EXPRESSION STUDIES ON WOLVES

Captivity Observations

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(With 57 Illustrations and 1 Table)

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The observations which form the basis of this work began in 1934. At first they concerned almost exclusively, and later always by preference, the wolf packs which were lodged in the Basle Zoological Garden until 1942.

The systematic study of the behaviour - in particular social behaviour - of these wolves extended over several years. In order to distinquish between established behaviour and accidental behaviour, and those behaviours caused by the special captivity conditions, it was necessary to enlarge the observations. In 1939, therefore, attention was paid to wolves and a pair of dingos in the Zurich Zoological Garden, in Basle to the jackal, fox and raccoon dog groups, further at the Eiger glacial station to a litter of polar dogs and finally to domestic dogs in the greatest variety of living conditions. Other mammals kept in special groups provided opportunity for valuable comparisons, especially large beasts of prey and monkeys.

The investigation of the behaviour of higher mammals for example, wolves - involves significant difficulties
with regard to the observation itself as well as to the
representation of the observed facts. Two considerations
must therefore be taken into account:

1. One/experiences the occurrence in effective captivity as being something obviously "understandable", and has difficulty in understanding its course objectively. "If we are witnesses to a profound excitement, our

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sympathy is so stongly aroused, that we forget, or it becomes almost impossible for us to make a careful observation," thus Darwin (1877, p. 11) described this experience.

2. Even if one can overcome this difficulty, the description of observations proves to be possibly an even greater problem. While it is possible with insects and fishes, and in part even with birds, to describe and give names to phenomena of the interaction of life quite (because of) objectively according to behaviour course thanks to their relatively clear and at the same time strangely attractive mannerisms, with higher mammals we are concerned with a system of concepts with a kaleidoscopic variability in significance: such as would serve for human society. Behaviour-form and function are often included together in the same word with subjective experiences - feelings, strivings.

The objective and clear-cut designation of the phenomena of social behaviour must therefore be considered an important task of the behaviour investigation. For individual phenomena - "imprinting", "threatening", "displaying", etc. - that has already been done. In the face of the wealth of social relationships in higher mammals, however, this beginning is only very inadequate.

I consider it absolutely necessary at this point to establish "expression" as a central concept of this work!

I designate as expression the function of structures whose "biological meaning" it is to participate in the orient-ation of interaction by influencing the choice, for example, as releasers. One specialized structure, which lends itself extremely well to functional analysis, was demonstrated first in birds by HEINROTH and LORENZ, analyzed and established in the literature of animal psychology as the "releaser". Today it is known that particularly in reptiles, fishes and insects the principle of the releaser is widely distributed. Doubtless more complicated possibilities of inter-individual reactions exist also; this applies in very great measure for the more highly organized mammals.

It seems to me that the here suggested definition of expression, on the one hand, encompasses all that which in biology is sentimentally called expression, and on the other hand it is really useful biologically in that - in pure functional orientation - it allows the best understanding of the many levels of expression phenomena from the structural and genetic point of view.

I shall attempt, therefore, to give account more or less of this multiplicity of the levels of expression phenomena by separating them as follows:

Peripheral expression structures
 (these are)
 - here belong the optically effective signs of
 form and colour ("dress"), scent organs and

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scent fields, signs of body surface which, upon touch, act on the skin senses.

- 2. Displays of non-deliberate behaviour expressions.
 non-deliberate, i.e. not oriented to an external object, are easily distinquishable, excitement-conditioned expression phenomena as hair and feather-ruffling, colour change, fluctuations in the secretion of the skin glands, eye pupils reaction, further non-deliberate motions of the limbs (stamping, trembling, jerking), changing in the breathing rhythm, a part of the vocal expression, etc.
- 3. Displays of deliberate expression actions.
 - such motions are, owing to their "addressee-ism" and the actor's obvious total participation, felt to be real actions; their closer study is the main task of this work. For examples may be mentioned, threat position, sham attacks, challenges to play, tenderness behaviours, etc.

Naturally we are not concerned principally with peculiarities. Peripheral expression structures can make non-deliberate expression behaviours, and together with these, deliberate expression actions become effective.

The sharp distinction between the three levels of expression cannot be made completely when one considers their functional connection one to the other. Apparently, however, the degree of participation of the central nervous

system, and likewise the degree of psychic determination, and thus the psychological intensity increases with deliberate as against non-deliberate actions in the functioning of peripheral structures.

With reference to the functional separation of the expression phenomena considered here, the observed expression performances of wolves in captivity will not be shown in their relation to subjective experience; rather an attempt is made to see these performances in the light of their social function, i.e. relating to the whole phenomena-complex of interaction. Therefore, the most important regulations for interaction must be our first interest.

II. ON THE SOCIOLOGY OF THE WOLF

A. The yearly society behaviour

Thorough studies of the sociology of the wolf outside of captivity do not exist, however, the animal novels of THOMPSON-SETON, JACK LONDON, ASLAGSSON, et al provide an approximate picture. In the detailed works of YOUNG and GOLDMAN (1944) an exact treatment of the sociology of the wolf cannot be found. In view of the partly controversial accounts of various zoo keepers, this gap is especially evident.

A yearly cycle governs the social phenomena. The pack formation starts with the beginning of winter.

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Chorus howling, joint wanderings and hunting, and fairly early rivalries concerning leadership and sexual partnership denote this period. During this time the pack becomes a closed (exclusive) society. Its core comprises the bitch wolf, presumably the only mature one of the pack, and the male "lead wolf". Whether the isolation of the mature female wolves from one another is the result of rivalries, what course these rivalries take in any event, and what effect they have on the formation of a pack is not known. The lead wolf and bitch more and more plainly become a pair - first in the pack group - then at winter's end, they separate from the pack and occupy a family area for the summer. Unpaired, weaker males and young animals stay together in small packs for quite some time. Each pair scrapes a three-meter long earth den with a chamber in an isolated place, and they raise their young there.

In contrast to behaviour of pairs in a narrow living space, the wider hunting area of a pair is rarely defended from individuals of the same species. It appears that territory marking with urine, which above all is practised by the pack, is not intolerant in character, but rather it represents a peaceful form of contact among neighbours. The conclusion of this summer phase, along with the running off of the yearly life cycle completes the

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independence of young wolves.1.

A comparison with domestic dogs in primitive keeping conditions - Eskimo dogs, street dogs, - enlarges this picture. Certainly in males the yearly sexual cycle is blurred. Furthermore, according to verbal reports from Tinbergen, pack organization in Eskimo dogs - perhaps because of the humanly enforced close living together - remains the same throughout the whole year, and these closed societies defend their own group territories. Under these circumstances the joint parental raising of the young does not occur; the female looks after this matter herself, whereby she digs an earth cave according to the habits of wolves. On the other hand, the males belong to the pack permanently, not to the family. They even endanger the raising of the young, in that they - according to

^{1.} The mentioned work of Young & Goldman (1944) brings to light another possibility of inter-relationship:

The parent animals form the center of a tightly closed family with their own area, living a monogamous permanent union. This family encompasses the young animals until they reach reproduction age, so that a family, i.e. a pack, encompasses "generally a pair of wolves and their yearling or two-year old offspring". (P. 120).

Tinbergen -frequently try to eat newly born pups.

The fact that the closed societies remain the same throughout the year may be fateful to the largest young animals, in that their non-deliberate belonging requirement, as it is found in young dogs generally, may lead to clashes with neighbouring packs. With maturing, this youthful requirement is changed from an active exclusive attachment to the parental society to a closed society of their own.

In the Basle Zoological Garden, where since 1934 I had an opportunity to make observations on two wolf packs which were kept continuously one after the other, up to ten wolves were kept together in a small area with a floor space of approximately 10 metres by 20 meters. Although the cyclic pitch became evident during the course of the year, the captivity conditions prohibited the normal biological course of society Each winter, living together became more intense, beginning with the increase of friendly Then there followed violent rivalries among relations. individuals of the same sex and pair formations. staying together of the original pair, in particular the tie of the dog, i.e. the lead wolf, to his bitch became ever more evident even after mating time; a separation of the pair, however, was prohibited by captivity conditions. Accordingly, all the individuals remained closely tied together in a structural society throughout the year.

With large important packs, breaking up of the society into sub-groups occurred, however this was - possibly also because of the restrictive living space - never clearly evident. Also, the actual dividing of space into group territories did not take place. On the other hand, this space as a whole was regularly defended against the zoo keeper by the whole pack.

Here, I should like to bring to mind a short account of the form of life of domestic dogs. They defend family territories throughout the year. A certain contact between neighbours exists, however, and becomes evident in urine spraying and nightly melodic howling which often brings forth answers from round about.

However diverse may be the forms of social behaviour which have been briefly sketched here, they do seem to me to indicate the same social tendencies. In extreme cases the outward living conditions are capable of shaping the structural closed society into a permanent whole, as it occurs with wild wolves in the winter, or they may influence the life in family areas or individual areas, as led by wild wolves in the summer.

Worthy of note is the elasticity of the social tendencies of wolves, a fact which will come up repeatedly. (P. 86)

B. Concerning the structure of wolf behaviour in the Basle Zoological Garden.

Up to the present time, only a few vertebrate societies have been thoroughly examined; but one can probably assert that the most important trait, perhaps even the foundation, of most structural societies is a social order of precedence. To be sure, according to Carpenter (134, p. 99), such an order hardly ever shows up in the free-living howling monkeys, although with regard to leadership, enemy evasion and defence of group territories their packs appear to be thoroughly organized. Moreover, one should not overlook the fact that orders of precedence of special type-specific character occur in individual animal species.

This also applies to the wolf. As the predominant number of its expression accomplishments - such as the social intercourse ceremony- are meaningful only from the point of view of the super-individual time-linked wholeness of the society, mention must be made of the known characteristics of the social order of precedence of wolves.

The societies observed by me indicated two sex orders of precedence when either sex was in a majority.

The all-winter phase of violent rivalries that followed the narrow social togetherness period has already been mentioned. However, it must now be added that these tense relations occur only among individuals of the same sex - and finally, in order to allay the situation, a status order is established.