating of excrement). The ground under the cage was of concrete, provided with a drain, so that it could easily be flushed.

Coprophagy in captive apes, especially anthropoid apes, presents a technical problem of zoo management, both from the point of view of its effect on the public and the danger of infection. It provides, too, a striking example of the hypertrophy of valencies (p 31) as a secondary result of confinement of space. In an essay on coprophagy among anthropoid apes C. Stemmler (1937) mentions various possible causes, among them the following. The ape, in his life in the trees, hardly ever comes into contact with his excrement, which usually falls at once to the ground. When he finds it on the ground of his cage in captivity he naturally examines it, at first with a bit of wood, then with his fingers. Since these get dirty in doing so he licks them, and we have the beginning of coprophagy. In other words, in the free anthropoid ape's world, its own excrement does not, so to speak, exist; nor is it seen in the immediate neighbourhood, as it usually falls to the ground at once and disappears from the animal's field of vision. In captivity, however, if the cage is not built on Brandes's biological plan, the excrement at once becomes part of this tree animal's surroundings and, as something new and striking, attracts the animal's
attention to an exaggerated degree. The less the animal's attention has previously been drawn to it, the stronger the valency, in W. Fischel's sense (1939: 62) i.e. the excitant effect of the excrement. Now in captivity there is little for it to occupy its attention, largely through the lack of necessity for avoiding the enemy which constantly occupies the animal in freedom. The few things on which attention can fall often hold it in exaggerated form, as in the case of excrement, a new sort of phenomenon interesting optically, olfactorily, thermically and physically. Preoccupation with this attractive phenomenon appears in an intensive form corresponding to its valency, as there is a lack of attractive occupations, of stronger diversion. The animal cannot detach itself from the object that has once arrested its attention. In this way the psychological side of coprophagy might be summarized. We shall return later to a discussion of other valency hypertrophies.

All tree climbing animals do not have the same way of excreting i.e. droppiing from a height. There are extreme arboreal animals e.g. the three toed sloth (Bradypus tridactylus), in the world of which excretion plays a very important part. H. Krug (1939: 291) observed that this sloth had a highly localized, social form of excreting and, moreover, that it took place on the ground. This sloth climbs down from the treetops to the ground for defaecation and excretes at a definite place, in common with various other individuals, so that regular mounds appear.

From the examples of the orang-outang and the sloth just quoted it will appear that excrement may have basically different significance in the subjective worlds of two extreme arboreal animals that are biologically related, and this must be taken into account in captivity. In the world of the orang, a branch climbing animal of the virgin forests, excrement simply does not exist, as we have pointed out; whilst in the world of the sloth, a climbing creature, hanging to branches, the excrement or its place of disposal becomes to some extent the focal point of the space-time system of several individuals. Krieg also observed deposit of excrement at the same place and time by several animals that had come from different directions.

The above example will serve, moreover, to show the difference between the two chief types of excretion, diffuse and localized. Comparison of these two types is not only of biological interest but is noteworthy from the technical side of the zoological garden (inspection and utilization of places for defaecation during cleaning etc). Incidentally, we may add that only those species with a localized method of excreting can be kept clean in their habits. With the diffuse type this is impossible. Thus it might be thought that by suitable training a new significance could be given to the excrement, but with such biologically deep seated behaviour habits it is extremely difficult to make
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changes through training, in fact, almost impossible. In the section on feeding (p 137) we shall return to these types of excretion.

A very peculiar and quite unpredictable result of keeping an anthropoid ape on an unbiological floor was discovered by M. Hilzheimer (1937). His careful analysis of the skull of Bobby, the largest gorilla ever to be kept in captivity in Europe, led Hilzheimer to the conclusion that Bobby, who arrived at the Berlin Zoo as a 35 lb baby and grew in seven years to a colossus of 600 lb, developed an abnormal posture of the head, and in consequence an abnormally shaped skull. The cause of the wrong posture was that in its infancy the animal was often carried about in arms like a human baby, so that in order to look its keeper in the face it had to bend its head right back. Things were even worse when Bobby was on the ground. Then his relations with human beings forced him to raise his head even more, for he always tried his hardest to look at the eyes or mouth of everybody who looked after him. Now his contact with human beings was almost continual, that is as long as he was small, since his keepers looked after him as much as they could. Thus he was constantly standing in the wrong body position with his head upraised, and eventually this led to the growth under continuous pressure of those parts of the occiput that were in full development and especially the muscles of the crista.

Hilzheimer's view is that in future care must be taken to see that young gorillas' quarters are fitted up in such a way that they can hold their heads in a natural posture, yet without depriving them of that peculiarly intimate contact with their keeper so indispensable for them. It is therefore a question of finding a suitable flooring at the right height above the ground. In principle, Brandes's orang-outang cage offers the desired solution. It is true that Hilzheimer's opinions need verifying for a larger number of individuals. The gorilla of the Basle Zoo, 'Achilles', has besides the keeper a chimpanzee as playmate and shows no such symptoms.

Many tree climbers require an empty space beneath them. This need must not be underestimated, as J. von Allesch (1931) has clearly shown for the lemur (Lemur mongoz). Like so many other climbers this animal has a strong dislike to being kept on the floor. The cage floor for animals of this sort must stand above the floor of the surrounding space, otherwise the animal cannot feel at home. The well being of many arboreal animals depends largely on the relative height of their floor above the ground. The lemur's cage was set on blocks at least eighteen inches high. As von Allesch (p 70) states, that was enough to give the lemur the feeling of being up in the air and of having plenty of space underneath him, and thus of ensuring his complete freedom of movement.

For months an opossum (Didelphis paraguayensis) was kept by the author on a table (1934a 41) on which a branch had been fixed
for climbing, so that this tree loving animal felt that it had a free space under it. Here we are dealing with a need which is too often disregarded. It is not confined to mammals but is also common to birds and reptiles, and even to some frogs. The climbing fish (*Anabas*) does not climb, we know, but the mud-hopper (*Periophthalmus*) is often found climbing at a considerable height above the ground in the stilt-like, almost vertical roots of mangroves.

It is not always easy to tell the difference between the mechanical effect of surfaces and the specific space effect of the floor beneath. What is stressed here is the importance of the relative height of the floor for the animal. The definite 'floor fear' of many arboreal animals may be so pronounced that it may even be useful as a barrier (Figure 19). In this way, J. von Oertzen (*1913*) kept a group of Colobus apes in the open in an isolated clump of trees from which they dared not escape as they would have had to cross a treeless level space.

Frequently, climbing animals in captivity have too few opportunities for climbing, especially brown bears. Their cubs, particularly, have a marked need to climb, their flight reaction consisting whenever possible of climbing. In the Berne bear pit, where giant fir trees renewed every other year are provided for the animals, this flight behaviour may be observed clearly. The bears find it much easier to climb up than down; individual bears, obviously less gifted, have never learnt properly and get stuck high up regularly. They then have to be got down by extreme measures when ready to be put into their dens for the night. One bear, in fact, had to be shot down because it regularly climbed too high and could never manage to climb down again.

Even in markedly arboreal animals, climbing has to be learnt individually and the necessary freedom from dizziness individually acquired. We should not assume without question the existence of these capacities in young animals born in captivity. J. von Oertzen (*1913*) looked after a three year old chimpanzee in Africa. This animal had been greatly plagued by sand fleas in its infancy and, thanks to its injured paws, had never dared to climb. Later on it suffered comically from dizziness. With infinite precautions it climbed up to seven or eight feet, then such a fit of terror seized it that it dared not move either up or down, and howled for help. In the first chapter it has been shown that certain lizards can only climb to a specific height up a tree.

It is a characteristic phenomenon that many animals, which in freedom are not classed as climbing animals, get into the habit of climbing in captivity, for example the fox (Figure 20), as well as hares, snakes, lizards etc. This eccentric behaviour is due to decay of the urge to avoid the enemy, conditioned by captivity, and to the energy thus released (p 31). This encourages activities which find no place under the tough conditions of life in freedom.
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*Life on the ground*—Animals that are strongly attached to the ground cause least trouble for the zoo technician, as far as barriers are concerned. The constant heavy friction against the flooring, however, causes fresh difficulties hardly known with climbing animals. The mechanical nature of the floor must be now hard, now soft, according to the nature of the body parts that are chiefly in contact with it. Contact organs and floor must be in harmony. If this harmony is destroyed it may lead to too much strain on the bodily organ in contact with it and cause foot sores or decubitus, or, equally serious, too little wear on hoofs, claws, and nails. This applies to all ground dwellers from mammals to fish. Decubitus (lying down) has been described by M. Plehn (1924) in carp. For them it means among other things the danger of infection, as it does for all fish.

The ungulates may be taken as an illustration of the chief points concerning the organs in contact with the floor. There are basically three possible lines to take in captivity; adaptation of the floor to the contact organ, in our example, to the extremity, or hoof; adaptation of the contact organ to the floor; or regulation by activity. The second method is practical only with domestic animals that allow themselves to be handled without special precautions. With the horse the extremity is adapted to the nature of the floor by the horseshoe. This is not possible with wild animals. For them harmonious unity of function is created in the natural biotope by the abrasive effect of the ground, the nature of the hoof (softness or hardness), the rate of hoof growth and the degree of activity (opportunity for wear). In captivity it is seldom possible to provide a floor of the same quality as in nature; moreover, the rate of hoof growth cannot be controlled. Activity is often altered and reduced compared with life in freedom, and this may lead to morbid hoof formation. In many hoofed animals there is a real problem here, since periodical treatment of the hoofs by direct capture often means considerable danger, not only to man, with animals that are not completely tame. Yet even the otherwise tame animal may be upset by capture, though this may be harmless in itself. In a state of excitement the original wildness i.e. flight tendency, is overstimulated and the animal may injure itself in its attempts to escape, or its heart may be affected.

Some years ago the Basle Zoological Gardens lost a giraffe from heart failure as a result of hoof paring. Now a special watch is kept on the hoof growth of the giraffes (Figure 21) and abrasive material is provided by spreading quartz sand even in the inner stalls. The importance of activity for hoof condition was very noticeable in a pair of Chapman's zebras at Basle. Both animals were living in the same enclosure or the same floor surface. The hoofs of the active stallion remained in perfect condition while those of the mare showed abnormal growth and had to be drastically pared. The mare was suffering from pulmonary
Figure 24. Distance and contact types, a Flamingoes do not tolerate contact. b Slow loris and galago in close bodily contact.
Figure 26. Contact behaviour between a Golden agouti (*Dasyprocta aguti*) and spotted paca (*Agouti paca*) b African cattle egret (*Bubulcus ibis*) and South American capybara (*Hydrochoerus hydrochoeris*)
THE GROUND

emphysema, was consequently far less active and so made much less use of its hoofs than the healthy stallion.

In other instances it is not lack of activity but simply too soft a floor surface that causes insufficient wear. This can happen even in nature, as R. Hesse (1924) has pointed out. In the wild sheep (Ovis moschata), introduced into Hungary and adapted for rocky ground, the hoofs grew into curved beak-like shapes (Figure 22). For a remarkable example of spiral growth in the hoofs on the forelegs of a free South African Cephalophus antelope, see R. H. Burne (1907).

Whenever in a zoo we have to deal with overgrown hoofs, the question arises whether treatment of the hoofs (e.g. paring, for camels or zebras that are kept on soft ground) justifies the risks mentioned. We must at all costs avoid producing an abnormal formation, by aiming at a suitable adaptation of the ground. In most instances this will mean an increase in the abrasive effect of the ground for ungulates. This is achieved by deliberately providing a hard floor of sand, broken stone, or cinder. By this means some adjustment can be made through the animal using only certain parts of the floor surface, the well beaten or less well beaten parts. O. Antonius (1929) describes the hoof treatment of a Chapman's zebra which was always an undertaking that endangered the animal's life. He therefore recommends a suitably strong abrasive floor covering of coarse, sharp granite chips the size of a nut. In another instance, that of a Hartmann's zebra (1937), O. Antonius greatly increased the activity of the animal during the hoof treatment, and for months made it run for half an hour daily over the coarse stones of its paddock. Thus by suitable contact with the animal's space-time system the desired adjustment of the hoof is often attained and abnormal growth avoided.

Though not to such an extent, the same problem may often occur with birds. A. Reventlow (1941) even had to have the overgrown claws of humming birds cut, and as a result of capturing them lost several through heart failure. The effect of the ground on these birds that scarcely ever alight upon it is naturally not felt. It is difficult to imagine what causes the continual wearing away of the humming bird's claws in freedom.

Other hard structures may undergo definite abrasion by the natural floor e.g. the eye teeth of the maned wolf (Chrysocyon jubatus). H. Krieg (1940a) has confirmed that in freedom this long legged wild dog often digs comb-rats (Ctenomys), squirrels and snails out of their holes, not with its long legs but with its teeth. In this way its eye teeth become worn right down; a long series of skulls confirms this. In captivity, however, through lack of these efforts at digging for food, excessive growth of the eye teeth may arise, as O. Antonius (1941) observed in his maned wolf, in which the long eye teeth were just as prominent as a barking deer's when its jaws were closed.
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Constant contact with the level floor among animals that live on the ground has further significance in captivity. Here we must again refer to the secondary effects of space confinement in conditions of captivity noted on p. 31. If a space with a level surface, one thousand times smaller than the size of its territory, is provided for an animal in captivity, this will mean a thousandfold increase in the danger of infection and re-infection; for the infectious matter falling into the enclosure shows a concentration increased a thousand times compared with life in freedom (Figure 23).

Infection by parasitic nematodes, which play such an important part among wild animals, is chiefly considered here. In freedom the chances of the moose, for example, again coming into close contact with its parasite laden excrement and being re-infected are very slight. In captivity, on the other hand, the likelihood is extremely great. Infectious matter is highly attenuated in freedom, highly concentrated in captivity.

This important secondary effect of captivity mentioned may be illustrated by a concrete example observed by A. Baumgartner (1937), and should be considered a classic example of it. For a long time Baumgartner attended breeding ibex at Interlaken-Harder as a veterinary surgeon, and in his work on intestinal strongylosis in ruminants he described the fate of the male ibex 'Max' suffering from severe strongylosis. At the end of May 1922 it was reduced to a skeleton and so anaemic and weak that it could hardly stand up on its legs. It had been brought up on the bottle and so was tame. In this sorry state it was taken up the Harder (about 4,000 ft) and let loose near the hotel there, in the hope that death would soon bring a happy release. But that is not what happened. The ibex visibly recovered, hung about round the hotel, and became the pet of the hotel keepers and the guests. At times it would come on to the hotel terrace, walk about the balcony, jump on tables, allow itself to be fed, drink glasses of beer and amuse the guests. In the late autumn, shortly before the beginning of the rutting season, it returned to the
enclosure of its own free will, presumably under the mating urge, and demanded to be let in. Next spring it fell ill again and repeated its cure on the Harder, and so on for a third summer. The change of place, with the removal from the source of infection, doubtless cured the ibex.

It would be hard to imagine a more clear-cut instance of the effect of different concentrations of infectious matter in freedom and captivity than this vivid account of Baumgartner's. The more natural the floor, the greater the danger of infection or re-infection in captivity, apart from relative size of space. Worst of all, often enough, is natural floor rich in humus. Again we see from this the danger of a false conception of 'naturalness' in conditions of captivity. Natural floor is often very difficult to keep clean and is therefore unsuitable. The right floor for the ibex is a hard surface, as free as possible from cracks in which dangerous parasites can develop. Baumgartner successfully used limestone flags, the cracks between being filled with cement.

Soft ground is known to be extremely dangerous for deer, moose and antelopes. Thorough disinfection of 'sick' soft ground by chemical means is still not possible even nowadays as M. M. Zawadowsky stated in 1930 (p 48). Fresh experiments in this connection are at present being made. As the eggs of parasitic worms are extremely resistant to chemical means, the application of a physical remedy is sometimes to be recommended, for instance, extreme heat from a flame-thrower. Of course, this method kills off all the vegetation as well as the parasites. Periodic changes of place, which are so desirable, are not possible to arrange in zoological gardens. In practice a floor is easier to clean the harder and freer from cracks it is. Thus the hardness of the material should be as much as the hoofs of the animal concerned can stand. Ideally, any droppings from parasitized animals should be scrupulously removed at once, though in practice this is not usually possible through lack of the necessary staff. The author has recently shown (1942a) how difficult the rearing of a young moose (Alces alces) with parasitized parents becomes on 'natural' ground, and how quickly infection by the dangerous nematodes follows. After two and a half months, and in spite of all precautions, eggs of all three parasites that had attacked the parents were discovered in the droppings of the young moose.

The following is worth quoting as psychologically characteristic of typical ground animals. Just as animals that live above the ground may have a real need of free space below them, certain ground animals must always feel solid earth beneath them. They find ground that sinks or shakes uncomfortable; elephants in particular are notorious for their sensitivity to this. True ground animals have their whole organization adjusted to a two dimensional existence in contrast to animals that live, so to speak, in space, and they cannot really understand the
third dimension. From extensive observations on freedom F. F. Darling (1937) 194 established that the space above the red deer lies completely outside its field of perception. M. Kakies (1936) 20 found the same to be true of the moose. It is strange, but it is a fact: the moose cannot look up very easily. Kakies says that it may even happen that he will walk beneath you unsuspectingly, although you are crouching on a branch without any cover just above him. R. Sommer (1925) 128 discovered a similar state of affairs in the horse, a domesticated representative of the inhabitants of plains. The horse’s perception of the space above it, according to Sommer, is primarily little developed if at all. Optical perception in the horse is only directed to the front, to the sides and to the back; the horizontally slitted oval pupils seem to be closely connected with this peculiarity and take in nearly the whole horizon at once.

This two dimensional adjustment may be characteristic for true ground birds. O. Heinroth (1938) 152 says of the partridge that those brought up as chicks and consequently quite tame may be trained to come up when they hear the tapping of fingers, a sound which more or less corresponds to the pecking of the adults to attract their chicks. After a time they will fly up to a window sill when it is rapped, provided it is obviously part of the wall below. They take this wall to be more or less an upward extension of the floor and use their wings to make their way up it. If, on the other hand, a table is rapped they run about under the place where the knocking comes from, and never learn to try intentionally on to a table top, even when they have often walked on it beforehand. If it is desired to prevent these determined birds from following through an open door into the next room, all that is necessary is to put wire netting across the door to a height of about sixteen inches; they will keep on running to and fro in front of this transparent barrier without attempting to fly over it, which of course they could do quite easily.

Life in the ground—Animals that live underground are difficult to keep in zoological gardens so that the public can see them, and at the same time so that their need for burrowing can be satisfied. Often an unsatisfactory compromise between the demands of the public and the needs of the animal results, the animal usually getting the worst of it. This compromise is unbiological. For the armadillo investigated by Holzapfel (p 88), we have already shown that keeping an exclusively burrowing animal on a smooth hard surface can lead to a chronic state of tension. A similar problem occurs with underground representatives of all classes of vertebrates, from fish to mammals; for instance, eels or plaice, horned frogs (Ceratophrys), sand snakes (Eryx), kingfishers and aardvarks. Pelobates fuscus is a good example of an intimate connection between organism and ground. This common spadefoot toad digs itself in quickly and safely, provided the ground is suitable.
By day it keeps to the hole it has dug, leaving it in the evening; in the morning it burrows at the spot where daylight overtakes it. For this it needs dry, or slightly damp, sandy ground. The close connection between type of ground and behaviour may be shown by experiment. If several containers are filled with different sorts of earth (mud, clay, garden soil, pebbles, sand), the toads choose the sand for preference and bury themselves in it deeper than in anything else. Eighty nine experiments out of a hundred had this result (G. Hinsche (1941) 26). Hinsche considers this burying in a suitable type of ground a reaction of vital importance. We must distinguish between species that live permanently or temporarily underground. In many e.g. the fox, only the home is subterranean, while other animals like the mole hardly ever come to the surface. Suitable biological treatment is more difficult the more the animal is confined to life underground. Small species such as the mole can be exhibited underground, at least partially, through glass. With larger types it is far more difficult, although here there is plenty of room for experiment.

Glass, as a barrier for the larger burrowing animals, should not be used too freely as its imperviousness to air can have a bad effect on the atmospheric conditions. B. Schaeffenberg (1939) 107) showed clearly for the mole (Talpa europaea) that up till now its usually short life in captivity is due to lack of oxygen through keeping it in wooden cases. Moles were kept alive for months in underground wire cages. Many subterranean mammals show a marked need for a damp atmosphere. On this point I. Krumbiegel (1938) 9), in his observations on the weasel, says that animals that live underground or buried for a considerable time breathe considerably moister air than they can be provided with in captivity. The increased dryness of the mucous membranes thus leads to a greater need for drinking in captivity. This is very obvious in hamsters and various species of mice. Of course, this increased need for drinking is absent in species adapted for desert life. F. Werner (1939) 174) kept an Egyptian sand snake (Eryx jaculus) which never drank a drop of water for six years.

It is obvious that still greater use could be made of glass to display animals that live below the surface. Consideration for the public, however, should never be allowed to jeopardize the well being of the animal. Often it is enough to have a special part of their enclosure for the burrowing animals to dig in. With larger animals (fox, marmot, aardvark) a grating is better than impervious material such as cement for the barrier below ground and on the sides to which the public do not have access.
Exogenous Factors: Biological Environment

Vegetation

Plants often play an important part in the qualitative details of the animal's surroundings, and may have various kinds of significance for the animal. Aquatic plants not only serve as oxygenators for fish in an aquarium, but are important in their world for laying spawn on, as nesting material (e.g. stickleback), for cover, and often, for food too. Among amfibias and snakes which are exclusively predatory, the food significance does not apply; on the other hand plants can be of importance for these animals (e.g. tree frogs, tree snakes) as perches, for climbing, and as dwelling material. Birds often use plants too as a perch or as protection from the sun. For captive animals vegetable matter may have many other kinds of significance. As an illustration of this many-sidedness a dozen examples may be given:

1. Food—leaves, fallen leaves, seed, bark, roots, stems
2. Support—opportunity for climbing, home, living space, sleeping and nesting place
3. Means of sharpening and abrasion—for incisors, tusks, beaks, claws
4. Rubbing posts—for bison, ibex, elephant
5. Secreting places—for marten, deer, chamois etc
6. Substitutes for partners in mock fights—stags etc
7. Playthings—for cormorant, sea-lion, monkey, elephant
8. Tools—fly whisk for apes or elephant
9. Building material—for nesting of fishes, alligators, birds, mammals
10. Cleanser—for stags to remove the velvet from their antlers
11. Cover
12. Camouflage—masked crab, the coating of algae in snapping turtles.

This short summary, which might easily be doubled, should show that proper attention ought to be paid to plant material in the formation of the environment, especially as it often has a significance for the animal.
of which man is unaware. Vegetable matter may not only be of great
importance for herbivores but for carnivores as well. Planting shrubs
in animals' enclosures is not done just for decoration.

The importance of plants as food is not under discussion here, only
their importance as a qualitative space-factor. Edible plants, which
thrive in the larger enclosures without the help of man, or in spite of
him e.g. poisonous plants, may sometimes be a danger to the animals.
C. Holz (1926/27) reports cases of death through poisoning
among Nubian ibex (Ibex nubiana) in Hagenbeck's Zoo. The exotic
ruminants found a poisonous nightshade plant (Solanum nigrum) growing
among camomile in their enclosure and died through eating it. In the
chamois and ibex enclosures at the Berne Zoo, in which the animals
are not only kept for years but also breed, this poisonous plant was
abundant but left severely alone by the animals. In contrast to African
game brought into contact with a foreign flora, the native species
obviously can tell the poison plants that grow in their own habitat. Two
observations can be made about these different experiences at Stellin-
gen and Berne:

1. The popular conception that an animal only eats what is good for
it is false—otherwise there would be no cases of poisoning
among animals.

2. It would be interesting, from the point of view of animal psy-
chology, to go more thoroughly into the basis on which the
herbivorous animal's knowledge of plants rests, whether on in-
herited knowledge of the species or on individual experience,
handed down by tradition from one generation to the next. A
good opportunity for investigating this problem exists in zoo-
logical gardens, and has not yet been sufficiently pursued.

It often happens in Africa that cattle are poisoned in the veldt
through eating poisonous plants. In fact, severe losses are caused
by this every year in tropical and subtropical districts, as R.
Östertag and G. Kulekampff (1941) report. They point
out that the question arises why farm animals in Africa should eat
poisonous plants when it is well known that in Europe they instinctively
avoid them. Animals in Europe leave such plants as meadow saffron
alone, and horses pick poisonous plants out of the chaff, even when
chopped up, and push them carefully into a corner when they are
feeding. Few poisonous plants are eaten by European animals, and these
perhaps from ignorance, an example being the needles of the yew
(Taxus baccata) which horses eat by mistake when they are tied to one
of these trees. Probably the animals mistake the yew for a fir tree.
Further examples quoted by these authors seem to show that knowl-
dge of poisonous plants is not inborn but gained through personal
experience and upbringing since it is always the freshly introduced
animals that first fall a victim to poisoning from pasture plants, more rarely resident animals and still more rarely their offspring. It also seems possible that animals may become more or less immunized in the course of generations. In any event, the study of the behaviour of wild animals towards poisonous plants is not only of interest for animal psychology but for the biology of zoological gardens, as well as for its economic aspect.

This gives us the opportunity of pointing out a mistake that is still fairly often made when zoological gardens are being planted out, and that is the setting of poisonous species inside and outside the enclosures. Plants such as yew (Taxus baccata) should be rigorously excluded from zoological gardens. A couple of needles of this dangerous plant is known to be enough to cause the death of a horse or pony if eaten by them. Some pheasants, among others, find these plants poisonous too. Even when they are growing outside the enclosures there is always the danger that a few twigs may be broken off by children or even adults and unsuspectingly offered to animals for which they are deadly poison. Wandering ponies or cart horses belonging to tradesmen or brought in during building operations may also snatch the chance to eat some of the lethal yew leaves when nobody is looking.

Not only poisonous plants are eaten by captive animals at times, both in the aquarium, the aviary and the ruminants' enclosures, but also plants which are not generally thought of as food. Among the latter we find trees that have been untouched for years suddenly stripped of their bark. The temptation to do this naturally suggests some sort of physiological change, some suddenly acquired appetite, as a reason for this bad habit. This may be so in many instances, but in others psychological not physiological causes are responsible. In a large red deer enclosure with hundreds of trees, bark peeling was so unpredictable that no connection could be traced between it and food, season of the year or any phase of metabolism such as moult, growth of antlers, pregnancy or lactation. It seems suddenly to occur to one animal to peel the bark off, and often the effect on the others is contagious. On the other hand it may appear as a curious sort of frenzy; the does rear up like female giraffes and tear off strips of bark to a height of nine feet or more. The bark stripping stops just as unpredictably as it began. Often there are serious epidemics of it, at other times it is quite insignificant. I. Krumbeigl (1930) thinks that examples of bark peeling among Cervidae are a playful activity psychically due to boredom. F. Goethe (1939) found similar motives for bark peeling and biting among wild sheep (Ovis musimon) where it was not an instance of specific peculiarity but of an individual acquirement that might spread to whole flocks. He suggests that tree biting should not always be put down to lack of a definite pasture. His observations show that it may develop from a casual occupation, perhaps as a consequence
of an urge to do something, into a permanent habit. This ethological point of view must be taken into consideration, since nowadays much effort is devoted to counteracting damage done by biting from the physiological nutritional aspect, through provision of the pasture plants assumed to be lacking.

In captivity attempts are made to remedy it by protecting the trees. Twisting wire netting round tree trunks has proved not only ugly but far too risky. In the first place the fastenings normally used to keep it in place become loose, fall to the ground and are highly dangerous, being only too easily swallowed by the animals with their food. In the second place pieces of broken, rusty wire that fall off constitute a further danger, easily causing perforation of the stomach. Passing animals can injure themselves on projecting bits of wire, in fact, camels have been seen with their eyes seriously injured by wire netting. In any event wire is unbiological material and is easily broken, even the strongest sort, by horns, antlers etc. Painting the tree trunks might conceivably be effective to prevent injury by the animals, but the author has yet to find the right preparation and doubts if one could be made that would stop a bison, for example, from rubbing a tree with its horns. For this reason, in Basle, stout curved boards are used enclosing the trunk, reinforced by strong galvanized iron bands of adequate width to protect the trees in the enclosures. No foreign bodies can fall from this wooden material and often in play or in mock fights male stags, goats, sheep, antelopes, wild cattle, bison etc like to rub against them. This provides the animals with the occupation and exercise necessary. Boards that get worn can be taken out separately. With large animals it is necessary to fix the two strong iron bands to a firm iron stake, cemented inside the wooden palings.

Defective wire netting is one of the worst sources of foreign bodies. These can be trampled into the animals' feet, or be swallowed and sometimes cause perforation of the stomach. We emphasize this danger most strongly. It must be made a rule for all workmen doing jobs in the gardens that their work is not over until they have made certain, after a careful search, that they have not left behind any pieces of wire, nails, hooks, scraps of tin, steel wool etc. In Basle a special poster is used to drive this home to all workmen in the gardens. It is displayed in all the service quarters and shows a full sized X-ray photograph of a camel's stomach in which all sorts of metal scraps caused fatal perforations. Birds often fall victims to dangerous bits of metal, too. In Basle a cormorant's intestines were pierced by a large nail it had swallowed. A marabou had several pieces of rusty wire netting sticking into the wall of its stomach preventing the bird from walking. In this case the zoo veterinary surgeon, Dr E. M. Lang, managed to remove them. The number of injuries from foreign bodies has dropped
almost to zero since the regular campaign against leaving nails or pieces of wire netting around was initiated.

In certain instances tree-biting is due to some psychical origin, such as lack of occupation, or hypertrophy of the valency of the bark of the tree. The question thus arises, whether it is time to experiment with psychically effective counter-measures in the form of simple training exercises for amusement and occupation. Lack of occupation always seems one of the most significant secondary phenomena of captivity (p 158), and must again be stressed. It can only be remedied by providing suitable occupation in the shape of occupational therapy. Naturally individual training of each animal, as in circuses, is impossible with deer and wild sheep in large enclosures, but group exercises along field boundaries and the like are possible. Particular animals may still prove responsive to intensive individual training.

Tree trunks are an important means of keeping the skins of many large animals clean by rubbing, and are often in great demand. M. S. GARRISON (1938) 34-36) mentions an American bison (Bison americanus) that went from the treeless prairie to the tree-clad banks of a stream to rub itself. When the first telegraph lines were taken across the North American continent the wooden posts offered grand opportunities for rubbing. They were so freely used by the bison that the wires were brought down for miles. Isolated boulders scattered over the prairie were also used as rubbing posts, and in the course of time they were worn as smooth as glass by the bison. The bison polishing here is similar to the prehistoric bear polishing. Rubbing not only produces feelings of pleasure, but also has a beneficial effect on the hair and the skin condition, similar to the curry combing and brushing of domestic animals.

The claws, a specialized skin structure, are not only regularly worn away by wild animals as they continue to grow, but are often sharpened too. F. W. CHAMPION (1934) 22) does not call it sharpening, but claw cleaning in the tiger, after it has killed its prey. He has a photograph of a tree showing deep claw marks of the tiger made with its forepaws as it stood on its hind legs. It is possible that this placing of marks may also have the significance of demarcation of territory, similar to the scratching of certain trees by North American bears described by J. VON UEXKÜLL and G. KRISZAT (1934) 72). The so-called claw sharpening of large cats on tree trunks has not been properly explained yet. It nearly always occurs during stretching, when certain muscles have been extended and relaxed. Clawing is therefore more likely to be the result of stretching and contraction than of intentional sharpening. O. ANTONIUS (1931) 333) gives an illustration of a tigress sharpening her claws and lying lengthwise on a horizontal tree trunk.

According to E. H. PEACOCK (1933) 85), Indian elephants have the habit of sharpening their tusks on trees, especially teak trees. They
show an intense dislike of having blunt tusks, and in a few days they sharpen them up again. In captivity, where the elephants have no trees to sharpen them on, the tusks often grow to grotesque lengths and shapes never seen in freedom. L. Heck (1930) found tree sharpening among rhinoceros. He says that one can easily tell by the horns whether the animal has been living in the forest or in a rocky district. Since they are in the habit of sharpening their horns, those of the forest rhinoceros assume very long, thin and dangerously projecting points, whereas the others horns become blunt and short through being sharpened on stones. Most captive rhinoceros have no proper opportunities for keeping their horns sharp. Of course, they can rub their horns against the communicating doors between the inner and the outer cages, and this usually results in a stereotyped movement so that little is left of their horns. By special measures, such as providing the door with suitable woodwork, removal of the stereotyped movements by psychical remedies etc. it might be possible for the captive rhinoceros to keep his trophies intact.

Many Cervidae (deer species) are in the habit of using certain branches for rubbing off the velvet, which sometimes hangs over their faces and gets in the way. In enclosures where there is a lack of undergrowth, special material should be fitted up for them in a stall at this season. Once the branches are provided they are immediately used by the animals for this purpose.

With birds care must be taken to see that the diameter of their perches or branches corresponds more or less to the size of their feet. Many birds prefer either rigid or springy perches. In New Britain the author watched a flock of cockatoos (Cacatoes galerita ophthalmica) for several weeks. They kept visiting a few bare branches of a certain tree in the forest, swinging themselves up and down on them for hours on end. Chamois often need branches on which to put the secretions of their antorbital glands during the rutting season. They have special branches put into their enclosure during this period. Elephants sometimes use twigs to drive off troublesome flies, and this has also been observed in freedom.

We shall add to these remarks the reminder that the surroundings of animals living in captivity often consist of non-biological material, such as smooth stones and metal, walls, wire netting, railings, iron bars, iron doors and the like. Vegetable matter in a variety of forms is often completely lacking. This lack can often be noticed in all sorts of ways. On the other hand a few branches, or a tree stump, can do a surprising amount to increase the animals' well being. A pine marten cannot be expected to sprinkle the netting provided with its anal secretion, nor a stag to clean its antlers on an angle iron. The fittings must have a definite biological character in order to release the proper reactions in the animal.
EXOGENOUS FACTORS: BIOLOGICAL ENVIRONMENT

Fauna

Kindred animals—Up till now the animal has been discussed chiefly as a single individual. Thanks to man, the individual in captivity usually lives in contact with one or more animals of the same or other species. So far the fauna among which the individual finds itself has been considered as one of the exogenously conditioned factors of the space-quality. The single individual is often merely an abstract concept. W. KOEHLER (1931) is quite right when he says that a chimpanzee, for example, kept on its own in captivity is not a chimpanzee at all. Very few creatures live truly solitary lives, and then only during certain phases of their life. Many need the company of their fellows or some substitute for it. Satisfaction of the need for society may be vital in certain circumstances. Solitary confinement is unbiological, although in a few species, such as the thunder fish (Malapterurus electricus), it is unavoidable, though we do not yet know enough about this animal's biology. Recently, H. HECK (1941) succeeded for the first time in making the piraya (Serrasalmus), which up till then could only be kept singly, swim in a shoal in the aquarium, under special precautions. It is of fundamental importance for every species of animal in captivity to be kept in a natural family group or in larger social groups.

Even pachyderms may, as C. G. SCHILLINGS (1920) says, 'have an urgent need for social life', though this is somewhat difficult for human beings to credit. He has noticed a strong social need in the rhinoceros and attributes many fatalities among newly imported wild animals to isolation. To counteract this he has got valuable young animals accustomed to living with goats, these dissimilar animals soon becoming remarkably dependent on each other, inseparable in fact. L. HECK (1930) mentions a newly captured young rhinoceros that became attached to a young white bearded gnu, and later could only be separated from it with difficulty. Of course it is difficult, even impossible, to point to this isolation from companionship as the direct cause of an animal's death; but from all that we know today about the importance of the social factor in keeping wild animals, Schillings' assertion does not seem at all improbable. It has, at any rate, been demonstrated experimentally that intake of food may be influenced strongly by the social factor, for in the wild animal intake of food is a clear indication of his relative state of health. We shall return later, in the section on food, to the social factor briefly touched on here.

The sociable wild animal in captivity has a natural claim to enough company of his own kin, since the same social laws hold good in captivity as in freedom. This is not the place to embark upon a sociology of wild animals. We can only give a summary of the relevant facts, as was the case in an earlier paper (H. HEDIGER 1941). In the chapter on social rank (p 23) it was pointed out that in most species each
individual fits into the social hierarchy of its kind in obedience to definite laws, and also has to behave according to its social position. In addition it was shown that scarcity of space, or excessive density of population, in freedom often increases social encounters until pronounced anti-social behaviour develops. The question now arises whether social structure and ceremonial can be changed, or even perhaps destroyed by captivity. We know for certain that it will not be destroyed, for exhaustive experiments have now been made on social behaviour in captive wild animals, as well as domesticated ones. The question of changes, however, in social behaviour as a result of captivity still remains unsolved.

From observations on baboons (*Papio hamadryas*) in freedom and captivity, S. ZUCKERMAN (1932) comes to the conclusion that the social behaviour of the captive animal is identical with that of the free one. Even if the character of social behaviour is not changed by captivity, various conditions of captivity may yet influence its intensity. Here, some of the secondary effects of captivity listed on p. 31 may come into play. Apart from increase of sexuality (hypersexuality) Zuckerman considers increase of socially conditioned fighting possible. In the comparatively crowded surroundings of captivity social rivals cannot get as far away from one another as in freedom. Thus after a fight the victor still has his defeated partner in his field of view, so to speak, and the defeated one cannot lose sight of the females belonging to his victorious rival. This state of affairs, together with the hypertrophy of valences generally at work in captivity, sometimes leads to the conflict never being settled as long as two or more rivals live together. In freedom the animals separate and can thus avoid a final solution of the conflict, but the only real solution in captivity is the death of the rival. For this reason social encounters in captivity, not only among baboons, are often far more intensive than in freedom. Animals which in social encounters are apt to be dangerous therefore require special attention to see that they are grouped harmoniously. This provides a new, perhaps unexpected, basis for revising our opinions, for example, about monkey terraces (monkey paradises) as well as about confined cages which are often so small as to cause overcrowding. Again we see how wrong it may be to gauge the well being of captive animals just from the size of the space available for them. O. ANTONIUS (1933) rightly says that real suitability to the vital needs of the inmate is far more important than the absolute size of a cage.

Among these literal necessities of life is the social harmony of the group, for example, the baboons; if this is not achieved there is a fight to the death between rivals. S. ZUCKERMAN (1932) gives concrete examples of serious losses among socially conditioned fights of this kind. In a large colony of captive hamadryad baboons there were
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many deaths not only among fighting male rivals, but even more among
the females. The fighting was partly about females and partly about social
rank. Of thirty three females that died during the period under obser­
vation thirty lost their lives in fights, only three through illness. The
chief conclusion to be drawn from such facts is that it is often more
suitable, and even more correct biologically, to keep species that fight
under powerful social stimuli in smaller harmonious groups rather
than together in over large numbers. This not only applies to
monkeys, but to many ungulates, predators, rodents, birds, and cold­
blooded animals (e.g. fish) as well. Of course it is often possible,
through careful attention to the proportions of the sexes i.e. plenty
of females, to keep together successfully quite large companies that
harmonize well. This is proved, for instance, by the baboon terraces
of H. Heck in Munich–Hellabrunn.

Statements similar to those of Zuckerman about baboons have been
made about wolves by R. SCHENKEL (1947) in the Basle Zoo. The
following conclusions may be drawn from these facts. In captivity
social encounters are intensified, first, because the animals cannot
avoid each other sufficiently (confinement of space), secondly, because
extra attention paid to the single individual through lack of diver­
sions (hypertrophy of valencies), and thirdly, because sexual behaviour,
closely connected with social behaviour, is very often intensified
(hypersexuality). In the wolf, the behaviour of the socially inferior
individuals is supervised by their superiors down to the smallest details
of change of position, carriage of body, and even of ears and tail.
Any neglect to perform the due social ceremonial for particular social
positions results in menaces, sharp punishment, and even fighting.

Generally speaking, the relative rank of the individual in the social
scale is of decisive importance for the whole conduct of life, as well as
for freedom of movement, choice of resting place, of places for excre­
tion and urination, for feeding etc. For example, the inferior of two
ibex kept together was not allowed inside the shed: it had to stay out
in all weathers while the superior ibex monopolized the shed. In
addition the inferior ibex was not allowed near the food. The only
remedy was to put the inferior animal into the small adjacent enclosure
at feeding time. In every zoo such facts are familiar.

If one of these socially low ranking animals (ω-animals) is tyrannized
by all the others to an exaggerated degree through confined space
under conditions of captivity, it will be left literally with neither
room nor food. Before succumbing it will perhaps try to resist this
unbearable state of affairs and perish from weakness in the ensuing
battle. This fate is all the more likely the greater the confinement
of the space available and the more intensive the resulting social
contacts. In practice this sad state of affairs only occurs in unsuitable
transport cases.
No animal in captivity ought to be exposed to such a fate through excessive social inferiority, and the destruction that inevitably follows. Here we have without doubt the most serious secondary effect of space confinement under captive conditions i.e. anti-social behaviour. Tyrannizing to the point of death is exceptional. In any social hierarchy it is obvious that one individual is bound to occupy the lowest grade; often, however, this situation is quite bearable, and does not exclude certain positive values, even advantages. Besides, the social $\omega$-position sometimes has more than one significance; in the following linear order of rank it has only one.

\[
\begin{align*}
O & \rightarrow O \rightarrow O \rightarrow \ldots \rightarrow O \\
\alpha & \rightarrow \beta \rightarrow \gamma \rightarrow \omega
\end{align*}
\]

Often the social rank is not linear, but may take the form of triangular, quadrilateral, or even more complicated figures, so that, for example, individual $W$ is superior to individual $X$, $X$ to $Y$ and $Y$ to $Z$, but $Z$ again to $X$.

The $\omega$-place may be shared, as it were, among several individuals (W. C. ALLEE (1938) 178).

It frequently happens, too, that $\omega$-animals show special skill in getting all they need, in spite of their social inferiority, and are often very resourceful. A group of three female ibex was fed from a manger with two compartments. The $\omega$-animal was chased off both sides and could only get at the food when the others had already eaten their fill. Eventually it found a solution: it jumped over the feeding animals into the manger and was able to eat its fill in peace and quiet. These original tactics never brought it into conflict with the other animals. It is often noticed how intimately $\omega$-animals get to know their keepers, thus getting various advantages. The author has seen this happen with the most widely differing ungulates (bison, ibex, red deer etc) and predators (tigers, lions, bears etc). We shall return to it in the chapter on the animal-man relationship.

The greatest attention should always be paid to social harmony as part of the eph-harmony (in Hesse’s sense) in captive animals. The social structure of the group therefore demands constant attention. It is usually impossible to avoid social fights, certainly when strange animals are introduced into a group. Besides, to do so would be quite unbiological, for the social animal needs a clear decision about its social position. It is quite possible, and much to be recommended, to try and reduce the excessive violence of the first encounter, though
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the result of such interference is often doubtful. The more drastically
they have been fought out, the more permanent social decisions are
likely to be. After fighting, social rank is often more permanently
decided than by a sham encounter; it may even be conclusive. The
vast number of experiments upon the hen, the classical subject for
social psychological investigations, have shown that resistance to the
existing social order is far more frequent when this order arises from
encounters alone than from fighting (D. Katz (1937) 222). Even if it
is not possible to avoid serious social fights during the formation of
social groups, occasional excessive tyrannization over an α-animal
should nevertheless be avoided by isolating the individual that has been
too much set upon. Indeed, this is the only time when isolation can be
defended biologically.

In a survey of social structures we must realize that servile behav­
ior is the result of despotism. Normally, serious encounters only
occur during the formation of fresh groups, when strange individuals
are put together, or when young animals belonging to an existing
group reach the age at which they make claims to a definite social
position, although they have not yet been accepted into the hierarchy.
When the inferior individuals give way to the superiors in a manner
suitable to their position, the social harmony is assured. Sharp reproof
only takes place when the ceremonial is transgressed. At all events
the socially superior individuals are not always tyrants in the bad sense,
but often highly tolerant. Generally, it is the rule that an animal is more
tolerant the higher he stands in the social hierarchy, and more brutal
the lower he stands i.e. the fewer the individuals over which he can
tyramnize (D. Katz (1937) 222). Finally, it is characteristic of many
α-animals, whether fish, hens or lions, that they will not tolerate
serious encounters, but separate opposing partners. This intervention
between fighting members of the society by the α-animal has been
called, mistakenly, peace-making. Far more likely it is a case of the
α-animal not wanting to be disturbed by such scraps in his vicinity.
The animal trainer, too, as the α-individual of his group, often has the
difficult task of recognizing fights between his animals as early as pos­sible and of suppressing them in good time by suitable handling. This
must be before the hostile animals have got their claws into each other
and no longer react to the strongest measures to separate them.

It also happens, in captivity as well as in freedom, that two or more
social systems can exist side by side in one enclosure, independently
and without friction, when two or more different species are kept
together. G. Kramer ((1937) 781) observed this in a company of
lizards of two different species. The social system of Lacerta melisel­
elens functioned quite independently from that of Lacerta sicula in the
same cage. During lively encounters within one species, members of
the other species remained completely unmolested. True, such a clear-
cut separation between the social behaviour of different species is not always found. It often happens that animals of different species are ranked according to the social system of one species and included in it; here it is not always easy to differentiate between social and biological rank. The following examples of triangular rank, quoted by D. Katz (1935, 224), are well known:

Duck and Goose —> Hen

Crane and Pelican —> Flamingo

The fact that creatures of different species may be included in the social hierarchy of one species, and treated as kindred, is of the greatest importance for the animal-man relationship. Man, too, may sometimes be treated by animals as kin, and be included in its social system. We shall revert to this in the chapter on the animal-man relationship.

**Causes of incompatibility** — It has already been stressed that man must ensure the necessary harmony of each group of animals living in captivity. This does not mean that he should interfere in every vigorous encounter; that would be senseless and unbiological. He should, however, prevent as far as possible anti-social excesses, not found in nature, from arising under the influence of space confinement in captivity. From the beginning we have underlined the fact that, for material reasons alone, losses through incompatibility should be avoided. Such losses are only deliberate during animal fights staged on purpose and which are thus unbiological. The reasons for so-called incompatibility may be very varied. It may be of value to give some of the principal causes, distinguishing two groups of incompatibility:

1. **Interspecific incompatibility** i.e. incompatibility between animals of different species
   a. Predator-Prey relationship
   b. 'Cat-and-Dog' relationship
   c. 'Singing-bird, bird of prey' relationship or mobbing
   d. Biological rank
   e. Differences between distance-types and contact-types
   f. Differences of appearance (expression, display)
   g. Differences of activity

2. **Intraspecific incompatibility** i.e. incompatibility between animals of the same species
   a. Social rank
   b. Territorial disputes
   c. Individual antipathy
   d. Sexual hyperactivity.
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From this incomplete list emerges the simple fact that representatives of different species may have more reasons for incompatibility for each other than animals of the same species. In other words, less incompatibility will be found within species than in relations between species. It will be obvious that many of the popular motives for quarrels among animals are not included here e.g. jealousy over food. Turning others away from the feeding place or chasing them away from food is usually a result of biological or social rank. Examples of true biological rank only occur in freedom with its natural overlapping of range and biotope. In captivity, on the other hand, there are only artificial biological ranks due to species that never come into contact in freedom living together under human arrangements. The decision about biological rank, as about social rank, need not be made by fighting. It may even be the rule of biological rank that decisions are reached on the basis of mock encounters, not fights, and are thus to some extent fought with psychological weapons. The author once kept a reindeer and a roe deer together in an enclosure. In every respect the reindeer was superior to the roe deer, even at the feeding place; but fighting has never been observed in these mixed companies of deer. From the start the roe deer, a newcomer, showed fear of the much larger, though quite harmless, reindeer; the latter was treated straight away as a person of respect. In another example a Chinese gander was superior to a roebuck.

We shall spend no time over the predator-prey relationship, which normally ends with consumption of the prey by the predator. There are, by the way, abnormal cases like those in which the predator and its potential prey are mutually bound by a companion relationship in Lorenz's sense (1935), when the predator-prey relationship is suspended. The best known example of this sort of relationship is the lion and its dog foster-mother. This state of affairs is so unusual that the zoo public often mistake the dog for the lion's food. It occasionally happens that a predator, for no known reason, spares its prey, when no companion relationship exists, gradually entering into a companion relationship with it. Thus in the Basle Zoo, for instance, as A. Wendt-Nagel observed, a stoat and a brown rat became companions; other rats were eaten in the normal way by the stoat. In a vipers' terrarium, a house mouse lived for months and, for some unknown reason, was never eaten by the snakes which otherwise fed normally. In the end the mouse was bitten by a young viper and immediately devoured by an adult viper.

The relationship between cat and dog is not yet clear. The popular idea that the two domestic animals are sworn enemies has not yet been properly analysed, nor is it certain whether similar relations exist between wild animals. Various indications show that it is not necessarily a question of long standing and proverbial inborn enmity,
especially as puppies and kittens can be very easily trained to live their whole lives together. It is possible that some species inherit an antipathy, similar to antipathies among individuals, but at the moment it is not proved. Many things seem to indicate it. Recently, R. MENZEL (1948) has made some interesting new investigations into the dog and cat relationship. A slow loris (Nycticebus) could not get used to a guinea-pig, but immediately reacted with the defensive, threatening stilt-posture. On the other hand, loris and galago could be put intimately together at once (Figure 24b). These two otherwise very dissimilar prosimians (half-monkeys) are, however, both extreme contact-animals.

The motive for the so-called 'mobbing' in birds is not clear (H. TOENHARDT (1935)). Biological rank may give rise to quarrelsomeness as has already been shown. In captivity, however, this is scarcely likely to cause difficulties if enough attention is paid to the inferiority of the species concerned, making sure that they have access to food and their own sleeping quarters etc.

Two extreme types of behaviour may be distinguished in all classes of vertebrates, namely, contact and distance types. Thus, for example, there are types in which individuals not only tolerate close physical contact with their fellows during rest, if this happens more or less by chance, but even deliberately seek such contact (wild boar, many primates, rodents, parrots, titmice, weaver-birds, cat-fish etc). These contact animals have no individual distance (H. HEDIGER (1941) 43). An individual distance exists in animals of the distance type (many ruminants, flamingoes, doves, sea-gulls, laughing gulls, starlings, swallow, pike etc). The representatives of these species only allow others to approach up to their individual distance (Figure 24a). They do not tolerate physical contact, apart from reproduction. Occasionally contact at certain definite places on the body is permitted, as for example, roe deer on the forehead and behind the ears, peacocks on the face. This may take place during play or in social contacts such as grooming the skin. Other examples of contact behaviour are illustrated in Figure 25 a, b and Figure 26 a, b.

It is evident that with a mixture of species, which may be very necessary for individuals in order to form a harmonious social group, attention must be paid to the type, contact or distance, to which the various partners belong. The approach of a contact-animal may be disturbing to a distance-animal; it thinks it must defend itself. In this way serious cases of incompatibility may occur. Very often, too, differences of expression may lead to serious misunderstandings. A striking example is quoted by H. WAGNER (1936). For reasons of space he wanted to put a giant red kangaroo and a South American stag of about the same size together for the winter. So long as the kangaroo remained in a crouching position everything was all right. But as soon as he sat
up in his typical manner, the stag would go for him, rearing itself right up on its hindquarters and thrashing the completely inoffensive kangaroo until he squatted down again on his haunches. Every time he sat up the fighting started again. The only possible explanation must be that the attitude and bearing of the attacking stag consists of rearing up on its hindquarters and letting fly with its forefeet. This attitude almost exactly corresponds to the behaviour of a kangaroo: the animals rear up, rest on their long hind legs and tail and hang their forefeet. That was what the stag saw and it felt threatened or attacked. In this case incompatibility simply rested on a misunderstanding of the appearance of an animal of another species.

Finally, differences in the rhythm of activity and rest periods may lead to incompatibility. The sleeping animals do not want to be constantly wakened by those awake, and react accordingly. This must be taken into account, too, in the formation of groups of animals of different species. Incompatibility among animals of the same species is the main reason for social quarrels which soon lead to harmonious agreement after fierce initial fighting. Fighting over infringement of territory is closely connected with these quarrels for social motives. Individuals of high social standing may tolerate infringement more easily than lower ones; on the other hand the occupier of a territory has more favourable chances in a quarrel than the newcomer. Here, too, agreement is conceivable. Lastly, individual antipathies may be among the causes of incompatibility. In this event no agreement will be reached, so that separation of the individuals is indicated if the incompatibility assumes dangerous forms.

Finally, sexual hyperactivity can only be included among the causes of incompatibility with certain reservations. This hyperactivity may lead to the injury, even death, of the partner. Properly speaking this kind of incompatibility is a result of excessive sexual irritation in one partner or the excessive sexual attraction of the other. Dangerous forms of sexual hyperactivity are only found among male animals, and demand special measures; these will be dealt with on p 144.

Animals of different species—Every zoological garden has to put up with unwanted animal visitors and such animals as take up permanent quarters in and around the enclosures. It is impossible to keep dangerous micro-organisms at a distance, and a difficult matter to do likewise for macroscopic creatures; one has only to think of the visits from fox, marten, polecat, stoat, brown rat, house rat, squirrel, house mouse, woodmouse, sparrow-hawk, hawk, crow, blackbird, sparrow, mallard, cockroach, cricket, flies, mosquitoes etc as well as the hosts of ecto- and entoparasites of a macro- or microscopic order of size. No zoo is free from a various assortment of commensals, epizoa and parasites. The damage done by these animals, for the most part undesirable, may be of various kinds:
Figure 26. Contact behaviour between a Golden agouti (*Dasyprocta aguti*) and spotted paca (*Agouti paca*) b African cattle egret (*Bubulcus ibis*) and South American capybara (*Hydrochoerus hydrochoeris*)
Figure 27. Deformed skull of wild gorilla due to pathological causes.

Figure 28. Weasel with tick (Ixodes ricinus) in the ear.
1 Direct damage. Injury to and killing of the captive animals by foxes, marten, rats, hedgehogs, birds of prey etc

2 Indirect damage. This may be caused by:
   a contamination of surroundings and food by pigeons, blackbirds, sparrows etc
   b robbing of food supply by squirrels, rats, mice, jays, crows, ducks etc.
   c disease carriers such as cats, rats, mice, sparrows etc
   d disease breeders, ento-parasites: helminths, protozoa
   e disturbance of the animals by rats mice etc.

The devastation done by rats may be illustrated by the classic example experienced by C. HAGENBECK (1909). He lost two elephants in one night. Rats gnawed away the soles of the feet of the elephants as they stood on a wooden floor and caused large wounds and severe bleeding. Next day, sixty rats were killed in the same house. Hagenbeck also reports that two ostriches were killed by rats. In the vivarium of the Berne Zoological Gardens, which are infested with house rats and brown rats, they even dived into the aquaria, destroying fish and water plants. Insulated cables for the electrical heating of the aquaria were often damaged. Elephants are commonly thought to have an inordinate fear of mice and rats, especially mice, because these rodents can creep up their trunks during sleep. In the course of his exhaustive physiological investigations on the elephant, F. G. BENEDICT (1936) went into this question of the specific fear of mice and rats among elephants. He came to the conclusion that nothing of the sort exists. On the other hand, elephants are known to be very nervous about any strange and unusual noises. A mouse, rustling a piece of paper, can make one get up and trumpet; whereas a mouse sitting on an elephant’s trunk, for instance, causes no reaction. Elephants trample mice and rats to death if they get the chance.

R. KOLLER (1932) gives many examples of rats as carriers of disease. F. SCHMIDT-HOENSDORF (1932) shows a connection between erysipelas in zoo birds and previous epidemics among mice. Mice may also have a share in spreading coccidiosis. B. J. BENCHLEY (1942) has to wage war against invading coyotes, foxes, racoons, and badgers in her zoo at San Diego (California). In the enormous grounds of Whipsnade Zoo a characteristic experience was had in this connection, reported by S. A. NEAVE (1945).

The first step was to erect a high boundary fence. At its top an overhang of barbed wire and wire netting was at first turned inwards to prevent the escape of animals from the Park. However, while no animals escaped, foxes, attracted by the birds in the Park, contrived to scale the fence and did much damage. Since then the overhang has been turned outwards and so far has defeated the foxes.
Parasites—One of the greatest problems of the biology of zoological gardens lies in the impossibility of keeping large animals in a pure culture. For them there is no such thing as sterile treatment. The fight against parasites thus gains prominence in the zoological garden. The number of animals that are sacrificed to parasites yearly is far greater than is usually assumed as G. Grimpe in his remarks on the works of E. Reichenow and G. Wülker suggests (1939).

Hardly a single large animal is to be found free from parasites in nature. When the parasitized animal goes from freedom to captivity, the new conditions are generally unfavourable to the animal, from fish to mammals, but favourable to the parasites. This may lead to a sudden increase in the latter. The change of food and decrease of intake due to disturbance are also unfavourable to the host, and may lead to weakening. It can be imagined that the organism's resistance to parasites is weakened through this. In addition there is the increase in the danger of re-infection, thanks to space-confinement e.g. in worm infections (p 115). All these factors are favourable to the parasites. The medium may also favour the development of parasites on fish (e.g. Saprolegnia).

Helminths have a special place among the parasites in the pathology of wild animals. We learn from an investigation by B. Murker (1939) into the deaths of wild animals (mammals and birds) in Basle Zoological Gardens that Helminthiasis was present in twelve out of 117 cases investigated i.e. in 10 per cent of the cases. Serious parasitization by worms, as is well known, can lead not only to severe digestive disturbances but to general anaemia and occasionally to intestinal obstruction. Even if it is not possible to exterminate parasitic worms completely, their numbers can often be kept below danger level by periodic treatment. This method has been used at Basle. Continuous parasitological supervision is one of the few opportunities for accurate observation the wild animal offers to the pathologist; therefore it should on no account be neglected. Even the many wild animals that have considerable residual flight tendency, and will not allow close observation without great risk or expense, at least provide their excrement for parasitological diagnosis and often take the necessary antidote for helminths in their food without trouble. The greatest possible use should be made of this simple diagnostic means of observation. In the Basle Zoo practically every species has a special record card on which the results of the periodic parasitical examination are entered.

The breeding of elks at Berne in enclosures on 'sick' natural ground was, at the beginning, almost entirely a parasitological problem, as has been recorded (H. Hediger (1943)). Both parents were attacked by parasitic nematodes. After some time, however, their parasitic content was kept within safe limits by periodic treatment. On 23 July 1940 a calf was born for the first time. Rearing it on this unsuitable
Figure 26. Contact behaviour between a Golden agouti (Dasyprocta aguti) and spotted paca (Agouti pacu) b African cattle egret (Bubulcus ibis) and South American capybara (Hydrochoerus hydrochoeris)
Figure 27. Deformed skull of wild gorilla due to pathological causes

Figure 28. Weasel with tick (Ixodes ricinus) in the ear
ground seemed doomed to failure, especially since, at the age of a few days, the calf ate earth and parental excrement in spite of all precautions. Its own excrement was examined each week by a specialist. On 17 September, after less than two months, eggs of the first parasite (Trichuris globulosa) were found in it. On 10 October, after two and a half months, eggs of the second parasite (Capillaria sp.) appeared, and on 16 October, the eggs of a third parasite (Oesophagostomum venulosum) could be identified. At the age of four and a half months the animal died of helminthiasis which, because of the intestinal inflammation and loss of appetite already established, could not be warded off. On 5 June 1941 a second elk calf was born, and kept under even more stringent precautions. It, too, was soon infested by two of its parents’ parasites. In addition, coccidiosis set in. Thanks to early diagnosis by periodic microscopic tests of the excrement, this was cured in time. Both species of nematodes, which later increased, proved extremely resistant. At any rate it was possible this time to prevent the parasite gaining the upper hand, but this was only possible through continual parasitological supervision from the beginning.

Worm infestation in zoos, although serious, is by no means a specific phenomenon of captivity. Parasitic worms are found in animals that live in freedom. In captivity, where conditions for parasites are usually more favourable, as we have indicated, special care must be taken. This leads us unexpectedly into the field of pathology. The first question to arise is a fundamental one—do such things as specific captivity diseases exist? Apart from serious phenomena of domestication which may be called pathological there are very few, if any, specific captivity diseases. Domestication phenomena do not concern wild animals, but only thoroughbred domestic animals. Possibly mouth-rot in snakes, for example, is a case of captivity disease, as it has not been found in nature, according to J. BURTSCHER (1931: 242).

Very few sick wild animals are found in nature if we except the occasional epidemics in game, when the small number of predatory animals cannot cope with the large numbers of sick ones. This is connected with the fact that every weakness, even the beginning of an illness, handicaps the animal so much in the struggle against its ever present enemies that it quickly falls a victim to them. For this reason wild animals rarely recover from serious illnesses. At all events, because sick wild animals are seldom to be observed in nature, we must not assume that they never become ill. The author has the skull of a very large gorilla; a friend of his came across the animal in 1937 on a narrow forest path in the Cameroons and shot it with his revolver. This ape’s skull shows striking irregularity of the eye sockets and lower jaw. According to the investigations of Dr F. KOBY (Basle), the animal must have suffered from infancy from a severe inflammation of
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the lachrymatory sac, probably with malignant tumour. The left eye-tooth is decayed. Through the opening in the pulpa, according to the dental report of Dr R. Bay (Basle), pulpa gangrene set in, with consequent ostitis, nasal fistula etc. This gorilla’s skull (Figure 27) proves that there may also be sick and suffering animals in nature. Here again the popular idea of ‘blessed freedom’ is incorrect.

An example of a chronic condition (cancer) in a free living wild animal, which should be mentioned, is that of an otter (*Lutra lutra*) found in March 1942 by Professor J. Seiler (Zoological Institute of the Federal Technical Institute of Zürich) at his fishing ground near Zürich. As Professor Seiler kindly told me, the otter was lying on a sandbank dying and was examined by Professor Riedmüller (Veterinary Bacteriological Institute of Zürich University). He reported that tumorous growths, from the size of a walnut to that of a child’s fist, with central (medial) softening in various parenchymatous organs and in many lymph nodes, were present. The histological examination of the tumorous growths in the Veterinary-pathological Institute of Zürich University (Director, Professor W. Frei) showed adenocarcinoma. The author considers this properly investigated case of a malignant growth in a wild animal significant because previously it was believed that in nature animals were spared serious illnesses, such as dental caries.

We cannot touch on the broad field of wild animal pathology, especially the pathology of zoological animals, but would mention in passing the comprehensive works of H. Fox (1923) and C. Krause (1939) in which a full bibliography is to be found. Figure 28 shows an example of a parasite attached to a wild animal.

This short section on parasites, which has brought us involuntarily to the theme of the pathology of wild animals, must not be left without a reference to the fundamental necessity for quarantine. This need is always present when freshly captured animals are to be introduced to an established group. It is less so with animals coming from other groups of captive animals e.g. from another zoo, though very often desirable here as well.

There are no animals free from parasites in Nature. When such an animal is taken into captivity, therefore, it is likely, in fact certain, that parasites have been introduced with it. True, all of these are not necessarily new or dangerous ones, but the possibility always exists that such new parasites may be dangerous for the existing stock. Here then is an unnecessary risk, an inexcusable one, easily avoidable by a suitable and simple precaution—quarantine. Every mammal that comes in should be examined for parasitic fauna by at least one analysis of its excrement.

For birds, too, quarantine is advisable. The author knows several instances of erysipelas being introduced by birds that had been purchased and put in straight away among the resident birds, resulting in
serious losses among the healthy stock. Even for fish, quarantine is desirable. In Switzerland the author found that not a single native fish caught with net or rod, or bought at the fishmarket, was free from parasites. The fish that are put into aquaria as food, too, should undergo strict quarantine to avoid the risk of endangering the existing stock.

For mammals, birds and reptiles blood examination is recommended as well, and delicate mammals e.g. anthropoid apes, x-rays and all the resources of medicine, diagnostic and prophylactic, veterinary and ordinary. These measures are all valuable at the beginning of quarantine as long as they can be used without too much danger to the animals. The aim is to find a compromise for each individual example between the medical diagnosis and the amount of handling, medicine etc that the animal can be expected to stand.

From the standpoint of animal psychology quarantine is a negative thing, because it prevents the animal, already exhausted by its journey, from building up its new home and mixing with its fellow species. On the other hand, for the biologist of zoological gardens, quarantine is indispensable, as has been said. It is one of those things, like everything else in the management of wild animals, that can be done more or less biologically. In the time just after capture or during transport much can be done by organization; by aiming at conditions that will count as part of the quarantine. The main thing here is to avoid unnecessary excitement and to keep unavoidable excitement below the danger line.

The animal can be spared a great deal by avoiding a repetition of tying it down and shutting it up at each separate operation, and by doing a number of operations simultaneously, such as skin cleaning, taking a blood sample, x-ray examination, dressing of wounds, and injections.

This is the place to stress the important fact (H. HEDINGER 1938a 1864) that for various reasons the treatment of wild animals often sets far more difficult problems for the veterinary surgeon and his assistants than the treatment of domestic animals. For one thing our knowledge about the diseases of the countless species of wild animals is far less than about the comparatively few kinds of domestic ones. Knowledge about the anatomical and physiological organization, indispensable for any therapeutic measure, is still completely lacking for so many wild animals and this organization can show marked differences between closely related species. For example, a thick layer of fat may seem, to the zoologically untrained veterinary surgeon, a pathological phenomenon, whereas the truth is that a physiological accumulation of fat may be an advantage just before hibernation or some other fasting period.

The possibility of direct comparison with the relatively familiar conditions of domestic animals or of man is often completely absent. This increases the difficulty of every surgical operation and of internal
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medical treatment as well. Often there is no guide as to the correct dose for medicines or drugs, or for diagnosis by pulse and temperature. The difficulties are increased still more by the psychical characteristics of the wild animal. In contrast to the domestic animal, it does not willingly allow every person to approach, and usually preserves a definite flight distance in man’s presence. Thus, unless perfectly tame, it can often only be brought along for examination by the use of brute force, and this causes excitement and a corresponding undesirable increase in the breathing and pulse rate. Even for completely painless minor operations (such as hoof paring for a zebra), anaesthetics must sometimes be used if only to keep the animal quiet so that in its attempts to escape or struggle it may not injure the investigator, the surgeon or itself. Anaesthetics have a much wider field of application with wild animals than with tame animals and yet far fewer experiments have been made on them so far. Recently E. M. LANG (1945), the veterinary surgeon of the Basle Gardens, published the results of his anaesthetic experiments on lions and tigers. We have, by the way, made a cage in Basle for operations on the large cats which, with suitable modifications, would do for other animals. It resembles a travelling cage but the rear wall and roof can be slid inwards with a little levering, and be fixed into any position, so that in a few seconds the animal can be held either ventro-dorsally or sideways against the opposite wall or the floor. The roof and all the walls are double, with iron bars inside and iron plates outside. Each plate as well as every bar can be removed separately so that only that part of the animal which the veterinary surgeon has to deal with need be exposed.

Many of our domestic animals’ diseases are familiar even to the outsider. With wild animals, however, it is sometimes very hard even for experts to recognize, as such, symptoms of disease, especially since newly captured animals are in a state of great tension, do not move about freely, and hide their feelings. Thanks to the wild animals’ special tendency to run away from human beings the distance barrier, which only disappears with tamed wild animals, can only be overcome by force. For this reason even the most elementary diagnostic aids such as auscultation, percussion, taking of temperature and pulse etc are useless. A. E. MOUQUET (1925) mentions that the investigator of wild animals must often be satisfied with diagnosis at a distance. Only in the rarest cases does the animal show by typical audible signs that it is in pain; fever and other symptoms of illness are often very hard to recognize. Inflammation of the lungs, for example, may suddenly kill off animals without any visible signs. Appetite is not a reliable guide to the state of health either. Many healthy animals refuse food through psychical excitement and sick ones often take it until they collapse and die. Lastly, there are animals that sham symptoms e.g. lameness, when there is no injury or sickness to cause it, as often appears when
they dash round perfectly normally in play. The problem of shamming is an attractive one for the comparative psychologist (E. Frauchiger (1945) 193, 236).

These few observations on wild animal diseases and their treatment show that it is essential to collect all the information in this field and make it generally available. It is a pity that lack of coordination still compels every zoo veterinary surgeon to find out so much for himself.
The Problem of Food

The animal does not live on bread alone. W. Fischel (1938) states quite rightly that feeding not only serves to provide material for metabolism, but also affords psychical experiences. Conversely, psychical experiences are of considerable importance in feeding the higher animals. The treatment of the question of food for captive wild animals has, so far, been too one-sided, too physiological and often too anthropomorphic. Accepted methods of feeding domestic animals have also had a hampering effect. Domestic animals have become extreme stenophages i.e. they take specialized food. They may even be monophages, eating one particular kind of food. Thus they are unnatural creatures, the more so the higher their breeding, and for this reason their food cannot be copied for feeding wild animals. This should not be influenced by experience with domesticated animals.

A short time ago a favourite classification of zoo animals was into hay eaters and flesh eaters. What wild animal, however, lives on hay or on cold, bloodless meat. S. Scheidegger and W. Wendnagel (1938) recently showed, in the case of the lion, most popular of all the beasts of prey, that the consequences of feeding it on nothing but blood-drained meat are serious and lead to pseudorachitis. Excess of potassium causes disturbance of the mineral metabolism. Most wild animals are almost unbelievably euryphagous and tend to eat a varied diet. This has already been shown for the howler monkey (p. 21), the red deer and several others. Our ideas about wild animals' food must be changed. We must get rid of many anthropomorphic conceptions, although in the last few years a noticeable improvement has been made in this. Nearly all zoological gardens have to think about economy. However unreasonable or foolhardy it may sound, it must be said, once and for all, that economy in the feeding of wild animals is basically unbiological, for the very simple reason that the wild animal in captivity should be fed on the optimum not on the minimum scale. Economy is only permissible when, for example, there is a cheaper choice between two equally suitable kinds of food. Even here there is one reservation, since periodic change from one of these kinds to the other may be important in itself. In principle the biological, not the economical, point of view should be decisive for feeding a wild animal in captivity.
THE PROBLEM OF FOOD

In most instances only the best is good enough. The best possible food obtainable is often inferior in quality to natural food and essentially below its standard. At best we can only offer the animal a more or less coarse substitute often with far too little variety. If need be the stock of animals, not the food, must be reduced. Methods of feeding animals have still to be put on a biological footing and need adapting to a natural diet. In practice this means first and foremost an increase in quality, a more careful choice of supply, and so an increase in price, and greater variety. We can assume, at any rate, that the increase in necessary items of food will be offset to some extent by reduced loss of animals and greater breeding success.

In the London Zoo the following deaths were caused by disease of the digestive organs (A. E. Hamerton (1937)):

<table>
<thead>
<tr>
<th>Year</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>1936</td>
<td>16.1%</td>
</tr>
<tr>
<td>1937</td>
<td>12.4%</td>
</tr>
<tr>
<td>1938</td>
<td>13.2%</td>
</tr>
<tr>
<td>1939</td>
<td>9.3%</td>
</tr>
</tbody>
</table>

B. Murer ((1939) 65) in his work on the causes of death of animals in the Basle Zoological Gardens already mentioned states that diseases of the digestive organs are usually commonest. The cause of colitis and enteritis can be established beyond question in only a few instances. It is often a question of alimentary intoxication. We see from his comparison of 117 cases that twenty eight i.e. approximately 25 per cent, were cases of enteritis (inflammation of the intestine).

The euryphagy of most wild animals cannot be sufficiently emphasized; far more allowance must be made for it. As for anthropomorphism, so disastrous for diet, let us quote a single example. It is often thought that the most suitable diet for all animals is food rich in nutrient and easily digested, just as it is for man. Such a diet is in fact bad for many species, since their whole organization may depend upon material that is hard to digest, even on completely indigestible ballast; in its extreme form, on stones. This is true for many fish- and grain-eaters among the reptiles, birds and mammals.

Feeding wild animals in captivity is, as has been said, not simply a physiological matter but a psychological one as well, especially with newly captured animals. On p 33 (Figure 8) is a diagram showing how even the most delicious titbits cannot tempt the animal if it is excited through constant flight tendency owing to the presence of man within its flight distance. With untamed animals flight comes before feeding, as explained in detail in the first chapter (p 19).

Feeding freely and satisfactorily in the presence of man is one of the most important proofs that an animal has settled down. Many animals, from fish to mammals, have been known to go on hunger strike in reaction to captivity. W. Wunder ((1927) 69) observed that large numbers of his newly caught pike took food for the first time after three months or even six. Sea-elephants (Macrorhinus) sometimes fasted,
after capture, for a hundred days or so (C. HAGENBECK). Newly caught
reptiles, especially snakes, and birds too, often have to be forcibly fed,
or else they would starve. This refusal to feed, the decisive factor for
self preservation, is psychically conditioned in all these instances.
Moreover, it is a characteristic of even the most stubborn food
refusers that they will drink water comparatively easily. Somehow,
water drinking seems to be undertaken with less ceremony than eating
food, a fact not unfamiliar, by the way, in human psychology. With
sensitive animals the danger of undereating, or rather of eating a diet
below the optimum, is greater than that of overeating, and so suitable
means must be found of increasing the food intake to the required
degree. As far as possible force should be avoided. It only increases
the animal’s excitement as a rule, thus, in the case of freshly caught
animals, destroying their chance of adapting themselves to the new
conditions of life in captivity. The best results are generally obtained
by ensuring as calm a frame of mind as possible, and a restful atmo­
sphere with lack of disturbance and darkness. Sometimes the social
factor makes all the difference.

The Social Factor

A biological fact lies behind the saying that a solitary pig will not grow
fat. It is a common experience, though often forgotten, that the amount
of food eaten by a single individual can be greatly increased when it is
in the company of members of the same species, or of other animals
accepted as such. This is of prime importance in the management of
wild animals, where great attention must be paid to an adequate
amount of food being taken. Its influence i.e. the result of this social
or companionship factor, can be traced through all the vertebrate
kingdom, from fish to mammals.

W. WUNDER ( (1936) 266) quotes an observation of Seiler’s,
according to which carp ate and grew far better when they were kept
together in an aquarium instead of in separate tanks. Wunder adds that
this observation has been confirmed by American writers in many
other species of fish. Fasting snakes can sometimes be induced to feed
by putting them with snakes of their own or different species that feed
well (H. HEDIGER (1941a)), Honigmann (quoted by F. HEMPEL­
MANN (1926) 374-) observed the same thing in tortoises.
The effect of this social factor on food intake has been the subject of
exhaustive experiments on birds, especially hens. D. KATZ ( (1937)
162) quotes Bayer’s experiments, which produced among other things
the following interesting results. A hen suffering from a known degree
of hunger is put in front of a heap of corn and eats until satiated. After
it has stopped pecking a second hungry hen is brought, and this one
starts to feed at once. The behaviour of the first hen depends on
whether it is socially superior to the new hen. If it is and it tries to stop the second hen from pecking, and if that does not succeed begins eating again itself; if not it at once starts to peck again. In either case the satiated first hen can be made to take more food through the presence of a hungry second one. Under the influence of the social factor the food intake may be increased over 60 per cent. The percentage may be increased still further by introducing more than one hungry hen.

These experiments show that isolation, in itself unbiological, may be serious in all those cases of fastidious wild animals, where adequate feeding is important to the keeper. Just in the same way as there is a sort of psychological feeding, there is also psychologically caused undernourishment. Isolation of separate individuals from a social group e.g. chimpanzees, is known to have producedfasting for several days (D. Katz (1937) 200). The author once had difficulty in getting a three months old elk calf to take enough food after isolation. The isolation was necessary for a closer observation of its metabolism. Here the effect of the social factor was perfectly clear by standing near the food trough with the young elk; it was found that the intake of food could be increased to a remarkable extent.

In addition it must be stressed that the feeding of a wild animal is not a physiological matter alone, but is intimately bound up with the social situation. In the examination of the social factor, as shown in the experiments with hens, we should not rely on increase of food intake through the presence of members of the same species; the composition of the social structure of the group thus formed must be taken into account. It may be surprising that such trifles should play so important a part among birds; it is even more so among fish that social rank should be so important in this connection. We only emphasize this here to draw attention to the fact that even among mammals these relations must be very complicated, which is something that is far too often forgotten.

W. Wunder (1936) 266 states that the effect of the social factor is basically different in carp and trout. Carp, as we have said, feed and grow far better in company than singly. What happens with trout is this. Kept with others in a restricted space, it will not rest until it has become master of this space by killing off the other fish. Trout are solitary fish, and show their impulse to be sole masters of their territory in this ruthless fashion, in contrast to the carp that lives in a shoal.

In many animals, especially fish, social order and territory are very closely linked. M. Meyer-Holzapfel (1941) has shown this for the Characin (Hemigrammus caudovittatus), and E. Dieschlag (1941) for pigeons, where this author found what he calls a localized social rank.

According to the experiments of W. Wunder (1927) 69, the pike behaves partly like the hen, partly like the trout. If, for instance, large and small i.e. superior and inferior, pike are introduced together, the superior ones take the food first. When kept singly, on
the other hand, the small fish take food long before the larger ones do. In company the weakest pike must expect to be eaten by the strongest, especially when few are kept together and there is a big difference in size.

Feeding Patterns

The idea still prevalent that the wild animal's food is monotonous is just as wrong as the notion that it takes it casually or mechanically. The animal does not simply eat; it takes its food in a very definite way, usually at a definite time as well. Peculiarities in the way it takes its food must be dealt with specially. H. Börker (1937) has made a careful classification, of great value for the zoological garden biologist, of the animal's search, recognition, grasping, chewing, swallowing etc of food. His analysis is primarily a mechanical one. In the author's opinion, in zoological gardens, however, we ought to distinguish between two extreme types of feeding, with intermediate links. Both of these are, psychologically and in their animal and war relationship, very different. These are continuous and occasional feeders. These two types are found throughout the animal kingdom, from fish to mammals.

The continuous feeder is represented by plankton-eating fish, toads, land tortoises, singing birds both grain- and insect-eaters, rodents, ungulates, Tylopodes (camel species), elephant, sea-lion, brown bear, and monkey. Examples of occasional feeders are predatory fish (pike), snakes, birds of prey, and great cats. Intake of food in continuous feeders is spread over a long time, of the order of hours, eating being interrupted by comparatively short pauses. Intake of food in occasional feeders is condensed into a short space of time, of the order of minutes, and is often interrupted by long intervals. As we might expect, the amount of food swallowed at a time by the latter is proportionately greater than that of the continuous feeder, which takes essentially smaller portions.

Most large predators, the great cats, may have one or even two fast days a week; the lion does not kill an antelope or a zebra every day in nature. The antelope, on the other hand, does not let a day pass without eating.

H. Krieg (1937) 306 says that herbivores cannot be made to fast without harm to their digestion, for example, by intestinal twist and constriction in fasting ungulates. They must be able to fill their stomachs with straw at least. In their natural state, plant-eating animals fill their digestive tracts daily with large quantities of food of comparatively little nutritive value. Fasts are unknown to them.

Intake of food like every important biological activity of the animal is part of its space-time pattern. The free living giant panda (Ailuropus melanoleucus) needs from ten to twelve hours to take sufficient food, in the form of bamboo, which is poor in nourishment. In doing so it wanders along its habitual tracks among the giant bamboo stems of its
FEEDING PATTERNS

comparatively small territory of a square mile, depositing one or more pellets of excrement every hundred yards or so. Apparently the main period of feeding is at night (E. Schäfer (1938) 29). In this animal, food intake is spread over time and space, and so is defaecation. The other extreme perhaps is a snake of the poisoned-bait trap type (H. Hediger (1941) 40), which does not move at all from one spot. It lies in wait at a particular time, during an appetite phase, at a particular fixed point of its system, until a victim appears. In a few moments this is killed and swallowed and the snake retires for a long time and devotes itself to digestion at another fixed point.

Even more striking is the way the ruminant fits intake and digestion of food into the space-time pattern. It is separated into two different actions, provisional and final. Each action is assigned to a particular locality and point in time. In deer, for instance, grazing often occurs early in the morning and at evening in exposed localities and consists of a hasty snatching of food. This can then be peacefully digested during the day in the relative safety of the resting ground under cover. The process of rumination is linked with a definite psychic situation, with maximum amount of rest and lack of disturbance. Rumination often takes place in a state of dozing. In the zoological garden, this need for a peaceful atmosphere for rumination should be properly catered for.

It is not enough, generally speaking, that there should be a sufficient intake of food. The best conditions for digestion should also be present. Intake and digestion of food are differently localized in the space-time pattern among ruminants, and to some extent among predators and monkeys, rodents etc. The predatory animal frequently finds cover to consume the prey it has caught; digestion may follow at a third spot, and excretion at a fourth etc. G. Brandes (1939) 10 found that his orang-outangs did not always put the scraps they found into their mouths, but often collected several together to be consumed one after the other in peace and quiet at a favourite spot. The cheek pockets of the monkey, hamster etc may here be compared functionally with the ruminant's stomach. They serve to separate intake and digestion of food and to assign each of these actions to a special locality. We shall have more to say about the method of fitting the intake of food into the space-time pattern later.

Here we shall simply summarize the importance for the animal and man relationship of both continuous and occasional feeders. We have already said on p 120 that even the best food will not be taken by the animal if it has flight tendency, and if the food presented is less than the flight distance away from man:

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<th>Food</th>
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Animal's Flight Distance from Man
THE PROBLEM OF FOOD

It must once again be stressed how very important it is in the zoological garden to have each animal as tame as possible, i.e. with the least possible flight tendency. We must, therefore, try to overcome this psychological barrier, the distance between man and the animal, by all possible means. In original undiminished flight tendency the attraction of food, as has been shown, will not be of assistance as flight takes precedence i.e. it dominates intake of food. In the course of the reconstruction of its surroundings, however, the animal's flight tendency, and hence flight distance, may be appreciably diminished. The power of food attraction may be used for drawing the animal and increasing the intimacy of the animal and man relationship. An increase of this sort is used in animal training. Here the difference between the attitudes of the two feeding types towards the attraction of food becomes clear. The occasional feeders (e.g. the large cats) react quite differently to the food stimuli compared with the continuous feeder (bear, sea-lion, elephant, and so on). These must be rewarded, as it were, for every single performance with food such as sugar for bears, and fish for sea-lions. Training sea-lions without fish, or bears without sugar, is unthinkable, though training lions or tigers without meat is, because with them food stimuli often play no part at all (H. HEDINGER (1938b)).

Quality and Quantity of Food

Here we cannot undertake to quote individual recipes, only to demonstrate a few basic points. I. KRBMBIGEL (1933) has given an excellent list of foods for various groups of animals. It is a kind of cookery book, in fact, for those who run zoological gardens. There are two facts to be borne in mind. In the zoological garden we must usually offer the animal:

1. substitute food, and
2. food that is often far less varied than nature's.

These two disadvantages cannot, or can only partly, be made good through greater nourishment content. Compared with the widespread europhagy or eating a variety of foods of wild animals, the food they eat in captivity is usually far too monotonous.

Individuals show a peculiar dislike of substitute food. For example, in specialist circles, it is still often considered a fact that the reindeer cannot be kept without 'reindeer moss'. In contrast to this we may add that a reindeer, acquired in bad condition, got no reindeer moss at all for two years, yet in this time developed into a strikingly handsome specimen. Its food consisted of crushed oats, thin slices of dry bread (larger pieces could not be chewed), dried potatoes, sliced dried turnips, occasionally some locust beans and, as a supplement, some dried
QUALITY AND QUANTITY OF FOOD

yeast, occasionally grass in summer, and extra vitamins (A, C and D) from time to time. After two years the animal began to grow thin, doubtless due to old age, and had a very poor appetite. To stimulate intake of food reindeer moss was provided for the first time and eaten with marked avidity. On 3 June 1942 the animal that had been acquired in November 1939 had to be shot, because of symptoms of senile decay, confirmed by post-mortem. In the Basle Zoo, reindeer have been kept for years without lichen and thrive remarkably well. It must not be assumed that reindeer lichen (Cladonia rangiferina) contains something mysterious that the animal could not otherwise get. Besides, this lichen is not, by any means, the sole diet of free-living reindeer. In his monograph on reindeer, A. Jacobi (1931) states that the consumption of lichen is considered a special characteristic. It is believed that it prefers this combination of algae and fungi to any other food, indeed the genus (Cladonia) gets its popular name ‘reindeer lichen’ from this. As he has shown, this generalization is misleading; the reindeer in summer feeds almost exclusively on green food, and only through its failure or inaccessibility in winter does it turn to the hardy lichen.

Things are different, for example, with the koala (Phascolarctus cinereus), a monophagous eucalyptus feeder. As A. Pratt (1937) found in the course of his investigations, botany and chemistry are not advanced enough for us to discover the exact species of eucalyptus which the free animal chooses with literally superhuman skill from the many different species. These seasonally undergo rapid changes in their chemical make-up and are vitally important to the animal.

The animal’s food must contain the necessary nutriment as well as suitable vitamins. These have now become familiar to those who run zoological gardens, and so much attention has usually been given to them that they need only be mentioned here.

A careful eye should be kept on adequate provision of mineral substances, especially with the larger animals. Many animals such as antelopes, buffalo, rhinoceros, elephants, kangaroos etc make periodic visits in free life to special spots in their territories or neutral zones to get various mineral substances. These are often in the shape of salt crystals and occasionally in surprising quantities. The addition of considerable quantities of bacteria to their food can sometimes be of vital importance too. An example of this sort is quoted by L. Nicholls (1938) in his valuable work on methods of feeding in the Colombo Zoological Gardens. There, a giant tortoise had been laying eggs repeatedly, but the young kept on dying shortly after hatching out. On one occasion, however, five survived, apparently because some rotting leaves were available which they greedily devoured. Nicholls says that it appears from this that newly hatched giant tortoises require bacterial action to take place in their food before it is suitable for them.
He further suggests that their digestive systems may not be sufficiently developed and they require bacteria to break up and partly 'digest' for them the plant proteins, or it may be that yeasts and other organisms are bringing much needed vitamins to their foodstuffs. The specific food requirements of many animals are often not the logical outcome of their body organization or way of life, but sometimes can only be discovered empirically. Thus, for example, E. Fabricius (1945) discovered that for certain young ducks (Nyroca fuligula, Somateria mollissima) and sawbills (Mergus merganser) a purely fish diet is quite insufficient and leads to hypofunctioning of the Glandula uropygialis. The young birds are then unable to grease their wings properly, their feathers get wet in the water and they drown. The experiments prove, in the author's opinion, that the Glandula uropygialis, in order to function normally, in the downy young of certain waterbirds is absolutely dependent on the supply of some specific substance that is especially abundant in insects and probably also in certain crustaceans, and that sensitivity to quantitative variations of this substance in the food is very great. The chemical nature of this substance is, however, not yet known and likewise the way in which the downy ducklings in nature satisfy their need for the substance necessary for the normal functioning of the gland requires further investigation. On the sea coast where insects are not available in sufficient quantities the rich crustacean fauna in the Fucus-vegetation plays, without doubt, an important part in this respect.

H. Madsen (1941) has had some surprising experimental results which cast an altogether new light on this question. The author first heard about them through H. Poulsen at the Copenhagen Conference of Directors of Zoological Gardens in 1949. Madsen showed that the uropygial gland plays no part in making the feathers waterproof. On the contrary, if the feathers are treated with the secretion from them, the finer feathers become stuck together and the bird gets wet. It also gets wet when it drowns beneath water e.g. when it gets entangled in a fishing net. The feathers seem rather to owe their resistance to water to the fact that the finer ones are kept at an equal distance apart by the action of the skin muscles so that air is trapped in between them and the water cannot enter. When the bird dies, the muscles cease to function and the bird gets wet. Moreover eider ducklings keep dry in the water even though their oil glands have not yet started to function. In addition, the oil glands of certain ducks (Anas platyrhyncha) were removed by operation; in spite of this, the new feathers that grew after the moult were just as water repellent as those of untreated ducks. The fact that oily substances e.g. those obtained from the food fish, can cause the feathers to stick together just as seriously as artificially applied secretion, is of significance here. In the Copenhagen Zoo it was very striking to compare two groups of small waders (e.g. avocets, Recurv...
Quality and Quantity of Food

tosta avosetta), one fed on fish, the other on a fishless diet. The latter had no opportunity of soiling their feathers with fish oil. They looked spotless and were harder than the rest. Perhaps the true interpretation of Fabricius's experiments mentioned above is that the chitin diet was markedly better than the fish diet in that it removed the possibility of smearing oil on the feathers. In the Basle Zoo we had disastrous results among puffins (Fratercula) the moment we added cod liver oil to their pieces of fish in order to improve their diet, thereby considerably increasing the danger of feather-soiling unwittingly. They all died with their feathers badly stuck together.

For the sake of completeness we should also add that the quality of food deserves attention because of certain incidental results. Frequently, in order to obtain or keep a particular shade of colour (flamingoes, for example), a mixture of materials is necessary, as these are responsible for the proper colouring. This also applies to fish and crustacea.

A further important secondary result of the quality of food may come from purely mechanical properties. Many wild animals, especially rodents, have their teeth adapted for a hard diet of definite abrasive effect. If this abrasion is absent in captivity, due to food of too soft a consistency, excessive tooth growth may occur. Many hoofed animals suffer at times from irregular wearing down of their teeth in captivity, as O. Antonius (1929) points out. In other instances, as in the maned wolf (Chrysocyon jubatus) already mentioned, excessive growth of the eye teeth is not caused directly through type of food, but through type of flooring (p 93).

The behaviour of animals towards dummy food is not only of purely animal psychological interest. Instances are known of porcelain eggs being taken away and hidden by stone martens (Martes foina). Experiments on tame stone and pine martens showed that these animals could not tell the difference between real and imitation hen's eggs (see H. Räber 1944). Porcelain eggs were treated by them as if they were real ones i.e. they carried them about for a long time in their mouths and tried to eat them. Apparently the egg is regarded by these animals purely as an optical shape, as in man. The tactile (touch) or olfactory (smell) test, that we might expect from the martens, is noticeably absent, or plays only a very limited part. The egg is registered in a similar way by some reptiles, namely the egg-eating snakes. C. R. S. Pitman (1938) quotes a case of an egg snake (Dasypeltis scaber) even swallowing a camphor egg and, of course, dying as a result.

A loris (Nycticebus) that had a partiality for cockchafers ate a real one, and then grabbed a chocolate one with cardboard legs, although it did not eat chocolate. It must have made a mistake; the imitation one was dropped after the first surprise and taken no more notice of. It sometimes happens that animals take food of a kind quite outside their normal diet, by intention, and not by mistake. This may eventually

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lead to pronounced allotriophagy (eating unusual and unsuitable things), frequently symptomatic of a deficiency disease, or that something else is wrong. D. Katz (1937) 173 speaks of perversions of appetite. These may often be valuable indications of errors of diet. According to a report of K. M. Schneider (1935) 249, a two year old lion in the Leipzig Zoological Gardens had to be given castor oil and enemas because it had swallowed part of a child’s coat. The celebrated lion ‘Coburg’ of the famous Marseilles lion tamer Henri Martin choked through swallowing a pair of slippers belonging to his master (H. Thetard 1928) 37. Coprophagy (excrement eating) is a strange form of allotriophagy, and it has become a zoological problem among apes (p. 88). E. L. Taylor (1940) has now shown that in the rabbit (Oryctolagus cuniculus) coprophagy is a normal phenomenon. Up to 90 per cent of the excreta is picked up again at definite times, and this constitutes a kind of pseudo-rumination. The pellets are frequently re-ingested straight from the anus. This remarkable phenomenon was described by the French investigator Morot as far back as 1882, but has since been forgotten. A morbid form of divergence from the normal feeding is autophagy (self-eating). Valuable animals fall victims to it in zoological gardens. In his report Schneider quoted a case of a male lion having to be shot because within a few hours it had eaten its tail down to a length of twelve inches. A lioness went even further. Schneider plans a comprehensive survey of similar cases that will be particularly welcome as no large zoological garden is free from serious cases of autophagy. The nature and methods of dealing with this present far reaching problems not yet solved.

Quite a different type of autophagy, sometimes noticed in snakes, occurs when, under conditions of feeding excitement, they take hold of visible portions of their own bodies and begin to swallow them by mistake. For example, C. Stemmler (1937a) 230 quotes a Natrix tessellata mistaking its own body, obviously smelling of fish, for its prey. It bit it vigorously and began to swallow its own body, which violently struggled against it. The more the body defended itself against the bites of its own head, the more vigorously the head attacked. Only when the adder had energetically punished its own tail did the two enemy body parts separate.

The quantity of food taken is controlled in freedom by a variety of factors, which, in captivity, do not have the same results. Through hypertrophy of food valencies in captivity exaggerated intake of food may occur, especially when excessive amounts are offered by the public. The removal of the animal from the functional sphere of food may thus, in captivity, lead to disturbances caused by valency hypertrophy, or as J. Dobberstein (1936) expresses it, by boredom. As a rule with sensitive animals there is a risk that they will take too little food rather than too much, so that their feeding should be
stimulated as far as possible by various means. These may include the social factor (p 122) and are further discussed. D. Katz (1937) found in the experiment on hens that by offering a larger quantity the normal intake of food can be increased above normal satiety. In this case a relationship exists between the quantity of food offered and eaten.

Frequently, animals of the continuously feeding type show a propensity for getting the greatest amount of food out of the public by certain tricks of behaviour; they invent various methods of begging. Here, interesting forms of self training often arise, although these really consist of training by the public. The tame animal recognizes the visitor as a potential food provider; yet the food is not forthcoming. In a state of unrelieved tension the animal must do something to gain the object it desires, as Koehler rightly says (quoted in E. Kuckuk (1936) 16). Therefore the animal makes some sort of movement to get the desired food, standing up or making the maximum approach to the goal, stretching out its forepaws, trunk etc. Or else, by chance, postures and methods of behaviour (such as turning round and round) etc which elicit food will be discovered by trial and error (or more correctly from the animal psychology point of view, by trial and success). Successful behaviour will be remembered and repeated at the next opportunity. Occasionally begging movements will occur between animals in the absence of man. A magnificent ibex could be observed, during the rutting season, turning like a compass needle towards the receptive female, but keeping a certain distance away, with the characteristic behaviour found at this period. During this process it sometimes happened to make begging movements at the female with its forefeet. Begging is not always a good thing in the zoological gardens. Geodor (1941 148) considered it a drawback that the animals at Nuremberg got used to begging under the influence of the public. He said that the magnificent spacious enclosures completely failed in their intended purposes at times. They ought to offer the animals opportunities of running around and playing with each other, just as in nature. Animals continuously fed by the public no longer do this. They keep standing and begging by the ditches or the fences, and waiting. The visitors, who, by constant feeding, have got the animals used to continual begging and have stopped their natural play activities thus lose the pleasure of seeing them playing about. The idea of animals playing in nature as we said at the beginning is clearly based on anthropomorphic assumptions.

In the Berne bear pit, each bear has a special way of begging (F. A. Volmar (1940) 358). One stands up with open mouth and hooks its right paw on to its lower jaw; another crosses its arms over its chest in a standing posture; a third stands upright and makes nodding or request movements with its head; another again lies down stretched
out full length; yet another sits like a rocking chair, with back bent, and clasping its hind paws with its forepaws. These methods have all been discovered by the bears themselves and have a surprising but understandable effect on human beings; from their nature they are highly unspecific. Basically, they are all variations of attempts at maximum approach and arousing of attention. A. HILFIKER (Basle) has, in the press, a comprehensive work on begging in zoo animals.

Many animals such as predators, rodents, Corvidae etc regulate the quantity of food provided by laying up stocks. In nearly all cases these are found again through subconscious not conscious memory (W. FISCHER (1938) 262, 272); i.e. a squirrel will neither 'remember' that it has hidden its stores all over the place nor the spots where they are hidden. When it needs them it finds them again while searching at random among the hiding places in question, or by smelling them when it chances to come near to them.

A fictitious increase in the quantity of food, prolonging, or repetition of the feeling of pleasure connected with feeding may be achieved through vomiting and eating again. Dr E. M. LANG (1943), the Basle Zoo veterinary surgeon, had under observation a sloth bear (*Melursus ursinus*) that regularly regurgitated its food more than a hundred times, only to eat it again with the gurgling and sucking sounds typical of these bears. Here, for completeness' sake, we might refer to the method of indirect feeding occasionally used in psychological experiments on animals. Thus H. W. NISSEN and M. P. CRAWFORD (1937) for example in their experiments on chimpanzees used automatic machines from which the animals could get food by inserting counters. In the London Zoo (J. HUXLEY (1937) 36) a slot machine was installed in the sea-lions' enclosure which, on the insertion of sixpence by the public, tossed fish into the pond. Similarly, the Barbary sheep could be fed automatically; on inserting a penny a handful of maize was automatically scattered. G. BRANDES (1941) mentions an old feeding machine for the female elephant 'Bupari' in Halle; the animal knew the difference between copper and nickel coins and could only be got to put nickel ones in.

We should distinguish between slot machines in which the coin, inserted by the animals, produces the food, and those in which the public puts it in. The former are without doubt more interesting from the point of view of animal psychology. On the other hand, the second has an important hygienic advantage, because it excludes direct contact between animals and public. This fact is important, especially with highly susceptible species e.g. apes. By the use of such machines, in spite of separation by a glass window, the public are not denied the pleasure of personal feeding. Both offer an advantage in that the machines can be filled with good food and thus help to avoid unsuitable and harmful food being given.
Food Presentation—Timing and Method

The zoologist can only gain by making use of the conclusions of animal psychologists about feeding—hunger, appetite, and so on. Many of these results are to be found in Katz's book, already frequently referred to. This writer discovered a method with hens and other animals which might obviously be regarded as psychological fattening. It consisted in taking left over food from a hen that has eaten its fill and immediately offering it again. This could be repeated eight times or more. Each time, the hens pecked at the freshly offered food. In this way the amount of food taken could be increased up to 67 per cent. The degree of hardness of the ground was also found to be important for the amount of food taken. Furthermore, a connection was found to exist between appetite and colour; sometimes warm colours, yellow and red, may favourably influence the appetite. To the animal biologist it appears again and again, from these and similar experiments, that feeding in animals is not just a physiological process. By appropriate modification of the circumstances where possible, many difficulties in feeding wild animals can be smoothed out or removed altogether.

A factor for many lower vertebrates which decides whether they will accept or refuse the food offered (i.e. recognize it) is whether it moves or not. The movement may be active, imitating living prey, or passive. G. Lederer (1939) says that many tropical marine fish, especially just after they have been caught, will only take food that is sinking in the water. This habit may mean careful feeding several times a day until they are acclimatized. Food lying on the bottom is often ignored. Once the fish are acclimatized, they learn to look for food on the bottom. This should mean, in Uexküll's sense, that food lying on the bottom does not exist in the world of these fish. Only during their re-orientation or adaptation to the new surroundings can the new phenomenon of food lying on the bottom be fitted into their reconstructed world. Many fresh-water fish, too, behave like this (e.g. Pantodon), failing to recognize food lying on the bottom. We find the same thing as well with many birds such as swifts, humming-birds and penguins and even mammals such as bats. It often requires laborious training before ground food can be introduced artificially into the animal's surroundings. Actively moving food simulating prey is necessary for many fish, amphibia and reptiles, since optically they are only able to notice moving things. D. Katz (1937) tells of frogs that starved by the side of a heap of dead flies; they see nothing edible in the motionless insects. We know how poikilothermal or cold-blooded vertebrates, while feeding, must have dead food artificially made to move if they are mainly optically orientated. In eighteen years' observation on his king penguins (Aptenodytes patagonica) T. H. Gillespie
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was unable to note a single case of them taking a fish from the ground. At feeding time every penguin had to be fed singly by hand. In any event, free-living king penguins never eat fish, but small crabs and especially cephalopods. Thus for this species of penguins fish form a definite food substitute.

The temperature of the food may be important for the most widely different groups of animals, even for fish. In the work on management of tropical fish already quoted, G. Lederrer (1939) states that all food, before it is given, must be suitably warmed, whether it is the fleshy part of mussels, live fish or insect larvae. It is absolutely necessary in the case of quick feeding fish for the food supplied to be of the same temperature as the water in their tank. Food temperature may also play an important part with many homeothermous or warm-blooded animals. For predatory animals that kill warm-blooded prey, a certain amount of warmth is natural in their food, and it is quite likely that cold or ice-cold meat is foreign to them and harmful. Eating cold flesh, temporarily at least, is only normal to the larger beasts that return to their prey when it has grown cold, after their first full meal off it, or in the case of carnivores that live largely on carcasses e.g. hyenas. Yet it must be remembered that prey grown cold in this way is far above the temperature of the refrigerator, unless we are concerned with arctic or antarctic conditions. As I. Krumbiegel (1935) has shown, warming of food and drink is indispensable for keeping weasels (Mustela). The danger of cold food to these sensitive smaller predators has long been known. For this reason the author was extremely surprised to see some free-living weasels (Mustela erminea) in winter regularly jumping up at some big pieces of half frozen horse meat that were hanging up outside, to save using the refrigerator during the cold season. The weasels used to tear off and eat as much of the cold flesh as they could manage. Apparently it didn’t do them any harm. Very few carnivores are used to eating cold frozen flesh. The husky dog is one; it swallows lumps of rock-hard flesh until the sharp edges can be felt through the walls of the animal’s belly (W. E. Ekblaw 1936).

Relative height of the food above the ground also plays a part in food presentation, especially with long necked leaf and twig feeders like moose, giraffe, okapi and many antelopes, for which it is unnatural to take food off the ground. This is in contrast to grass eaters, many bovines, deer etc. In his monograph on giraffes, I. Krumbiegel (1939) refers to this fact. He observes that feeding off the ground or from food troughs that are too low causes unsuitable posture of the neck and has a harmful effect on the flow of saliva. In the giraffe this is normally copious and sticky, and tongue exercise, by means of feeding racks placed high up, is in the long run necessary for health. Occasionally there is an overwhelming need for dry foodstuff, moistened by a
FOOD PRESENTATION—TIMING AND METHOD

strong flow of saliva. The giraffes which were observed by the author in the Belgian Congo (Garamba National Park) in 1948 fed not on high trees but low shrubs, their necks bent low and their forelegs sometimes spread wide apart in the typical manner.

The importance of timing is also a consideration in the presentation of food. Most birds are adapted for seeking food by daylight, while many mammals prefer to feed at twilight or by night. Many nocturnal animals can undergo a considerable change in habits in the physiological, optical sense, whilst the opposite in birds, for instance, is impossible since they cannot see well enough in the dark. Here, attention must be paid to day and night rhythms of activity and rest, as well as to rhythms of longer duration. There is no better example of this than the snake, an extreme case of an occasional feeder. Quite apart from seasonal rhythms, summer activity and winter rest, we can observe a definite three-phase rhythm in the snake, and this must be taken into account in their management. These three phases are: sloughing, feeding, digestion and sloughing once more. Moreover, this rhythm is fitted into the snake’s space-time pattern, or rather it forms a part of it. Feeding, digestion and sloughing as a rule take place at definite times and places, and correspond to a specific psychological situation. The sloughing snake behaves either with apathy or on the other hand very irritably, which is very different from the snake creeping when seeking its food or the one that has retired to cover for digestion.

As a rule snakes only respond to food stimuli during the phase that follows sloughing. With many species (e.g. colubrines, boas), eating and digesting may be interchangeable, but even in these instances, greater feeding activity will be noticed after sloughing and a reduction in it before the next sloughing. With large boas, vipers and others, the prey will often be taken only once during an eating phase, or else repeatedly at short intervals, and then digested as a whole, so that here the eating and digesting phases are more clearly marked off. During the sloughing phase snakes have only rarely been known to feed. In such cases, the space-time pattern must be strictly observed if artificial feeding has to be resorted to with fasting specimens. It is no use cramming the food in; it must be done at the right time or else the snake will throw it all up, and the risk taken in any forcible feeding, especially with highly venomous snakes, will have been in vain. There is also the likelihood that the snake that has been crammed at the wrong time will not be able to digest the food taken.

Among extreme occasional feeders for which feeding is, as it were, an event, details of presentation are very important. It has been told elsewhere (H. HEDIGER (1941a)) how in the case of fasting snakes a fatal sequence of events may occur; activity becomes impaired through fasting and is followed by a condition of apathy. During this,
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with no prospect whatever of food being taken, there is continual slowing down of the metabolism and increasing weakness. This vicious circle must somehow be broken and there are two lines of approach. First, activity, and hence indirectly, metabolism, can be powerfully stimulated by the so-called 'disturbance treatment'. This may include frequent change of place, changes in external surroundings, addition of other snakes or animals etc. Secondly, metabolism can be directly influenced by forcible feeding. Recently we have tried to stimulate the appetite of rattlesnakes that were off their food with a solution of grape sugar. The animals liked licking the drops off the blunt cannula of a hypodermic needle. Insulin injections are aimed at creating artificial hunger, since some way must be found of avoiding forcible feeding, always a rough and disturbing operation for the snake, and often involving serious risk for the keeper.

This important chapter can only be dealt with here in a few suggestions. Care must be taken with ungulates with very large horns (ibex, watusi etc) or antlers (e.g. reindeer) to see that the animals can get at forage boxes and mangers in comfort; they must be a sufficient distance away from the wall etc. The author has seen gardens where big reindeer could only manage to reach their food after all kinds of twisting and turning. If possible, the protected zone of some animals such as certain birds of prey should be catered for. Notice should be taken of the fact that in free life these birds only catch their prey at a certain distance from their home. Animals like these should thus be fed as far away from the nest as possible. There is an extensive literature about the breeding of animals most often used for food in zoological gardens. Here we should like to mention only Praktische Futterkunde (Practical Information on Feeding) by H. Geyer (1940) for aquarium and terrarium animals and the excellent U.F.A.W. Handbook by A. N. Worden (1947) and his many collaborators on The Care and Breeding of Laboratory Animals.

Excretion

Intake of food must be followed by digestion, and this again by the deposit of its end products, excrement and urine. In the zoological garden supervision of excretion is as important as that of intake of food. Apart from constant inspection for parasites (p 114), in suspected cases, consistency, colour, smell etc must be examined regularly so that possible digestive troubles may be treated at once. In many instances excretion is not a simple matter of metabolism any more than the intake of food. It often occurs not from physiological pressure, but with quite a definite meaning like demarcation of territory, at a fixed time and place, and is thus incorporated into the space-time pattern (H. Hediger (1944b ). A peculiar product of metabolism is the pellet. It is found primarily among day and night hunting birds of
EXCRETION

prey, as well as among butcher birds, herons, some reptiles (Varanidae) and mammals (Mustelidae), and is expelled from the mouth. Pellets are usually balls of hair and feathers, with fragments of bones or chitin. Their formation is essential for the health of many animals; hence these must be given food of a sort that will allow pellet formation. The food should be hairy, feathered or chitinous. Hyaenas and other carnivorous animals often expel sharp pieces of bone and cartilage.

On p 89 two types of excretion were described. The following are examples of diffuse and localized types:

**DIFFUSE EXCRETION**
- Phasianidae (pheasants)
- Passeridae, Oscinae (song birds)
- Anatidae, Anseridae (ducks, geese)
- Bovidae (cattle species) some
- Cervidae (deer species)
- Monkeys

**LOCALIZED EXCRETION**
- Sloths
- Many rodents
- Many predators
- Procavia (Hyraxes)
- Tapir
- Rhinoceros
- Lama
- Hylochoerus (Giant forest hog)

The localized type is of practical importance, since it may considerably ease the task of cleaning, especially if the defaecation places can deliberately be incorporated into the layout by fitting up artificial ones with warm water, or with a sample of droppings and urine. Such a place will then often be used by the animals, for if it has the significance of a marking place it must be used and sprinkled. Disinfection is very closely linked with defaecation and urination.

Since excrement often contains parasites, thus leading to fresh infection or re-infection, it must be removed where possible. Automatic cleaning of the floor by periodic flushing might be used far more with individual species of animals. De-odorization, the neutralizing of disturbing and harmful smells, is closely connected with disinfection, and is used where there are enclosed animal houses and menagerie tents, especially if offensive smells from ammonia etc cannot be immediately removed by ventilation. Often the problem of de-odorization arises in open enclosures as well as, for example, foxes' enclosures. Strangely enough, the public is often far more sensitive to animal smells than to chlorine, which is freely used as a disinfectant. B. J. BENCHLEY (1942) 277 uses chloride of lime once or twice a month to disinfect the cages. R. HILTY (1974) 66 draws attention to the fact that creoline or any of the coal-tar derivatives are dangerous to any animal of the cat family, on account of the cresylic acid content. Hilty mentions a circus lion being killed through its cage being saturated with a creoline solution to keep down the flies. Naturally the greatest care must be taken with deodorizers to see that they are not only harmless, but also not
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objectionable to the animals. When skunks are kept, the scent glands are generally removed by operation (C. B. Moore (1937) 366). It is possible to overdo the cleaning of cages and enclosures as has already been shown with the slow loris (p 46), which, like many another animal, only feels at home in surroundings that are more or less impregnated with its personal smell, namely of its urine.

Breeding

Reproduction is part of the normal behaviour of a healthy animal. Since isolation is unbiological, as has been said, the successful breeding of captive animals follows inevitably with proper biological treatment. For the animal biologist, therefore, breeding is something like arithmetical proof for a mathematician. Without breeding there is something wrong with the treatment; if it occurs then it is at least a guarantee of definite and continuous good health in both parents. Therefore biological treatment of animals must aim not at keeping separate individuals, but generations. The problem of breeding wild animals in captivity appears simply as a kind of super-individual metabolism, but the rearing of young is first and foremost a problem of feeding, once the space requirements are satisfied. Thus the problem of breeding will be treated merely as a supplement to the food problem. Like the latter, the problem of breeding is interwoven with questions of the animal-man relationship as well as with the space problem. We shall show this by an extreme example, all the more striking on that account.

It is a peculiar thing that many native i.e. mid-European species of animals can hardly be kept in captivity, let alone made to breed. One of these is the capercailzie (Tetrao urogallus) an extraordinarily difficult bird to keep. The squirrel (Sciurus vulgaris), too, common everywhere, in the forests as well as in the city parks, does not take at all kindly to captivity. Nor does the hamster (Cricetus frumentarius), though on the other hand its near relative, the Syrian golden hamster (Mesocricetus auratus), does. The house sparrow (Passer domesticus) does not breed in captivity, although it often brings up its young under the roofs of human dwellings. One of the most interesting instances of non-breeding animals until recently was the common European hare (Lepus europaeus Pallas), in spite of being one of the commonest wild animals in Switzerland, and being shot yearly to the tune of fifty or sixty thousand. Apart from one or two apparently chance instances of breeding at the end of last century, no success had been had either in breeding or keeping it alive for long in captivity until G. Notini (1941) reported some results in Sweden. Because the hare presents such an extreme case for breeding, it will be dealt with at greater length, especially as, after trial experiments in the gardens at Berne, the
BREEDING

author succeeded in solving this breeding problem in the Basle Zoological Gardens quite independently of NOTINI's experiences, so that by 1948 three generations had been produced in captivity. A detailed report will be found elsewhere (H. HEDIGER (1948)).

The difficulties of breeding from hares were of two kinds:

1 parasites, and
2 psychological.

This animal has many external enemies as well as many internal ones in the shape of parasites. On account of these, especially the Coccidia, it is necessary to move the hares on to fresh ground at least once every forty eight hours, to avoid re-infection. Frequent cage cleaning is impossible because every time it happens the hare is so badly disturbed by it that it dies of excitement by breaking its neck or knocking in its skull. A. USINGER ( (1933) 23) pointed out this danger. The problem is therefore to find a way of doing the necessary cleaning as often as possible without causing the usual disturbance. The solution, as shown in the first (German) edition of this book, was found to lie in the back to back cage with alternative compartments (Figure 29, 30a, b).

In principle this cage consists of two symmetrical halves, back to back. The plane of symmetry is formed by the vertical shutter in the middle. Each half consists of a double cage, one part covered by boards and the other open but covered with wire netting. Thus there are two simple cages arranged so that the protected compartments are adjoining. The common wall has for its lower part a movable shutter. This allows changing the hares over from one side to the other for the hares soon learn to hop through under the slowly raised shutter going in this way from one covered compartment to the other. The shutter rests on a sill about eight inches high. Very young hares that cannot follow their parents over the sill for the first few days are guided through under the partly raised shutter, after the adult hares have already moved over. In this way the adults never come into contact with the keeper. The latter is forbidden to enter an occupied compartment under any circumstances, or to walk past the open side of a cage. Access to the front of the cages is prevented by an unclimbable barrier, four yards in front. The back consists of a wooden wall with spy holes in it to left and right of the drop partition, through which the hares can be watched.

In the double cage only one half is occupied at a time therefore, and by a single pair of hares, possibly with their young until the age of three weeks. The unoccupied half is carefully cleaned out immediately after it is evacuated, disinfected and left completely empty until it is to be re-occupied. The hares are changed over every two days, or in the case of badly infected droppings every day, i.e. they change over each time to a perfectly clean floor and by this means cannot be re-infected. The
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disinfected part of the cage is liberally supplied with straw for the floor just before re-occupation and with food enough for one or two days, so that the door of an occupied cage need never be opened. In this way smaller hatches, through which feeding troughs used to be put, are

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![Figure 29. Lay-out of the double cage, as used in the Basle Zoological Gardens for breeding hares](image)

Figure 29. Lay-out of the double cage, as used in the Basle Zoological Gardens for breeding hares

dispensed with. On each of the narrow sides there are two big doors, filling up the space completely. They are only opened, as has been said, when the compartment in question is empty.

It has been found that for a double cage, a total length of fourteen feet is enough, with a depth of three feet and a height of seven. Anyone with experience of a rabbit cage examining a hare's cage of this sort
Figure 30. Breeding cages for hares in the Basle Zoological Gardens. 

Figure 32. Biological training. The bear, completely free, shows to a high degree the skill of this species in keeping a finely adjusted balance.

(Picture by Thalia Theatre, Wuppertal, of Edith Crocker’s Roar Art)

Figure 33. The positive significance of man to the tame animal. The brown bear, being afraid of lions, shelters behind the trainer.
first of all thinks it is too high. Yet a height of over six feet is necessary because the hares, if they do once in a way get too excited, jump to this height. If the cage was only half the height it might be possible for the hare suddenly leaping up to bash in its skull. Others consider the double cage too small compared with the space needed for a free living hare to move about. This need is greatly exaggerated, as most observers usually see the hare in flight, streaking away over great distances at full speed. Yet the hare obviously does not run about for pleasure. For nearly six years the author had the chance of watching completely free wild hares almost daily. They usually sat in their forms, for many hours a day, and only browsed nearby. Their territory was suprisingly small and, as a rule, they only left it in flight.

The extraordinary sedentariness of the hare has been proved in freedom by experimental marking. We found confirmation of this in comic fashion in the Basle Zoo through the behaviour of some specimens we had released from the breeding cages. Although they found abundant food outside, they were always being found by their cages for months afterwards. A hare that had been taken outside the gardens was shot by a sportsman months later less than a mile away.

All these observations go to show that two square yards of floor space are ample for a family of hares. Anything larger increases the difficulty of cleaning and thus the danger of infection. As has been said, a natural floor surface is very dangerous because it cannot be cleaned properly and favours the development of parasites. The unbiological wooden floor with a thin coating of cement and a layer of straw, and measuring seven feet by three feet for each half cage, has proved best for the hares after years of trial. Perhaps a layer of insulating material under the cement might be worth trying. The cage must be as smooth as possible inside so that the hares cannot injure themselves against projecting corners, bolts, screws etc. The most suitable feeding racks for the hay are those that can be fixed to the doors, and they must be provided with sloping roofs so that when the hares leap about they cannot drop into them, catch their legs in the netting and break them. The best size of mesh for the front has proved to be three quarter inch. Care must naturally be taken that mice cannot get in.

After we had succeeded in keeping hares for years in captivity, and in continuously breeding from them, it was at last possible to discover the exact length of pregnancy, hitherto unknown. It is forty two days. This can only be determined with certainty in captivity. Whilst we were breeding wild hares, a quite unexpected phenomenon was observed, namely super-foetation as a normal event i.e. the fact that a gravid female very often allows itself to be covered again three or four days before a birth. If such a doubly pregnant hare is separated from the male, as we have done repeatedly, it can, after being isolated, bear young for a second time within an interval of about thirty nine days.
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It is thus possible for pregnancy and heat to appear simultaneously in the wild hare. So the academic concept of corpus luteum hormone, especially of the effects of the sex hormone, does not apply to the hare. Incidentally the author, to his great astonishment, has just had pointed out to him that the phenomenon of super-foetation in wild hares was described quite clearly by Herodotus 2,500 years ago!

No doubt the hare is an extreme example of flight behaviour and parasitism. Yet it is an obvious conjecture that the method successful with it, might, with the necessary changes, be adapted to suit other species that seldom or never breed in captivity, for reasons of animal-man relationship. It often happens that in captivity nearly every normal relation between one animal and another is spoiled by the constant presence of man, with consequent failure to breed. The following diagram illustrates this fact:

Figure 31. The disturbing effect of man on the animal-man relationship. The moment the enemy, man, appears, all relations between the two animals are broken off, and replaced by stereotyped flight or defence reaction in the presence of man the enemy.

Thus all sensitive animals, or those that never completely get rid of their flight reaction to man, ought to have the chance of being able to feel safe from disturbing stimuli in some definite part of their surroundings or home. Significantly enough, difficulties of this sort are unknown to domestic animals. The tendency to escape from man is foreign to them; no disturbance whatever is caused by man in their relations to each other, especially in their sexual behaviour. In addition there is one fact about the domestic animal described by K. Lorenz (1943). The innate behaviour bound up with pairing has become considerably simplified under the influence of domestication. He points out that with the wild animal, elaborate conditions in its external surroundings must be provided, the choice of a mate, founded upon highly differentiated systems of inborn behaviour methods, must be observed etc. With the domestic animal a narrow stall and an acceptable individual of the opposite sex are enough to ensure breeding.

For wild animals it is not enough to bring together two animals of different sexes to breed from them. Usually, a series of conditions must be fulfilled before successful mating takes place (p 25). In the first place it is essential to ensure:

1. a physiological readiness
2. a psychological readiness
3. a definite standard of milieu or quality of surroundings.
in which the potential physiological and psychological methods of
behaviour can take place undisturbed.

The physiological readiness of the two sexes is usually connected
with definite seasons, the rutting periods. This is in contrast to most
domestic animals, and these periods must be carefully taken into
account. In typical instances, individual readiness can only occur
within this period of heat.

Psychological readiness is at least as important as physiological, and
depends on many separate factors, especially on a sympathetic adjust­
ment between the two animals. Individual antipathies can create an in­
surmountable obstacle to mating among the most different animals,
even among fish. O. ANTONIUS (1936) for example, writing in
this connection about his experiences with wild horses, says that one
of the chief difficulties in all breeding experiments with wild horses
lies in the stubborness of many stallions, that refuse to mate with cer­
tain mares, either of their own or of different species. We already
know from the literature on the subject about Falz-Fein's Chapman
Zebra stallion that was 'in love' with every female horse, but would
have nothing to do with its own mare, which it eventually bit to
death; or the London stallion 'Kiang' which would not mount his own
mare so that it had to be covered by an onager stallion. With couples
of different species, difficulties already mentioned elsewhere arise
even with stallions that are willing to mount. These are due to the
different mating ceremonial of individual species.

In fish this ceremonial can be surprisingly complicated and, as with so
much biologically important behaviour, is often firmly incorporated into
the place-time pattern. A single example will illustrate. K. LORENZ
(1940) carried out an excellent investigation into the behaviour
of the mallard (Anas platyrhynchos). He describes how in this species
mating occurs after protracted courtship, unusual and highly differ­
entiated social meets of the drakes and active choice of mates by the
females. While the drakes, gathered in great flocks on the surface of
the water, are absorbed in the complicated dance-like series of move­
ments of the meet, the females, especially the unmated ones, gather
close by and watch the actions of the males with obvious attention.
Weeks and months may pass while these mating gatherings occur at
definite times and places. Eventually they are increasingly interrupted
by one individual female going up to a male, swimming behind him
and, with a characteristic bleat-like cry, warning off another drake over
her shoulder. Lorenz says that this so-called incitement is a very com­
mon instinctive behaviour among the order of Anatidae. The drake
may react differently to the incitement according to his inclination; if
he complies regularly with the demands of the female, by accepting at
least a symbolic threatening attitude, then the two may be considered
as firmly mated.
Ceremonial may undergo definite simplification under captive conditions, as happens to an even greater degree with domesticated animals. Yet no mating ever takes place among wild animals without the special ceremonial for the species. Even the least complicated relationship between animals, and one with least ceremonial, can be fundamentally upset by the presence of man, if the animal has no chance of finding a place free from disturbance. The only exception is with completely tame individuals, no longer influenced at all by man's presence. R. Bigalke ((1939) 42) did not succeed in breeding with African hunting dogs (Lycaon pictus) until he took them away from the public. He had similar experiences with other predatory animals. The mating behaviour of captive animals is not always disturbed by the presence of man alone, but often by the presence of other animals as well, even of the same species. A. Kortlandt ((1940) 449) quotes Portielje's observation on the lapwing (Vanellus vanellus) that these birds, a large flock of which were kept in a comparatively small cage, never managed to breed. As soon as the company was reduced to two pairs, courtship began immediately. Similarly with mammals. It seems obvious that, basically, conditions in captivity must on the average have a harmful effect on the development of mating ceremonial and especially of reproductive capacity. In fact, there are many species of animals (e.g. gorilla, cheetahs, flamingoes, giant turtles, boas, thunderfish) which can be kept in captivity, but never, or practically never, be got to breed. The assumption with all these animals is that something is wrong with them in captivity. In addition to referring to the importance of ceremonial for many species, it must also be said that in the search for what is wrong we must also take into account physiological and psychological considerations. We can take it for granted that at times we shall have to deal with only apparently unimportant trifles. We can also safely assume that in the near future many decisive factors hitherto unknown will be discovered, as can be inferred from the developments of the last few decades. Chimpanzees could hardly be kept alive previously, nowadays they breed in many places, in America, in fact, for the third generation since 1933 (R. M. Yerkes (1940) 336). The elephant was still quoted by C. Darwin ((1910) 2,172) as a classic example of a mammal that will not reproduce in captivity. Up to 1932, on the other hand, according to H. Hvass ((1932) 191), nine elephant births had been recorded in Europe, and their number has greatly increased since then. Also the first African elephant, 'Adam I', has since been born in a European zoo, on 11 April 1943 at the Hellabrunn Zoo near Munich. The first rhinoceros (Diceros bicornis) ever to be born in captivity appeared on 7 October 1941 in Brookfield Zoo, Chicago.
Hypersexuality

Whilst animals have a tendency not to breed in captivity, as C. Darwin (1868) states in detail in his sterility hypothesis, there are also animals that do, and on them captivity has the unmistakable effect of hypersexuality. The biologist of zoological gardens must thus balance the claims of breeding as a guarantee of correct biological treatment against the need for preventing hypersexualization brought about by captivity; for hypersexuality is one of the obvious phenomena of domestication, and any signs of domestication in the wild animal are highly undesirable (p 168). The keeping of wild animals in zoological gardens is not concerned with the breeding of fresh mutations but of genuine wild types under artificial conditions and surroundings. Apart from this basic fact of the biology of zoological gardens, hypersexuality has such far reaching and at times unexpected results, like change in periods of 'heat' with harmful consequences such as winter births, that the greatest attention should be paid to it.

The state of domestication, which can only be achieved by keeping the original wild forms captive, and to which the wild animal's life in captivity forms, as it were, the first step, shows hypersexuality in an extreme form. It is seen in the strikingly precocious maturity of many domestic animals i.e. in the faculty of being able to breed at an earlier age than in nature (M. Hitzheimer (1926) 37). This author quotes as typical the case of steers which can often be used for breeding at an age when they are scarcely three quarters grown. When they have reached the peak of their physical development they are too heavy for mating and are therefore slaughtered at the age of five, six, or even earlier. Extreme hypersexuality among domestic animals also shows itself in an increased wearing out of the male's sexual powers, in a spread over of the heat cycle, in disregard of the seasons, and in an increased rate of births (O. Antonius (1922) 70). This spread over is also remarked on by L. Krumbiegel (1931) 227). He says that heat periods in wild animals are much more sharply defined than in domestic ones, which may be on heat all the year round. K. Lorenz (1940) 22) in contrast to wild animals, found that in domesticated animals mating reactions are often greatly increased.

The symptoms of hypersexuality just mentioned are found more or less in many wild animals which will reproduce in captivity viz mammals and birds. S. Zuckereman (1932) 44) indeed maintains that the breeding season in mammals is controlled by factors independent of external conditions. He is thus of the opinion that we can tell the breeding season in free life from data about births in captivity. This is certainly not so generally, only at any rate for certain species. From observations in the Cairo Zoological Gardens F. S. Bodenheimer
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(1938) 152) thinks the hypothesis a likely one for various gazelles. He has found that in the Cairo Zoo where food supply and climate are even throughout the year and where no rainy season occurs at all this rhythm of the habitat persists with regard to births. He thinks he can establish a correlation between the monthly percentage of gazelle births in the zoo and the rainy seasons in the natural geographical range of the various gazelles. These are Gazella dorcas, G. leptoceros, G. arabica, G. sommeringi and G. ruficollis.

In the author’s opinion, however, the graphs illustrating all this are not convincing. They might be considered rather as evidence for the disappearance of breeding seasons, for with Gazella dorcas the zoo births are spread over nine months, with Gazella leptoceros over six, and with Gazella sommeringi in fact over eleven months! There can be no question of a seasonal fixation of sexual activity and a retention of the deeply fixed seasonal rhythm of the natural habitat in captivity, at any rate with these particular gazelles. Allowance should also be made as to whether the births used for Bodenheimer’s statistics are of animals that were freshly caught, perhaps even pregnant, or that had been kept in the zoo for a long time, possibly even for generations.

Disappearance of the breeding season is often more marked in each generation.

Before describing two typical examples of the disappearance of the breeding season, in the wild boar and American bison, it should be stated that there actually are animals the breeding behaviour of which is not affected by this tendency to disappear, characteristic of many animals. The polar bear is an outstanding example of an extremely conservative animal with a fixed breeding season. On the basis of a large number of polar bear births, eighteen of which were in German gardens, or Stockholm etc. K. M. Schneider ((1933) 156) has shown that the breeding season of this arctic animal shows a spread of six weeks at most. An interesting account by G. Speidel ((1949) 235) on the famous breeding of polar bears in Milwaukee Zoo confirms the fact that in North America too polar bear births keep closely to a fixed season. The nine births of the polar bear ‘Sultana I’ from 1919 to 1935 varied between 24 November and 27 December. The three births so far of her daughter ‘Sultana II’ between 1944 and 1948 occur from 11 to 29 of November. In Zurich polar bear births regularly came at the end of November.

Thus the polar bear, without any doubt, represents a type of animal the heat and breeding seasons of which fall within narrow limits. On the other hand there is just as little doubt that animals exist with heat and breeding seasons spread over the whole year i.e. where births can occur at any season in captivity. Thus a list of all the available data on giraffe births in European and American zoological gardens has confirmed that births can occur with this animal in any month of the year.
HYPERSEXUALITY

A. REVENTLOW (1949) has published an interesting account of the various births among the giraffes in Copenhagen Zoo, in which he shows that they are spread over practically the whole year, namely from March to November. A. URBAIN (1944) established that young baboons (Papio papio) were born at any season to adults acclimatized to Paris. Many more examples might be quoted.

Fixed and variable types can also be distinguished among birds, although it remains to be seen whether the apparently fixed types such as black swans (Cygnus atratus) and emus (Dromaeus novaehollandiae) may not yet prove capable of adaptation. Up till now both these Australian birds have always laid eggs in the winter in Europe so that many clutches have been frozen. An examination of the exact data about the year of import would be most instructive here. It does not seem impossible for a change to occur in the course of generations similar to the striking example T. H. GILLESPIE (1932) observed in the king penguin (Aptenodytes patagonica). These birds, transferred from the antarctic to the Northern Hemisphere, each year gradually advanced their breeding season, or the moult intimately connected with it, to the early summer and in this way adapted themselves to the conditions in their new locality. In contrast to this certain birds of paradise described by H. G. MAURICE (1946) proved conservative and kept to autumn and winter for their breeding season in England.

Generally speaking the fixed type i.e. the animals that keep closely to their mating and breeding times in captivity like the polar bear, is not affected by hypersexuality. The variable type, on the other hand, even though it has a very limited season for mating and breeding in free life, soon changes the rhythm and duration of its breeding behaviour under the influence of conditions in captivity. Possibly the fact that there may be one or two breeding times a year in freedom also plays a part. Then an extension of the breeding season in captivity would be more or less understandable, but not the quickening up in the rate of births (hypersexuality) usually connected with it. It would be attractive at any rate, in view of the large body of material, to compare the habits of as many animals as possible in this respect. Possibly an important biological problem lies here. At any rate it would not be at all easy to decide whether many animals, especially tropical ones, have fixed seasons for mating and breeding in nature. We do not know the facts about this even for certain European animals e.g. the otter (Lutra lutra). H. PRELL (1937) considers that some rutting in the otter is caused by eating fish in spawn or by the sex hormones in these fish. Here is a hint of the possibility of help through sexual hormones for animals that are slow to breed in captivity. This is apart from use of vitamin E, already often used in practice.

A few more remarks must be made on hypersexuality conditioned by captivity or the extension of rutting season closely connected with
THE PROBLEM OF FOOD

Any generalization from particular instances, as happens occasionally in the literature on it, is most misleading here, because there are obviously such different types of reproductive pattern in nature, and because these again are differently affected in captivity. From the wealth of data, the following three groups of facts may be emphasized as important for this study of the biology of zoological gardens:

1 There are animals of which the reproductive pattern is negatively influenced by captivity (non-breeders) e.g. gorilla, cheetah (Acinonyx jubatus), Malayan bear etc. At least three cases are known of male gorillas where the genital organs were greatly underdeveloped. This was so with 'Bobby', the Berlin gorilla, which died on 1 August 1935, having reached a weight of nearly 500 lb (W. Koch (1937)). Another case was that of 'Alfred' the gorilla that lived at Bristol Zoo for seventeen years and which died in 1947 of tuberculosis, as Dr R. Clarke was kind enough to tell the author in a letter of 2 September 1949. The small, underdeveloped testicles of this 35 stone animal weighed only 1.5 gram. The third case is that of 'Mbongo' of the San Diego Zoo, 'the greatest gorilla that has ever been known to man', as it was called by B. Benchley (1942). This gorilla, which died of a fungus infection, weighed 618 lb, was sixteen years old and still sexually immature. A glance at the history of zoological gardens shows that an increasing number of those species previously considered non-breeding can be made to breed by suitable measures. Often, failure to breed is a question, not so much of a biological problem, but simply of organization, keeping animals separately instead of in pairs. In all probability gorillas and some other animals during freedom eat oestrogenous plants which they would not get in captivity. Many species show marked hypersexuality in captivity. We thus find life in captivity has both a hypo- and hypersexualizing influence.

2 Two types of species breeding in captivity can be distinguished: the fixed type, with an invariable season for rutting and breeding (e.g. polar bear), and the variable type, with elastic seasons, capable of adaptation, both in rhythm (e.g. king penguin) and duration (e.g. ibex). Here we must carefully distinguish between those species which are limited by their space-time system to fixed times in nature (e.g. European deer, wild boar) and those which breed continuously or nearly so the whole year in freedom (e.g. giraffe, anthropoid apes).

3 One of the most striking manifestations of hypersexuality through captivity is the extension of the rutting season i.e. the excessive spread of the rutting season in comparison with life in freedom, and consequently of the breeding time, with quicker sequence of births. Here again not all individuals and groups of given species react in the same way. In Basle Gardens the wild boars behaved as in freedom. Although both sexes had lived together for years, the young appeared every year in March or April, just as in free life, while elsewhere a
HYPERSEXUALITY

marked spread of the reproductive cycle had been observed in these very animals.

In Berne, the wild boars and bison among others are examples of the spread over of the heat cycle due to captivity and the tendency to quicker and quicker births irrespective of the seasons.

In nature wild boars are on heat from November to January and accordingly have their litters in April or May after a pregnancy lasting about eighteen to twenty weeks (W. Bieger and A. Wahlstrom (1938) 52). In Berne in 1937 three wild boars of that year were bought freshly caught and kept together. One of the females (Mädi) had her first litter on 3 May 1938, her second on 25 February 1939. The ones born in February died at once because of the cold. Shortly afterwards the animal came on heat again; it then had another litter on 10 August 1939. This was obviously an instance of a marked change and increase in the rutting period.

The other female (Rösi) had her first litter on 10 January 1939 and naturally they at once froze to death. Immediately afterwards she was on heat and had her second litter on 7 June of the same year. A similar thing happened the following year. The cold killed a first litter on 13 February 1940; on 26 July 1940 a second one was born. In this animal a double period of heat and littering was observed. The spread over of the heat cycle caused the fatal winter births. In order to bring the heat cycle back to normal again the enclosure was enlarged so that the boar could be separated from the sows on 25 May 1940 and the middle of February 1941 that is, during normal rutting, correction of the disturbed cycle did not occur. True, the boar had served both sows in December, yet neither became pregnant. Clearly they must have been in non-oestric condition, that is, not in rut. Not until the winter of 1941-42 could normal mating be achieved with the result that one sow (Mädi) had a litter on 24 April and the other (Rösi) on 4 May 1942. In 1943 Mädi had a litter of seven young on 15 April. A daughter of hers, born on 24 April 1942, gave birth to four young ones on 9 July 1943.

The disappearance of a circumscribed period and intensification of the mating behaviour could also be clearly observed in the bison, the rutting season of which in nature, according to M. S. Garretson (1938) 38, takes place between July and October. The cows calve, after a pregnancy of nine to nine and a half months, somewhere between April and June. We must assume that in freedom the bison cow does not calve every year, but every other. Unfortunately the origin of the Berne bison is not clear. At all events the first specimens came in 1914 from the Mülhausen Zoological Gardens. True, the bison in question had long been living in captivity. It will be seen from the adjoining table that there is a definite tendency to calve every year.
out a birth are few. There is also a tendency to spread the heat periods, and thus the calving times as well. The appearance of calves at the end of September is a striking symptom. The increase of births nevertheless occurs during the normal time, particularly May.

F. F. DARLING (1937) in his observations on the red deer in nature, found that June is the chief time for calving, but that odd calves, born of young kids and thus conceived late, can appear in August, September and even October. They then have poor prospects of living through the winter. This may also be observed in captivity. Calves born late in September have not sufficient time to grow their winter coats properly, and prove weakly. In nature a rigorous selection prevails, for young born out of season die, but elimination of this sort is not so strict in captivity. There is nothing to stop an extension of the period of heat, but it should be avoided by artificial separation of the sexes outside the mating season. This must be done with many animals, especially those where the males and females only live together during the breeding season, for example, red deer, chamois ibex etc.

Fundamentally, segregation of the sexes should occur in captivity the same way as in nature. In contrast to many other ruminants the male bison (M. S. GARRETSON 1938) for example, stays with the females in the mating season, as well as when they are calving. After the calf is born the steer assumes protection over mother and young and does not leave them until the calf is about five months old, returning again to the cows at the next mating season. In many animals e.g. the polar bear, strict segregation of the sexes is essential, otherwise
the cubs may be killed. In other species, again, the rearing of the young is exclusively the business of the male (e.g. stickleback, certain mouthbreeders, emu). Here the female may be dangerous for the younger generation. For these reasons, also, periodic separation of the sexes should be observed in captivity, as in nature.

Keeping the natural heat cycle by separation is essential, not only to prevent births in winter but because important periodic metabolic processes are linked with this cycle; e.g. moult and antler growth, which depend on the season of the year for proper development. A whole series of other physiological phenomena may thus be seriously disturbed by a spread over of the period of heat.

We can see the hypersexualizing effect of captivity in this spread over, and in a certain precociousness, found both in young born in captivity and in animals captured young and brought up in captivity. Berne offers a typical example of this. Up till now it has been assumed, from observations in the wild, that the ibex only begins to breed in its third year i.e. when it is two and a half years old (A. RAUCH (1937) 119). A flock of two young male and three young female goats, caught as new born kids, were therefore kept together without hesitation during their first year and a half. At the age of two years, each goat, strange to say, produced a kid. Thus the animals must have come on to breed at a year and a half. The kids of these precocious parents were obviously not fit to live, and the instinct of the parents for looking after them did not seem at all developed. They did not take to their young, butting them with their horns, or taking no notice whatever of them. The following year, however, births and upbringing were normal.

In captivity it is often noticed that the first birth or rearing of young fails. The offspring simply has the significance of a negative, disturbing or even threatening object for its mother. The harmonious sympathy between mother and baby usually so characteristic is often not even hinted at in primipares, so that the first birth gives the impression of a preparation or dress rehearsal for the second, which usually follows a completely normal course, distinguished by much maturer behaviour of mother and young. Marked immaturity among primipares of various animals, such as lions, has been described by A. Urban (1945) 213. In particular in the Indian black buck (Antilope cervicapra) immature mothers will not allow the kids to suckle or even come near. Ability to suck is not developed in the young, and the sucking reflex of immature young of this kind cannot be induced artificially.

The ibex (Capra ibex) is a particularly good example of the hypersexualizing effect of captivity. It shows this by extremely precocious maturity, and twin births, already noticed as a result of domestication or a phenomena of captivity by E. Backler (1917) 449). In a large ibex the author noticed persistent dermatitis between the forelegs as a very troublesome additional phenomenon of hypersexuality i.e. of a
mating season extending for months. During the rutting season the ibex, just like deer, chamois, many antelopes etc have a habit of retaining their urine and then squirting it hard under pressure against the belly and forelegs. In nature this phase may last a week or two. At all events it does not result in damage to the skin, but that may occur when squirting continues for many weeks. The ibex in question eventually had to receive medical treatment for extensive dermatitis.

It is likely that hypersexuality in the Indian elephant shows as early maturity. It used to be thought that these animals matured at an age of twenty to twenty five years (G. H. Evans (1904) 7), but recently in several European zoological gardens ability to reproduce has been observed when the elephant was ten or even eight. In apes, too, one suspects precocious maturing due to captivity.

Hypersexuality is most clearly seen in the many examples of sexual over-activity. S. Zuckerman ((1932) 217) thinks that regular provision of food in zoological gardens releases energies in the animal that are then used up in other ways, possibly in more intensive sexual behaviour. Captive birds, too, show a similar increase. Thus for instance, A. Kortlandt ((1940) 447) found far stronger sexual excitement in young captive cormorants than in wild ones. Even old ones showed increased sexuality in captivity compared with those in nature. A well known form of sexual over-activity in captive animals is excessive chasing of the female by the male, for example in the Cervidae or antelopes. Here, too, hypertrophy of valencies (p 31) should be taken into account. A female on heat attracts the attention of the male to an exaggerated degree, owing to absence of other diversions, lack of interesting objects in their surroundings, and their own lack of occupation, so that he cannot keep away from the female. Efforts are made with deer to prevent the harmful effects of this too vigorous pursuit by fitting up a barrier or selective compartment, which prevents the stags with their big antlers from passing, but allows the smaller does to slip through easily. This method is only useful with animals that show marked sexual dimorphism i.e. unequal size of body in male and female. It is a practical illustration of the hyper-activity mentioned. With chamois which often show strong sexual over-activity, and have no obvious dimorphism, O. Antonius ((1933b) 68) used a different method. At Schönbrunn in order to avoid injury to the female chamois after many unsuccessful efforts, he eventually made the active male wear a regular cap of vulcanite on his horns. At Basle the horns of the vigorous males were shortened by one and a half to two and a half inches and they were filed smooth, though this certainly had the effect of spoiling the beauty of their trophies.

Sexual over-activity at the breeding season is so widespread among many ungulates in captivity that provision must be made for it in fitting up their enclosures, especially by the avoidance of any sharp corners.
HYPERSEXUALITY

in their confined surroundings. Corners and angles into which the male could drive and keep the female must never on any account be allowed in their enclosures, states A. Usinger (1933) 14. The danger of sharp corners in enclosures was shown in the Berne moose paddock during a period of great activity. The female, once driven into such a corner, had no chance of regaining the open enclosure without butting hard. It even happened that a stag moose hoisted the cow on to his antlers and tossed her, so that the animals had to be separated for a time. Similar experiences have been had with antelopes in several zoological gardens.

In 1908 O. Heinroth published a summary of periods of gestation and breeding in a large number of species which is still of importance for biologists of zoological gardens today. The most comprehensive data are to be found in S. A. Asdell's book on *Patterns of Mammalian Reproduction* which appeared in 1946.
The Animal’s Relationship with Man

Degrees of Relationship

Relations between animal and man, naturally, may be very different in quantity and quality. There is a great gap both in the frequency of relations (quantity) and in their type (quality), between man and the free wild animal, that responds with flight reaction at the sight of him, and between man and the trained domestic animal that reacts sensitively to the slightest changes in his actions, voice or even mood. If we attempt to represent graphically the possible stages in the animal-man relationship we arrive at the following diagram.

Table VI. Diagram of possible Animal-Man Relationships

<table>
<thead>
<tr>
<th>Wild Animal</th>
<th>Transition</th>
<th>Domestic Animal</th>
</tr>
</thead>
<tbody>
<tr>
<td>wild</td>
<td></td>
<td></td>
</tr>
<tr>
<td>intermediate (half wild, half tame)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>tame</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Of course, this diagram does not show all the niceties of the animal-man relationship, which may occur individually from time to time with these stages as a basis.
Particulars about this table on the relations of animal and man may be found in previous works (H. Hediger (1935), (1938) 31). Here we merely summarize what is important for our present context. The plan shows all the degrees of relationship, with connecting links, which the wild and the domestic animal can have with man. These are arranged in an order corresponding to the stages of relationship in time, and in the frequency of connections between animal and man, which are undergone as a rule by a tameable wild animal successively until it has reached a state of tameness. These stages appear on the left hand side of the table. Here we can follow one and the same individual straight through from freedom to tameness and see how one stage of relationship leads on to the next one higher and more intimate.

We may disregard the right hand and horizontal part of the scheme, as it concerns the domestic animal. The wild animal, in its two possible basic forms of relationship—wildness and tameness—is what interests us. We should like to stress that terminologically speaking, tameness and domesticity are two fundamentally different characteristics. Tameness concerns the wild animal, domesticity the domestic one. The expression 'wild animal' is used here as the opposite to 'domestic animal'; by wild animal we mean the representative of a species of animal which has developed without the help or interference of man, while the domestic animal belongs to a species that has developed through interference by man, through his breeding methods. Thus domestic animals, in contrast to wild ones, are anthropogenic creatures. They are without exception the descendants of wild animals. The term 'wild animal' should not be mistaken for 'beast of prey'! A real wild animal is not necessarily a predator. A wild antelope or one newly caught, a wild hare or one freshly caught, are wild animals; that is, with the undiminished flight tendency of animals in freedom. Wildness means neither blood-thirstiness nor lust for killing but just flight tendency. The tamed wild animal is different from the wild animal because it has no flight tendency, that is to say it is emotionally stable. The wild animal in an intermediate stage of behaviour still has a certain amount of flight tendency, though much less than the animal in a natural state.

To adapt an animal to captivity means to reduce its flight tendency, to lessen its flight distance as far as man is concerned. Adaptation thus means reduction of the original tension caused by the presence of man; it means the breaking down of the physical and psychological state of nerves resulting from a constant need for flight without any hope of that need being satisfied. Adaptation is often judged in practice by the animal's willingness to take sufficient food, undeterred by the presence of man at a given distance. This, to be exact, is its original flight distance. During the intermediate stage of behaviour the decisive change of surroundings takes place (p 27). Half this change has been success-
fully accomplished with the acclimatized animal; all of it with the tame animal. Not every animal captured wild can make this change or accomplish the various stages of adaptation and taming. Those that cannot do so never recover from being captured, but die from extreme tension in the first stage, often of heart failure. This, as already mentioned, is the usual fate of old moose captured wild (L. Heck (1934) 7).

Taming means artificial removal of the flight tendency by man, and this intermediate stage leads to tameness. Tameness means lack of flight tendency and thus of flight distance, that is, it means emotional stability. The flight distance of the tame animal is zero; it allows man to approach it directly, to touch it, and even encourages active contact such as stroking, rubbing, and transference of warmth if it is of the contact type. Tame animals that keep a fixed distance away from others (distance types) allow neither man nor individuals of their own species to touch them. In spite of this their flight distance is zero, since the remaining limit of approach is made up, not of flight distance, but of individual distance.

Training represents a transitional stage through which the animal passes to reach the fullest kind of relationship with man; the state of being completely trained. For our purpose, training means special treatment of an animal with continuous use of favourable mental factors so as to produce certain actions at a particular personal command. These actions are natural to it, at least their elements are, but would never be released in freedom by the same stimuli or performed under the same conditions. (H. Hediger (1938b) 243.)

We need only add that tameness and training, in the senses just defined, can only be produced by man, and that the animal tends to change from a multiple relationship with man to one that is poorer. In certain instances, therefore, this weakening process can be stimulated by appropriate measures. The animal in nature tends to run away from man, it has a flight tendency. The captive animal tries to escape as long as it is still in a wild state. Again, the tame one may turn wild, and the one trained eventually forget its accomplishments.

**Meaning of Tameness**

Compared with the wild state, tameness for a wild animal in captivity has only advantages. It must therefore be strongly stressed that tame animals alone should be kept in zoological gardens. In contrast to the untamed animal objectively and subjectively suffering from considerable restraint, in a chronic state of tension, and hiding whenever possible, the tame animal appears quite unconcerned with complete subjective freedom of movement. It feels at home in the new surroundings,
MEANING OF TAMENESS

has shaped its world to fit the new conditions and enjoys complete ent­
harmony (harmony of the organs) and eph-harmony (harmony with its
surroundings). This double harmony is a necessary condition for nor­
mal reproduction in captivity.

The tame animal takes enough food without any fuss; its food intake
can be watched at close quarters. Its state of health, too, can be super­
vised far better. There is no need for remote diagnosis (A. E. Mou­
quyet (1925) 11). Unlike the untamed animal, in fact, it enjoys being
examined and, if necessary, handled as well. C. Stemmter (1941) 39
for instance stresses the advantages of tameness in the care of chimpan­
zees. He says that without protest they allow their wounds to be treated,
their ulcers incised; they can be bathed, which would be quite impossible
with untamed apes of this size, and even allow their bad teeth to
be pulled out. With the tame animal anaesthetics can sometimes be
avoided during essential operations, although they would have to be
used on the wild animal, not because they were necessary for the
operation itself, but in order to prevent it from struggling to get away,
a danger both for animal and operator (H. Hediger (1938a) 1846).

Finally, tameness in large animals is of great advantage when attend­
ing to them, changing their quarters, and especially when handling a
number together. With animals that have no urge to escape there is no
need to fear panic on such occasions, no attacks on their keepers, no
attempts to break out or incidents of that sort. It is obvious that there
is far less risk in handling tame animals than wild ones, though it is
impossible to eliminate accidents in dealing with animals; this is not
only the fault of the animal, but of man as well: first because of his
lack of ability to understand the animal’s position; secondly because
it is impossible to keep constantly on the watch. The ideal thing would
be to foresee the reaction of any animal in any situation; the experi­
enced animal expert comes very near indeed to this ideal. If such a per­
son meets with accidents in spite of everything, the reason is that
human watchfulness cannot be constantly exerted, and can only be
kept at its maximum pitch for a few seconds at a time. The animal
cannot be expected to do something unforeseen just at the moment
when the attention of its human partner is at maximum concentration.
There will more likely be times when his attention flags. It is probable,
too, that the animal is capable of recognizing the times when man’s
attention is strained and slackened or when he is absent-minded and
acts accordingly. The number of accidents is a measure of the man’s
understanding of the animal’s situation as far as attentiveness is con­
cerned.

To sum up the advantages of tameness; there are three reasons for
stressing the need for tameness in as many animals as possible in zoo­
logical gardens: tameness is attractive; tameness is healthy; tameness
is expedient.

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Meaning of Training

When we consider that the wild animal in nature is constantly pre-occupied with the impulses to avoid enemies and to seek food, and that both these highly important elements suddenly disappear in captivity, it is obvious that this change must have far reaching consequences. The captive animal's most important occupations are taken from him. Enormous amounts of energy are thus released and must somehow be restrained.

Clearly one of the most urgent problems in the biology of zoological gardens arises from the lack of occupation of the captive animal. This lack may have harmful results in various ways. Some of the secondary effects of captivity listed on p 31, which we should do our utmost to remedy, are very closely connected with it; especially the hypertrophy of valencies, which can appear in the shape of excessive anti-social behaviour, in dangerous sexual over-activity, in stereotyped movements (p 76 et seq; Figures 17, 18) etc. F. ALVERDES ((1925) 92) rightly pointed out some time ago that captive animals are condemned to inactivity. He came to this conclusion in connection with the analysis of particular behaviour patterns of monkeys; but the same thing applies to many other animals as well, such as predators, ungulates etc. It is clear that dangerous inactivity and harmful poverty of surroundings of this sort must be avoided at all costs. The captive animal must be given a new interest in life, an adequate substitute for the chief occupations of freedom. In the author's opinion this substitute can take the form of biologically suitable training and assumes the importance of occupational therapy.

These animals obviously often try to find something to do themselves. This has been observed countless times among mammals as well as birds. O. HEINROTH ((1938) 119) has something interesting to say about this. In nature, he says, parrots that mimic are unknown. It may be that through the boredom of cage life a desire to mimic is awakened in these birds and it can become so great that as soon as you say or whistle something in their hearing they sidle up, ruffle their ear feathers and listen very hard. Sometimes they even practise afterwards.

Naturally, the more highly organized the captive animal the more its lack of activity will be noticeable. No wonder, then, that training exercises were first tried out on apes. In progressive zoological gardens they have gone so far as to give large predators, as well as elephants, occupation through training. We see no reason why certain ungulates also should not have the physical and psychological benefit of suitable training. These animals could include one- and two-toed hoofed animals such as deer, antelopes etc.

There is no doubt that animals need more thorough biological treatment in this particular field. One of the main obstacles to an increase
MEANING OF TRAINING

in the use of training is, of course, a financial one; an expanded training programme needs personnel. From the biological point of view we can say once more, as with the problem of feeding, that saving money on this is unbiological. The captive animal should be kept under the optimum conditions, not the minimum, possible. As with feeding, there is every indication that here too increase in training exercises will be repaid to a considerable extent by the improved health of animals kept under optimum conditions, with consequent increased span of life and success in breeding. The majority of the four hundred or so zoological gardens in the world have a struggle against financial odds, and this shows that an investigation is needed; its significance has not yet been appreciated. First and foremost the position is due to the fact that fatal mistakes have been made in the financial calculations of newly established zoological gardens: usually minimum conditions instead of optimum ones, as well as measures for saving money which are biologically unjustifiable, have been planned. The financial calculations of zoological gardens must therefore be based on completely fresh grounds, namely on the optimum treatment of the animals. In future, new establishments running into serious difficulties can be avoided to a great extent by proper regard to this. Even nowadays zoological gardens for which there is no real need, and which have no financial support either, are being opened.

In the animals’ own interests we cannot refrain from saying that certain societies for the protection of animals would do far better to insist, where possible, on good i.e. biologically suitable, training; they should foster understanding of this in the widest circles rather than oppose blindly any training of wild animals on the basis of arguments that have long become completely untenable. Through their opposition to the training of animals they do them real disservice. On biological grounds alone, as has just been shown, the captive wild animal must have a certain amount of training.

The commonly held opinion that training is unnatural is wrong and is based on the mistaken notion of the natural treatment of animals which has already been dealt with in the chapter on the quality of the environment. Natural i.e. biological treatment, does not mean a pedantic attempt at imitation, either in the matter of space, or food, or the animal-man relationship, but an adequate substitute for natural conditions and a sensible interpretation of them. This does not imply forcing the animal that lives in a confined space in captivity to be actively engaged in constantly avoiding its enemies and struggling hard to get food, as would be the case in freedom. It consists rather in substituting activities suitable to the conditions of captivity, and this means training. Regular training exercises are not only necessary for many animals psycho-hygienically, but are to the animal’s advantage from the physical point of view. Training for captive wild animals corresponds
more or less to the sports and athletic competitions of civilized man. Physical stimulation of the kind produced by proper training will succeed at least to some extent in preventing, or at any rate reducing, the appearance of various symptoms of captivity. These may take the form of reduced size of body, weaker muscles, lighter skeleton etc. Training will also counteract the complex changes due to captivity and domestication.

The more complex the animal's organization, the more it feels the enforced lack of activity in captivity and the sooner does it try to do something for itself for lack of suitable occupation and amusement. In the bear pit at Berne, where the animals are not trained, and have no suitable playthings, a bear was seen in winter spontaneously making a snowball and playing with it (F. A. Volmar, 1940, 377). Begging, too, often represents a kind of misguided occupation. In 1934 the author watched a chimpanzee that was kept on its own at Hagenbeck's. It drew the visitors to its cage by screaming, then put a brick on its back and walked round its cage with it for a while. When a large enough crowd of onlookers had gathered the chimpanzee got hold of the brick and threatened the delighted crowd with it. Suddenly, it dropped the brick, which it had never been able to throw through the bars, and as quick as lightning picked up a handful of sand from the floor and scattered it among the spectators, who ducked screaming but who soon came back again. The chimpanzee repeated this sand throwing several times, always pretending to throw once when his hands were really empty. The lightning retreat of the spectators at this make believe sand throwing appeared to give the animal great delight; this was the end of a game which the author was able to observe for a considerable length of time.

The imperative need of the captive animal for something to do follows clearly enough from the analytical comparison of freedom and captivity, and shows itself unmistakably in practice. It is an important task of the biologist of zoological gardens to satisfy this great need. The most suitable way is by training.

Through training the impoverished surroundings of the captive animal become enriched by new interests; the animal's attention is divided so that there are no longer excessive hypertrophies i.e. extreme and often morbid fixation of the attention on a single part of the surroundings, or on a few parts. The predatory animal, for example, no longer devotes its attention exclusively to food; its interest is aroused in the training itself, in the preparations for training by the man it comes into contact with during training etc. Animals that have been trained have often been seen going through their training exercises spontaneously alone. During a pause in an exhibition of training for a group of bears, when the exhausted trainer was sitting down on a stand to get his breath back, the author watched a bear, obviously in
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less need of a rest than the trainer, get on its scooter and begin to do a few rounds on it all by itself.

The disastrous monotony of the captive animal's life is pleasantly interrupted by training. Contact between man and animal is intensified, often so much that the man is eventually accepted as a member of the same species, and incorporated into the social structure of the group. This intimacy with the animal has interesting psychological possibilities and often practical advantages as well, similar to those of tameness, but to a greater degree. In addition the material value of an animal, or of a group of animals, can be greatly increased through training because groups of trained animals have more show value than raw animals. From all this we can see that as far as the interests of the captive animal are concerned, training is a necessity. Like tameness being trained is healthy, expedient and attractive.

The aesthetic importance of training and trained animals is still often under-rated. Not enough spectators are capable of appreciating the artistry of the performances of a good man or woman trainer. The attention of the public is focused too much on the primitive danger element, or the technical side e.g. with performing tigers. Yet there is another way altogether of regarding first class performances. The good trainer creates something out of the inimitable movements of the wild animal, just as the artist does with his colours or the composer with notes. The quality of this artistic creation lies in the harmony of the animal-man relationship, in the delicacy and precision of the animal's achievements in individual performance, in the pattern of group performances to form an original blending of individual biological movements. For this reason, the performance of an outstanding trainer might be compared with the work of a composer of music. The latter, using his special gifts, carefully chooses and combines the various instruments of the orchestra, and from his musical experience knows how to demand from each instrument at a given moment just as much as he needs for a harmonious ensemble. In the same way the trainer skillfully groups his animals, and by carefully arranging the interplay of their actions and counter-actions, with the help of biological factors, produces the reaction from each of his animals that the performance as a whole requires.

It is obvious that standards as high as this should not be demanded from practical training in zoological gardens, cannot, in fact, be demanded. Indeed, a performance of the sort just outlined (see Figure 32, facing p 141) means such extreme exhaustion for the trainer that his daily work would be nearly swamped by it. In zoological gardens only simple occupational training can be undertaken; performances of a high standard may safely be left to the circus.
Pathic Attitude towards Man

It is well known among keepers of zoological gardens that the same animal sometimes reacts in quite different ways, even in opposite ways, to two or more men of apparently identical behaviour. Even in the street we often notice that many dogs bark at some people but not at others. B. M. Klein (1939) gives a full account of the various reactions of a Siamese cat to the people it came across. The African elephant 'Madi' of the Basle Zoo will accept only three keepers and we have been unable to introduce a new one. A fine specimen of an ibex took a dislike to a new assistant keeper; it stubbornly blocked his way into the feeding shed with its powerful horns and resisted every attempt of his to enter. It had to be fed temporarily by a keeper from another department. Birds, too, and even reptiles, sometimes react in this way. From the very start, a person is either sympathetic or antipathetic to the animal.

This fact is of the greatest importance in keeping animals. It is in the best interests of both man and animal for the relationship between keeper and charge to be as positive as possible. It makes for avoidance of accidents, and simplifies running of an establishment. In addition to the purely individual sympathies and antipathies between animal and man just mentioned, there are certain kinds of men who are unusually happy in their relations with wild or ordinary animals, whilst others meet with constant difficulties. This does not always depend on the right sort of training; there are born 'animal men'. Often, certain categories of people are preferred by the animals. According to D. Katz (1937) for instance, Koehler's chimpanzees preferred children to adults. The same thing was noticed in one of Yerkes's gorillas; among adults it preferred men to women. In other instances the reverse is true. The author has already shown (H. Hediger (1935) that this is not an example of the so-called 'rule of contraries', i.e. the theory that men are always more successful in dealing with female animals, and women with males.

Here we must be careful to distinguish between a genuine pathic attitude of the animal towards man, that is, its basic attitude, and secondary preference or inclination for certain categories of people or individuals based upon experience. In reference to this basic attitude D. Katz goes so far as to say (1937) that animal behaviour of this kind may even provide a new basis for a classification of human types. The importance of the pathic attitude of animal to man for zoological gardens is greater than its promise for human psychology, since it is something we have to make allowance for. The animal should not be given any keeper, however well qualified, but a man who appeals to it pathically. This pathic attitude must be positive on the man's side.
Everybody has not the same emotional attitude towards every group of animals.

The zoological garden and the circus are diametrically opposite to laboratory experiments in animal psychology as far as the sympathetic attitude between man and animals is concerned. In scientific experiments, any emotional influence of the investigator upon the animal under experiment is carefully avoided, but these emotional relations play the chief part in the zoo and circus. Consequently two completely different sides of the animal’s psyche emerge from this, either of which by itself is incomplete, and hence misleading. Just as the chemist wants to know the properties of a substance in as many different combinations as possible, the biologist, especially the animal psychologist, is intent upon observing the behaviour of the animal under as many different conditions as possible. In contrast to the principles of animal observation with maximum exclusion of the animal-man relationship, essential for experiments in the laboratory, in the zoological garden, as well as in the circus, the animal-man relationship should be allowed full play. During this intimate intercourse, the positive pathic attitude of the animal to the keeper is often clearly shown. Every trainer has had experience of animals defending a trusted human being against the attacks of other animals. Heck has described in detail (in a newspaper article) how his keeper was successfully defended by Toto, the chimpanzee, against an attack from Bobby, the powerful gorilla, living in the same cage. The pathic attitude between animal and attendant can sometimes help to save life in an emergency. On the other hand there are many cases of animals afraid of other animals seeking the protection of the man they trust. The author watched a bear in a mixed group of bears and lions taking refuge from the lions by its trainer’s side and sheltering behind the man it trusted (see Figure 33, facing p 141). When Yerkes (quoted in D. Katz (1937) 226) was walking past a lion’s cage with a gorilla, it took cover behind its human escort.

Assimilation Tendency

A characteristic of men as well as animals is the tendency to regard animals of different species, between which there are intimate relations, as if they belonged to the same species. This is particularly so the more primitive the type of man in question. This tendency to assimilation, appearing in man in the form of a variety of anthropomorphisms, occurs in the corresponding form of zoomorphism in animals. It has already been discussed from the aspect of comparative psychology in two previous articles (H. Hediger (1940a), (1941)). We are dealing briefly with it here simply because of its effects on the biology of zoological gardens.

Anthropomorphisms—This form of tendency to assimilation is much better known than the corresponding zoomorphism of animals. We
have already shown how wrong, from many points of view, are anthropomorphic methods of observation in biology. It is also necessary to get rid of a lot of the anthropomorphic tendencies still current in the practical management of wild animals, and in the biology of zoological gardens. To do this, a complete reorganization of the treatment of wild animals on biological lines is urgently needed. The problem of space has been dealt with at such length in this book because people still approach this subject with an anthropomorphic bias, especially with regard to the free-living animal. Fatal anthropomorphisms also affect the treatment of the food problem. It is natural, therefore, that in the third group of problems, the animal-man relationship, discussion of the common anthropomorphisms should be unavoidable. Only a few essential points can, of course, be touched on.

All anthropomorphisms in the treatment of animals are fundamentally wrong. Since there is a natural tendency for them in every human being we must keep on asking ourselves, whenever we are dealing with animals, whether our attitude is the right one for the animal, and free from anthropomorphisms. There are two things which can be dangerous for the animal; one extreme leads to pampering, and the other to the venting of human spite.

This pampering can sometimes develop into the grossest forms with pets such as dogs and cats, which may be turned into social, even erotic or sexual, substitutes by man. There is less danger of this with wild animals chiefly because of their greater flight tendency and capacity for self defence compared with pets. The young tamed animal is more exposed to this danger than the full grown wild animal. Both for space, food and the animal-man relationship, pampering leads to treatment of the animal that is quite unsuitable i.e. completely unbiological. It often results, among other things, in those forced contacts which animals of the distance type find quite unbearable.

Here we must add that children are often brought up with an anthropocentric attitude to animals. They learn by experience to have a highly anthropomorphic attitude to toys (H. HEDIGER (1941) 53); one has only to think of dolls, rag animals etc. The same thing applies equally to live animals that have to act as play-things. There is no doubt that the children's zoos that have been the fashion in recent years have sometimes had a harmful effect. By children's zoos we mean special enclosures to which children have access and in which young animals are kept, mostly domesticated, kids, lambs, young pigs, besides rabbits, guinea pigs and others, and occasionally quite young wild animals too.

The idea underlying all this is to allow children to have the most intimate contact with the animals; of course, only quite harmless and inoffensive animals are used. The way this basic idea is put into practice in many places is wrong educationally and from the point of view of
ASSIMILATION TENDENCY

animal psychology. Instead of children being taught to approach animals with respect and the greatest possible understanding, they are actually encouraged in children's zoos to order the defenceless animals about and to treat them just as they like.

True, many animals are very fond of being stroked and scratched, and like the transference of body heat etc. This will be true for contact animals. On the other hand there are many animals that find it unpleasant or intolerable to be touched by human beings or even by members of their own species. These are the distance animals. Children should be taught that love of animals does not consist in making complete nuisances of them, but in getting to know their characteristics and their needs. Through understanding and appreciation, they should be persuaded to give up wanting to satisfy subjective anthropocentric desires, usually aimed at excessive petting.

Friendship between animal and man, in the sense of intimate positive relations, can only be achieved by unforced, voluntary approach on the part of the animal, and not through the irresistible force of contact. The danger is that in children's zoos the basis will be laid for that wrong and stupid pampering, that selfish pseudo-love of animals which can appear in such revolting forms in adults, where it sometimes leads to excesses that are a real torture for the animal. By love of animals we mean a healthy delight in the animal, but with the greatest possible consideration for its biological situation.

Naturally there are children's zoos of a very different kind, where under sympathetic control children are responsible for certain domestic animals, especially popular fairy-tale figures, in a practical and valuable educational way. The value of a children's zoo, or the lack of it, is largely the result of the care taken by the staff in charge, and here plenty of staff should be provided, as they should everywhere else in the zoological gardens. It is also important for suitable explanations and introductions to be given to the children by teachers or other persons with them, even more so here than in their visits to other sections of the zoological gardens.

In the olden days animals considered sacred, as in ancient Egypt, such as lions, baboons, crocodiles etc suffered from a special type of pampering. These animal gods were often kept in temples and surrounded with pomp fatal to them. They were provided with food chosen on the basis of what would suit human tastes; were bathed, anointed and perfumed. Many of these animals were provided with sunshades inlaid with gold. Food was offered to the lion god in the sun temple at Heliopolis to the accompaniment of hymns. The sacred crocodiles of Lake Moeris that came up at the call of their priest keepers were decked out with bangles and necklaces (G. Loisel (1912) 15). This unnatural treatment of animal deities caused pathological changes in many, as Lortet and Gaillard (quoted by Loisel,
have pointed out in their exhaustive researches on mummified animals.

The other kind of humanizing in extreme instances leads to the venting of human spite on the misunderstood animal. If possible it is punished in a human fashion. The critical reaction of a predatory animal driven into a corner, for instance, is sometimes misinterpreted as viciousness or treacherous attack, as vengeance or blood-thirstiness etc. Actually it is simply the normal result of a type of behaviour following a biological impulse. An animal that disobeys commands, for example, during change of quarters, or in its attitude to its food, or in its deposit of excrement and urine etc is regarded as vicious or stupid. It is, of course, prevented from obeying man's orders by its flight tendency or by other biological circumstances, or else it completely fails to understand man's meaning. The dangerousness of an animal, even in written works, is still often thought of as viciousness, an idea not only quite wrong in theory, but invariably leading in practice to unbiological anthropomorphistic remedies. The so-called dangerousness of large wild animals is almost entirely caused by critical reaction, the demands of social rank, or may even be purely accidental, as for instance, in play, taking food that is offered, and so forth.

Zooanthropism—The humanizing tendency of man, as we have said, corresponds to an animalizing tendency of the animal; thus the animal sometimes considers a man as one of its kind, and consequently treats him as a member of the same species. The man then enters into the social organization of the corresponding animal group. Whether he likes it or not, he must play the part thrust upon him in accordance with the ceremonial peculiar to that species. It goes without saying that among larger animals man must at all costs assume the a-position and always keep it. He must be ready for social disputes, even with completely tame, harmless individuals. A great deal of so-called in-calculability, cunning etc is in reality nothing but social crisis induced in the animal by biological impulse. The animal must know whether it is socially inferior to its partner or vice versa; without a definite decision the animal is not, and cannot be, at ease. If the man puts off, or, through mistakenly interpreting the facts, intentionally neglects a decision on the social situation between himself and his animal partner at the proper moment, he at once gives the initiative to the animal, and it will then take it at the least expected moment. This is obvious for all animal tamers (H. Hediger (1938b) 249); yet among outsiders it is often unknown or underestimated. It is well known, for example, in the training of dogs, and various writers mentioned it long ago, for instance, F. Alverdes (1925) 77). He says, for chimpanzees, the man they have accepted as a friend belongs to the group. Furthermore, keeper and pet form an organized alliance, in which the former is 'despot', the pet the 'subordinate' (in Schjelderup-Ebbe's sense);
the social rank is decided once and for all (p 129). D. Katz too (
\(1937\) 225) has pointed out that man can sometimes be incorporated
into the animals' social rank.

The fact that man can be incorporated as a fellow member into the
social organization of animals has practical advantages and disadvan-
tages. Its theoretical psychological importance will not be dealt with.
The disadvantages consist chiefly that the man accepted by animals is
involved in disputes or scenes over social precedence and is, therefore,
bound to assume the premier social position himself unless he is willing
to give up close contacts with the animals for good. As a socially
inferior creature, a man would not only be a dubious figure, but would
be in serious danger in a group of big animals. They would take any
liberties they liked with him. It is lucky for man that quarrels about
social rank among higher animals do not always depend so much on
physical superiority, which would mean fights to the death, as on calm,
unruffled behaviour, that is, on psychic qualities. When two creatures
meet, the one that is able to intimidate its opponent is recognized as
socially superior, so that a social decision does not always depend on
a fight; an encounter in some circumstances may be enough. Man can to
some extent control the intensity of the encounter by suitable measures;
this would not be possible if physical superiority were the decisive factor.

Where the animal is clearly superior to the man, physically, con-
siderable effort is needed on his part to behave at critical moments like
an unquestioned superior. Yet man has definite possibilities of preju-
dicing the result of social encounters in his favour by making them
take place in surroundings foreign to the animal. Earlier (p 8), we
stated that unfamiliarity with surroundings has a depressing effect
during fights between animals, and decreases the prospects of success;
familiarity with the surroundings on the other hand stimulates i.e.
improves the prospects in a fight.

The ideal place for this is the circus ring. With difficult animals the
trainer first openly takes possession of it, so to speak, before allowing
the animal in: it is in an inferior position in its surroundings com-
pared with the man standing in the centre. Here again, the circus ring
proves a highly suitable place. Lack of corners removes all chance of
the animal taking cover; thus the man can give his superiority full play
and drive the animal back at will. In contrast to the circus, the animal
in the zoological gardens is usually in its familiar cage and the man is
let into it. The psychological situation is now less favourable for him
and is only possible with a young or completely trustworthy animal. A
more convenient arrangement and therefore one to be used with all
difficult large animals is that the keeper should go into an empty cage
and afterwards the animals be let in from a neighbouring enclosure.
The presence of corners, obstacles etc in the cage is an obvious draw-
back here, compared with the circus ring.

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For the man accepted by the animals, the advantages of being accepted into their social organization are of various kinds, assuming that he occupies the α-position. The man enjoys all the privileges that the α-animal in the group possesses, in particular, complete freedom of movement. All inferior animals must obey his orders without question. The superior man can, to a certain extent, interfere within their ranks, subdue quarrels, and, if necessary, protect individuals that are being bullied too much. It is a common experience that animals occupying a low social standing attach themselves unusually intimately to men. In the circus training groups the ω-animals are usually the best to work with and in the zoological garden the ω-animals prove the most faithful and in most need of company. This applies to predatory animals, and to many others as well, and holds good for bisons, red deer, wild sheep, ibex, monkeys etc. Often the ω-animals go to man for protection, as W. Köhler (1931) noticed with his chimpanzees. Illness results in a drop down the social scale, and so a specially strong attachment to man is noticeable in sick animals (W. Köhler (1931) 293); often very useful for giving suitable treatment.

In practice, an unpleasant result of the animal's tendency to assimilation is that the favoured man is not only accepted by them as one of their own species, but is considered and treated as a fellow member of a particular sex; thus during the breeding season they either try to fight over him or to mate with him. The animal is often wrong, too, in its diagnosis of sex. When a tame roebuck has a tendency to drive off every rival, he will fight fiercely during the rutting season to remove all rivals of his own sex. The roebuck always regards man as a rival of the same sex so he tries to attack him vigorously. This is the reason for the so-called viciousness of all tame roebucks. Other species sometimes mistake the man they have accepted for a female of their species and try to mate with him. A tame emu in the Basle Zoo regularly tries to mate with its keeper during the mating season in winter. If, as was once observed, it happens with a moose, the man concerned is in some danger. Here the tamest and most trusty animal can become a danger to the man. This behaviour has nothing at all to do with viciousness.

The animalization of the man is usually only found first when a certain degree of intimacy (tameness) exists between animal and man, and secondly when they more or less correspond in size. We are not yet sure how great the difference in size can be. Small animals often make a partner of only a part of the man; an otter, for instance, of one leg only of a man; a cock, of only his shoe etc. An otter, brought up on its own, regarded its keeper's leg as a mate, and it was surprising to see how completely the innate mating behaviour was transferred to this substitute. Clearly the otter bites the back of the female's neck during mating, because this particular male invariably grasped hold of his keeper's trouser leg during his attempt at copulation and seized a
fold of the cloth between his teeth. K. Lorenz (1935) 311, who thinks the frequent animalization of men by birds is due to the phenomenon of treading, described by him, gives an account of a ring dove (Streptopelia risoria) for example, that attempted to pair with the human hand. The young of mammals and birds may identify the animalized human being with parents of their own species. Man can have for them the significance of a parent companion in Lorenz's sense (1935). H. Brull too (1937) 69 speaks of human beings as parent companions of young birds of prey. T. H. Gillespie (1932) 132 gives an illustration of a young king penguin that forced itself between a man's feet just as it would have done with its real parent. The author has not yet come across an instance of reptiles where the young regarded human beings as parent companions. Among species with a highly developed care for their young e.g. the alligator, this does not seem to be unlikely.

Both Sides of the Zoological Garden

It happens even now that zoological gardens are opened without the founders realizing that in these days they are not just a local entertainment centre, as earlier individual menageries were. Zoological gardens cannot have isolated existence today. They are necessarily linked up with the long history of development which the keeping of wild animals has undergone in the course of centuries, and this means they have responsibilities. Every zoological garden is a part of the whole system and must fit into the picture along with all other zoos. The important knowledge gained in past and present zoological gardens demands suitable recognition. As in medicine or in technology, the biology of zoological gardens allows of no slap-dash individual experiments. In short, the keeping of wild animals in captivity implies responsibility, historically conditioned. The zoological garden should not be solely a place for the amusement and entertainment of the public; it has also the duty of acting as a centre of popular education and is thus bound to keep up with research and to take an active part in it. This means that a zoological garden not only has to function so to speak as a technical service internally, but must keep up externally the most active interest in educational establishments and research. Thus the zoological garden has two sides and two spheres of duty to fulfil.

The inside--This includes the whole internal organization; administration, buildings, technical side, stock of animals, personnel and public. Administration has least connection with biology and so will be discussed no further. Buildings and the technical side have already been dealt with from their most important biological aspects in the section on the problem of space. A fundamental difficulty is often met when attempts are made to fit the demands of the architect in with those of
the biologist or of the animals. In the long run the biologist’s demands, acting on behalf of the animals, must decide. The architect’s demands must logically receive only secondary consideration in the zoological garden. The director must not give in to the architect, says L. Heck ((1941) 358) with his unique experience of zoological gardens. The ideal is without doubt a real symbiosis, or harmonious understanding, between biologist and architect.

As far as the stock of animals is concerned their rearing, feeding and treatment have already been dealt with from the most important biological aspects. There is one fact of a biological nature concerned with administration that we should like to mention, and that is the list of animals in stock, treated by individual zoos in widely different ways. This record should contain the greatest possible number of details about the greatest possible number of individuals in stock if it is not to be purely an administrative instrument instead of also a valuable biological one. The problem has been tackled by H. B. Peters ((1933) 192). The difficulty lies in the fact that the list of animals in stock, without becoming unwieldy or losing clarity, ought to give continuous information about a number of similar animals, as well as about many completely different ones. It should not be confined to the individual, but should include the ancestors, the progeny, and record important events in its life such as illnesses, growth etc.

There is a great deal to be entered about some species while others have little worth recording. Thus the register of stock must contain the biographies, so to speak, of as many individuals as possible. Here again inequality of material about the animals compared with their length of life raises difficulties which can only be solved by maximum elasticity and strict impartiality. The basis for a biographical record of a single individual is its distinctive characteristics. This is a simple matter with popular big animals that have well known names; others must be given special marks (e.g. ear marks) where necessary. Birds can easily be ringed; individual reptiles can sometimes be recognized by peculiarities of colouring or of scale structure. It is harder to tell individual amphibians and fish or many invertebrates, and it is only possible to keep partial records for them. In the Basle Gardens all birds are ringed and individually entered in the register; most reptiles, too, are individually recorded, as well as amphibia, many but not all fish and occasionally a few invertebrates. The register consists of a file containing two kinds of cards 10 in by 15 in (Figure 31). The white cards contain individual particulars; the green ones are the so-called record cards on which biographical data are kept. Both kinds of cards are serially numbered and on the first the number of additional sheets is entered. The record cards of one species are placed next to the white cards of that species. All important details are noted on the record cards e.g. with stags, the time of rubbing the velvet off their antlers, of rut, and
Figure 31. Reduced facsimile of record cards of the animals in the Zoological Gardens, Basle. Only headings (translated) are shown. 

- **a** White card for individual particulars; 
- **b** Reverse of a; 
- **c** Green card for chronological entries of biological details; 
- **d** Red card for constant parasite check.
of shedding their antlers. Illnesses and their causes are noted as well as special behaviour, accidents, changes in social organization, important growth phenomena etc. All animals are periodically weighed and measured providing this does not mean too great expense. A third type of card (red in colour) serves for entering the results of the periodic parasite check of faeces so that the parasitic state of any animal can be seen at a glance.

From the biological point of view the personnel should be selected first and foremost from ‘animal men’ (p 162) as far as keepers are concerned, though not, of course, for technical or administrative staff. We ought not to have to refer to this obvious requisite; yet it is obvious that even now there are many zoological gardens where people are employed as keepers who would be far better in other jobs. Suitability for the job is particularly important in zoo staffs, for they have to deal not with inanimate objects but with living things. The wild animal is a particularly sensitive creature, and its happiness depends to a large extent on the innate and acquired qualities (e.g. the pathetic attitude) of the keepers. Equally dependent on these factors is reliability in working on which depends accident risk, settlement of disputes etc.

The public is the chief reason for the existence of most zoological gardens, but experience teaches us that it also provides the greatest source of danger for the inmates. The duty of the animal biologist thus not only lies in taking appropriate measures to protect the public from the animals but also, conversely, to protect the animals from the public. There are three reasons for this. First, because the public is the chief source of infection for delicate species of such illnesses as influenza, tuberculosis, colds etc. This applies especially to apes, which in practice can only be kept free from infection by the use of glass partitions. The second serious danger lies in the offering of unsuitable food by the public. The third is the possibility of direct harm or indirect damage to the animals by worrying, teasing, frightening, or exciting them.

B. Murer (1939) refers to the fact that after days when the number of visitors has been large, more digestive disturbances, for the most part not fatal, occur than after days when the number of visitors has been small. C. Stemmler (1941) observed among the apes he was attending that the state of his charges' health was favourably affected by the absence of the public owing to an outbreak of foot-and-mouth disease at the Basle gardens. He says that during this long period he was unable to observe the slightest change in the health of any of the five anthropoids; in normal times one or other of the apes was upset once a week on the average. For the first time that winter all his larger monkeys were free from colds. As already mentioned, the apes in the Basle Zoo are kept in conditioned cages behind glass. According to J.
Dobberstein too (1936), after days when there had been large crowds, cases of serious indigestion occurred regularly, sometimes with fatal results. It must be confessed that the titbits brought did not always fulfil the demands of a perfect diet. He goes on to state that unfortunately there is a mistaken notion, impossible to eradicate, that tainted food no longer fit for human consumption can be eaten by animals without harm. Mouldy bread, spoilt vegetable refuse, rotten food, cause just as serious disturbances in health to animals as to man. How great the ignorance of visitors is in this respect can be seen from the fact that a polar bear contracted severe enteritis with haemorrhage after it had been fed by a woman visitor on putrid sea fish, brought expressly for the purpose.

The public’s anthropomorphistic idea of what constitutes a titbit is particularly dangerous. Sweets are offered to the most unsuitable animals. In spite of strict rationing during the war, lumps of sugar were found in different enclosures. Many animals contract gastritis or enteritis through eating too many carbohydrates, especially sugar (B. Murer (1939) 18).

The most serious thing about public visits to zoological gardens concerns those people who, from malice or a morbid disposition, deliberately maim or kill animals (e.g. with poison). A case of malicious poisoning of this kind by a morbidly disposed visitor was noted by J. Dobberstein (1936) during the 1914-18 war, among several young bears in a zoological garden in east Germany. The historic giant sea-elephant bull “Goliath” of Hagenbeck’s was the victim of a similar crime in 1930. In its stomach was found a broken beer bottle which had caused severe perforations killing the powerful two-ton animal after a dreadful death struggle. Other cases were a seal’s eyes poked out with a walking stick and a bird’s beak, a shoebill (Balaeniceps rex), famous for the striking shape of its beak, smashed with a hammer. Several years ago in a North American zoo a man with a mania for publicity was caught in the act of taking a cobra out of its cage during the night and putting it into an empty violin case brought on purpose. In the zoological gardens at Geneva, now defunct, the elephant there was given an apple by a member of the public in which were sticking a lot of pins. In her excellent book, B. J. Benchley (1942) 308) mentions a number of similar sinister examples. Razor blades were found in the otters’ and sea-lions’ pool in different zoos. A roebuck was stabbed by a walking stick. A magnificent moose stag was poisoned after it had already suffered from several malicious attacks. Six months previously its beard was cut off by some unknown person along with a strip of flesh the length and breadth of a finger, and thrown into the hedge. An abnormal case was that of a man who had developed the habit of urinating straight into the moose’s mouth; he was eventually sent to prison. Even seventy years ago there were remarkable cases of
poisoning in the Berne animal enclosures. Between 11 and 19 July 1872 seven of the deer then kept in the city moat died through mercury and copper poisoning (H. Putz (1872)). Experience shows that no zoo in the world is safe from such regrettable incidents.

In all ages and places menageries and zoos have attracted not only men with a healthy interest but all kinds of abnormal ones upon whom the zoo seems to act like a magnet. If one were to classify these undesirable elements, and no zoo in the world is safe from them, the following headings might perhaps serve as a starting point:

1. Petty criminals
   a. Trespassers. In this category come all those who squeeze through the turnstiles, climb over the walls or get into the zoo by any other illegal means such as skeleton keys, back doors etc.
   b. Damage and destruction. This includes the numerous visitors who wilfully damage or destroy the garden's flower beds, technical fittings, name plates, notices, automatic machines etc. In addition the number of people that unscrupulously feed the animals with bad food, or when it is expressly forbidden, and quite obvious that by so doing they may endanger the lives of valuable animals.
   c. Thieves. All kinds of small animals like rabbits, birds etc or even eggs, frequently disappear from the gardens through visitors running off with them, or through people breaking or climbing in at night. What has been stolen (usually domestic animals) can be eaten or sold to breeders; but the theft of valuable exotic animals or exhibits of trophies (e.g. the prize stag's antlers at Hagenbeck's Zoo) by many collectors and animal lovers obviously has other motives, and often comes under the following heading.

2. Psychopaths
   a. Sexual perverts. These play a certain part in zoos. The most harmless ones for the management are the 'voyeurs' that specialize in animals. They devote themselves to watching the sexual activities of the animals openly and for long periods. Representatives of another group, related in some ways, are those in the habit of standing by the cages and enclosures and insulting spectators of this type. Much annoyance is caused by those aggressive men visitors who make advances to women or children in the darker parts like the aquarium or open aviary. Usually complaints about such molestation only reach the zoo authorities long afterwards so that it is often very difficult to catch these undesirable elements.

The most serious sexual perverts in the zoo are, without doubt, the sadists. From the point of view of the management they are the most dangerous visitors as they have a pathological desire to torment, injure, or even kill the animals. They are the ones who stick knives, hatpins and similar instruments into the unsuspecting animals, offer the animals pieces of meat with fish hooks, open safety pins etc.
them, push a stick or an umbrella through to put an animal’s eye out or injure its sexual parts etc. These people can also be extremely dangerous because they may throw stones and sharp or pointed objects, use catapults or finally give poison. The closest possible watch is the only remedy for them.

Sodomites are far rarer but do occasionally work their mischief in zoos, especially at times when there are few visitors about. Often their intentions are defeated by the railings. Sometimes the most unexpected animals are chosen by these perverts, not only monkeys, ponies etc.

A case was known in Basle of a visitor giving trouble to a male Beisa antelope known to be dangerous.

Other psychopaths. Completely unexpected and unpredictable incidents can occur through people with a mania for publicity. They do something quite extraordinary as for instance the nocturnal cobra theft mentioned, simply to focus sensation on themselves. Much less harmful are certain religious maniacs like the ones observed in Basle that threw religious tracts into the snakes’ terrarium, apparently in order to banish sin in the shape of snakes to these persons. Just as harmless, though sometimes a bit of a nuisance, are those psychopathic animal addicts who, for example, want to play music to certain animals in the zoo in order to brighten their existence, or who bring their pet tortoise to the zoo and put it into the terrarium with other tortoises tied to a string so that the lonely thing can have company.

Weakminded and Idiots

If these are not properly watched or are left on their own they may be a special danger in those zoos where the public has free access to certain animals e.g. deer, tame antelopes and the like. Their abnormal behaviour, bearing and gait have been known to over-excite many animals, so that people of this sort have suddenly been attacked by animals usually quite reliable. On the other hand the danger with such visitors and with drunkards too is that they may open doors and go into enclosures, cages and service quarters, if these are not kept properly locked, and so cause all kinds of accidents.

Murderers and Suicides

The foregoing naturally makes no claim to be psychiatrically correct but was written rather from the zoo managements’ point of view. Fatal accidents are bad from any angle of course, and the zoo must do all it possibly can to avoid them. The use of wild animals for accomplishing murders is fortunately restricted to novels. On the other hand rare cases occur of zoological gardens becoming the scene of serious crimes. Very exceptionally they are chosen by suicides to perform their tragedies. A particularly dreadful case of this sort happened in 1944 in the gardens at Zürich; a woman mental patient climbed in at night, gained access to the elephant house through a window and was killed by the young bull Indian elephant ‘Chang’. The body was torn
to fragments by the animal and trampled flat. The elephant had to be shot later (1947) because it injured several keepers and killed one.

Quite apart from pathological cases of these kinds, the people that visit zoological gardens must be taught a new attitude towards animals. If they are to be emancipated from the primitive tendency to humanize they must have a truer, more positively biological attitude towards zoological gardens. Nowadays a garden is not just a place of amusement but a biological institution as we have said. Thus its task is to spread biological facts of a special kind. Whoever, nowadays, just wants to study the animal itself will find the opportunity in those museums where the various types of animals and the characteristics of their morphological organization are displayed with such commendable clarity. The modern zoological garden has something else to show besides that; not only the animal itself, but the animal in relation to time and space; not the animal as an object any longer, but the animal as a subject.

Instead of only asking the question 'What does the animal look like?' better suited to museums, the public should also ask 'What does the animal do?' This question at once raises a large number of matters relating to space and time, and many biological details which link or help to link men closer to animals. The greater the range of contacts, the deeper and more fascinating will the experience of man's relations with animals in the zoo be, and the more comprehensive his understanding of animals; in short the greater the effects of a visit to the gardens. It is true that after conquering its original emotion and amazement, historically considered, the public has shown more interest in the active animal than in the one at rest, but for the wrong reasons. The public thought it had the right, once the entrance money was paid, to see every animal at all times, if possible at feeding time, or during some other vivid and entertaining activity. The important thing was not the unusualness of the activity but rather its degree, its intensity. This traditional idea of an eight hour day for animals must be given up by the public; it must be replaced by a more intelligent biological attitude towards the animal. Just as the animal's external appearance differs from man's, obeying its own laws of growth, so does the same thing apply to its behaviour, to its whole way of life. This fundamental fact must not out of mistaken kindness be kept hidden from the public who visit the zoological gardens, but be made absolutely clear to them. Thanks to its function as a place of popular education, the duty of the zoological garden is to demonstrate this biological fact.

Detailed descriptive notices are a valuable aid in this connection. They can be so much more than mere labels. It is a fact that many visitors fail to notice the most conspicuous labels and ask the nearest keeper the names of the animals in front of them. Nevertheless, descriptions are very important in a zoological garden, in one sense as important
as the animals themselves. An appropriate notice affords a means by which the authorities can keep in touch with the public. At Basle after years of experiment the author has introduced the following pattern for the larger mammals and birds: a rustless metal frame contains a glass-fronted area 8 in by 12 in, divided into three horizontal spaces. The top one is intended for casual visitors and contains the ordinary German name of the animal in big type; this is the main item. The scientific i.e. Latin, name is put above in smaller type, as well as the English and French names (with a view to foreign visitors to Basle Zoo). This notice is printed from metal type on a special machine and is replaceable. If there are young in the particular enclosure, a piece of paper with the date printed on it can easily be inserted. The second horizontal space is divided vertically in the middle. The left hand half shows a photograph of the animal, not a passport photograph, as it were, but one in which the animal can be seen, for example, shortly after birth, or in an unusual attitude or on its journey after capture, in short, as the visitor never sees it. Use is often made of a picture of its biotope or of an old chronicle, or piece of natural history etc. The right hand half of the middle section contains a typed account of about fifteen lines. This is intended for serious visitors as well as teachers, students etc and consists of a summary of the most important biological features of the animal concerned, the history of its discovery, the date of its arrival, a short genealogy or the like. The third, bottom section contains a small world map, printed on a card with the animal’s geographical distribution in red.

This kind of descriptive notice seems to stand the test. It has been described in detail because labels in zoological gardens have always been a thorny problem. Years ago an attempt was made at a conference of zoological garden directors to find a general solution i.e. a standard type, for all animals in all the gardens where the same languages were used. The author still thinks that each zoological garden should have its own way and bear in mind the special wishes and needs of its own visiting public.

A very different significance still attaches to the show value of the animal. This show value has been traditionally built up from all those characteristics that fit the public’s primitive anthropomorphisms. The biological treatment of animals essential today and the conversion of the public to such a view will mean fighting these traditional sterile anthropomorphisms. Such animals as the king of the desert, or animals that are especially dangerous, beautiful, elegant, familiar and, in the day time, lively, have show value, as well as those that are well known story-book characters; the ostrich for example, or again, huge animals like the elephant, rhinoceros, hippopotamus etc. Ideas about show value are due for revision; they need putting on a proper biological basis. The fact that at least 90 per cent of the public that visit
Swiss gardens cannot tell the difference between roe and red deer; that as many do not know, and some will not even believe, that the stag casts its antlers every year; further, that a large number of visitors think the stag is the male of the roe deer; all this clearly shows how necessary it is to give a new biological basis to the showing of animals, and how urgent it is to guide the public’s interest. For example, as soon as the miracle of casting the antlers is pointed out in a proper way the ordinary deer suddenly acquire show value.

Till now all animals with marked nocturnal habits, sleeping in the day time, have been thought of as having little show value; but why shouldn’t the public be clearly told that there are animals that are active at night and that rest by day? This information can be given on suitable notices and cages can be specially built to allow the sleeping animals to be seen. K. M. Schneider has demonstrated promising new ideas about this at the Leipzig Zoo: burrows with holes let into the sides; passages in which the animal feels more or less safely hidden, at the same time remaining partly visible to the spectator during its period of rest. Even an animal that is asleep or hibernating can be of interest, because of the way it sleeps, the length of time, the position it adopts etc. The public has shown itself keenly interested in the intimate affairs, the personal details, the lives of zoo animals. Fortunately some gardens give people that are interested an opportunity to visit the animals during certain hours of the night. In this way it is possible to watch the true nocturnal animals in full activity and also to get to know the individual sleeping habits of many day animals, provided of course these night visits are arranged so as not to disturb the animals.

Usually only feeding times are advertised as a special attraction. The public should have its attention directed to the whole space-time system of the animal. Could not interest just as well be aroused in the regular resting periods of many animals, in the time and place of cud chewing, in places for excretion and demarcation, in biological and social rank, in regular tracks, in the home and in many other typical ways of behaviour? Why is the queen bee always provided with a distinctive mark in the insect house while the α-animal in the wolf pack or in the herd of bison is never made known or mentioned on the label, nor is the home of a fish that is constantly being occupied and defended in the aquarium?

Once the zoo public realizes the laws of the space-time system and the relations between the animals, principally through the use of labels, guides, tours etc much that previously seemed dull or unimportant will appear interesting. Ideas about show value will change from sterile anthropomorphisms to interest in biologically important facts. The observer who is familiar with these facts eventually notices that there is a definite biological meaning underlying nearly every movement of an animal, and consequently many of the animal’s actions and reactions
BOTH SIDES OF THE ZOOLOGICAL GARDEN

can be predicted and regulated as they occur. What seemed merely a matter of chance now appears obedient to laws; what was apparently without order now seems according to plan and thus worth watching. Possibly the number of visitors may increase through this means of educating the public. Many visitors only come to the gardens when there are fresh arrivals to be seen; then for a long time after that they have 'seen everything'. When however their interest has been aroused on the lines suggested, say in the social disputes of a group of monkeys, predatory animals or ungulates, or in the space-time system of some animal that shows it more clearly than others, then visitors are attracted again and again, for now there is always 'something to see'.

To know something about the social intercourse of the animals and their space-time system is not less worth while for the public than to study the geographical range of a species of animal in the museum, the number of its toes or the formation of its teeth. A drowsy herd of bison to the visitor who has been converted to the new biological show value is no longer a number of individual animals standing about or lying down as though they were stuffed. Now the grouping of the animals is the expression of a system of laws, of social rank. Such a group of animals, especially their positions in the enclosure or cage, can be best compared to a game of chess; each pattern has a special meaning and the moves of the separate pieces change the whole situation according to definite rules of play. It is obvious that for the man who knows the rules of the game i.e. of social ceremonial, the biological way of looking at animals is most attractive; for him the show value will depend upon qualities very different from those which the public bred in the old fashioned anthropomorphisms can appreciate. In a similar way hereditary laws as well as laws of behaviour, and many other basic facts of biology, could be made clear as has already been done in several zoological gardens.

The outside—A zoological garden of which the internal affairs, administration and technical side, work perfectly is not by any means performing its full functions. Just as mathematics means far more than the gears of a calculating machine, the biology of zoological gardens extends far beyond the railings of a single zoo. Apart from performing his ordinary job, the zoological biologist has to keep in contact and in close cooperation with all those branches of knowledge that are concerned in any way with the biology of zoological gardens. The first essential here is to get the maximum possible value out of the animal material. It has countless possibilities, from its value for parasitology to its value for comparative psychology, from artistic value to value for the anatomy of the brain. None of the precious material in the zoo must be wasted, neither the animals themselves nor the material for observation. It is one of the internal problems of the zoologist to see that nothing is lost on the material side. To get the best value from the
THE ANIMAL'S RELATIONSHIP WITH MAN

scientific side is not less important and this is one of the external problems. Therefore connections with other zoological gardens have to be kept up as well as with all cultural and educational institutions that can have any sort of interest in the material. Incidentally the production and exchange of animal and observation material should be increased as far as possible.

Often enough this external side of the keeping of wild animals in zoological gardens is not understood by the authorities, or not properly appreciated. The general public's interest in this usually under-rated task of zoological gardens should thus be aroused by suitable propaganda written and oral. This will include the press, tours, lectures etc. Nowadays, it is not enough to put animals into enclosures. External problems are not of secondary importance; they are among the principal problems we have to tackle.

This is not the place to discuss the value of the external side of zoological gardens, their importance as places for research. That has already been dealt with by various writers, and the literature is voluminous. We shall merely stress one fact which throws light on the prime importance of the zoological garden for the basic questions of human life. It is surely of value to realize that keeping wild animals in zoological gardens (and their forerunners) affords, next to the production of domestic animals and cultivated plants, the oldest example on the most grandiose scale of man's activity in experimental biology as B. Klatt says pertinently in the preface to his work (1927) on the Origin of Domestic Animals.

The changes in wild animals through captivity and the phenomena of domestication in domestic animals are very closely related; so also are the phenomena of domestication in animals and the harmful effects of civilization on civilized beings. In the collected works published by H. Zeuss and K. Pintschovius (1940) this fact very clearly emerges and it is a striking thing that the zoologist is given the opportunity to speak first. In his introduction H. Nachtsheim (1940) refers to the changes in the animal through captivity, phenomena parallel to the harmful effects of civilization on human beings. He also states among other things that just as parallel changes in the hereditary nature of man and animals in the state of domestication can be shown, we can also draw a parallel between the harm done to man in his natural state when he comes into contact with civilization and the changes that the wild animal undergoes when it is kept in captivity. The fact that this striking parallelism between phenomena in animals and men is emphasized should not make us under-rate the differences that exist as well.

For the sake of clarity in terminology we should here like to emphasise, with Nachtsheim, that true domestication takes place through changes in hereditary characteristics, and that changes in the wild animal due to captivity represent only non-hereditary phenomena.
accompanying domestication. Thus these non-hereditary changes due to captivity on the one hand must be carefully distinguished from the typical signs of domestication on the other. In other words, modifications, mostly so-called distress-modifications, like smaller body size, must be distinguished from mutations.

Having referred to this, the author would like to conclude by pointing out the close connection between the study of wild animals in the zoological gardens and questions of human existence and life in general. In this connection the many parallel phenomena or possibilities of comparison have a bearing from the physical aspect and also from the psychological. It is not necessary to stress the fact that zoological gardens do not exist principally for the study of these important questions; but they do afford unique opportunities for the investigation of these problems that so directly affect man. These problems include comparative biology, pathology, psychology etc.

Responsibility

It is important for the visitor to find recreation and entertainment in zoological gardens, but that in itself would not be sufficient reason for keeping wild animals in captivity and cutting them off from the free surroundings of natural life. F. Schmidt (1941) rightly remarked that mere curiosity on the part of visitors does not in itself justify the interference by man in the animal's life, by turning it into a captive in a cage or enclosure; but it is possible to defend the transfer of single animals from the abundant stocks of wild animals to captivity under the best possible conditions in order to help man in his understanding of nature.

Every capture of an animal means exclusion from its surroundings and man incurs full responsibility for preventing waste with all the power in his means. The isolated individual must not be altogether a dead loss to its own species; the species, especially when rare animals are concerned, must somehow or other be compensated for the loss. This loss can be compensated most directly and in concrete form by breeding from the isolated specimen and eventually releasing its offspring, in return for the individual lent, as it were, by nature. This simple remedy can only be applied in comparatively rare instances. Re-stocking the Swiss Alps with ibex from animals born in captivity is one of the best examples.

In other instances, the need for capturing more wild animals can be avoided by using stocks bred in captivity, since capture very often means heavy losses with certain species. Thus the species may be indirectly indemnified in this way. We must assume that successful breeding will take place among animals deprived of freedom. It has recently been shown in this connection that isolation is not only
unbiological but inexcusable. There are still many species it is true which cannot be made to breed in captivity. Experience shows, however, that successful breeding is constantly occurring for the first time among species hitherto not known to breed, as our knowledge of the peculiarities and treatment of the species concerned increases. Isolation and the keeping of species normally regarded as non-breeding may thus be justified on the assumption that everything should be done to find out the conditions under which such isolated specimens can be induced to breed. In the interests of the maximum breeding potential of the stocks of animals in the four hundred or so zoological gardens, close cooperation on an international scale is desirable, quite apart from its significance in many other fields. By bringing together rare specimens e.g. gorilla, rhinoceros, or antelopes, considerable success in breeding might be gained, and this would materially increase our scientific knowledge. The possibility of compensating the species does not cease with the death of the isolated individual. Scientific diagnosis of the cause of death can often lead to improvement in the conditions of captivity, thus avoiding future losses. Here, too, international cooperation would be highly desirable.

Many species of animals owe their existence today to facts learnt about them in zoological gardens, or to efforts made in the garden on behalf of species exposed to danger in freedom. The American bison (M. S. Garretson (1938)) and the koala (A. Pratt (1937)) are examples of this. Many species of animals, now extinct in freedom, continue to live in captivity, as for example, the European bison, the wild horse, the Père David deer, the Barbary lion. Experiments are being made with latent hereditary material in zoological gardens to resurrect species that have died out naturally. Such species could be aurochs and tarpan. The help that National Parks and other wild animal preserves have received from zoological gardens is mentioned incidentally. The assumption that the animal can only gain through the spread of knowledge about animals and of love of animals due to zoological gardens has been fully justified. In any event the chief duty of the biologist of the zoological garden is to prevent sterile isolation and to combat by all possible means the harm done to the species through capture.
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