

EXPRESSION STUDIES ON WOLVES

Captivity Observations

by

R. Schenkel

(Of the Zoological Garden, Basle and
the Zoological Institute of the Univer-
sity of Basle)

(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 distinguish 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 - (P. 82)
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/^{co-}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

sympathy is so strongly 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 objectively according to behaviour course ^(because of) 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 orientation 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.

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

1. Peripheral expression structures

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

scent fields, signs of ^{the} 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 distinguishable, 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 ^{here} 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

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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.

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

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

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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 (interaction) behaviour. Each winter, living together became more intense, beginning with the increase of friendly relations. Then there followed violent rivalries among individuals of the same sex and pair formations. The 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.

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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.

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.

Both sex orders of precedence govern the total life management of the pack; above all, however, they decide the ownership of "sexual rights". A bitch and a dog as top animals carry through their rank order and as single individuals of the society, they form a pair. Between them there is no question of status and argument concerning rank, even though small frictions of another type (jealousy) are not uncommon. By incessant control and repression of all types of competition (within the same sex), both of these " α animals" defend their social position. In the first pack which belonged to one bitch alone - without rival - I was once able to observe that this repression of the one status-high dog worked in favour of the other. (P. 87)

Social orders in wolf packs are by no means definitive and clear cut; they are far more equilibria among uninterrupted and interacting forces.

The periodically conditioned change of pitch and changing of pack composition or of living conditions disturb the equilibrium and often allow rivalry to blaze up into power. Each new social situation created by these fluctuations leads to the re-strengthening and re-establishment of dominance relationships. The dominance status order of wolves is conditioned by situations.

Every mature wolf has an ever ready "expansion power", a tendency to widen, not necessarily his personal territory,

but rather, his own social behaviour freedom, and to repress his "Kumpans" of the same sex. Consequently, he maintains a constant watchful interest in all socially important happenings within the pack. In particular, status quarrels are never private affairs between two individuals; the whole society takes a more or less active part in them. Individual differences of social initiative and the power of adaption to momentary situations are very clearly evident. For the status of the individual wolf these are of the greatest importance.

The status order with all its details is a result of the interaction of all forces in the whole society.

Even if great fluctuations do not destroy the labile equilibrium of the social order, the maintenance of a not-quite-classless status requires constant self-assertion. This is maintained by expression accomplishments which have the character of imposing (a demonstration of the social potential) or of threatening (scenes).

Whereas with relative stability of social relationships the measurement of opposing forces is restricted to expression as a "barometer", or measuring stick of the potential energies; on the other hand, a maximum disturbance of the equilibrium can bring about a spilling out of the fully locked-up kinetic energies; i.e. a real battle. As a matter of fact, this occurs generally only among contenders for " α position", and

then only in relatively few instances. In general, the usual conflicts of opinion remain somewhere in the middle between the two possible extremes (status demonstration - battle).

Those expression phenomena, which we characterized as demonstrations of social potential and as aggressions, however, are not just a few sharply defined expression postures and intention movements. Such expression elements in wolves are extremely full of nuances and occur in various combinations. They are always, however, only the subordinate, showy ingredients of complex expression behaviour and behaviour results. Again, these do not allow themselves to be limited by the environmental life behaviour pattern.

The whole behaviour pattern. i.e. the relation of each individual within the same social environment, is expression. Environment is taken into account in expression, is given socially conditioned implications, and thus attains a "social field of force" with renewed significance. The rank precedence of an individual manifests itself in very definite ceremonies and in freedom of behaviour in the social field of force. These are as much status-determined as status-establishing.

Firstly, therefore, the "enjoyment of the social position" is a type of status demonstration and is, hence, status preserving. It is only during fluctuations of the social equilibrium that additional controls (mixing in) and threats, i.e. motions of intention to battle,

are added to these expression values. A severe disturbance of the equilibrium finally brings about real battle.

A stable social situation (or clear-cut hierarchy) indicates a weak development of energies in social relationships and, vice versa, a disturbed equilibrium indicates a great development of energies.

With relationships of equal status, then, forces are continuously checked in development in such a way that aggressive energies cannot be used up within the framework of rivalries by wolves with initiative and of high status. In the packs under observation, specific release battles, which were sometimes characterized as "dry runs" and at other times as "energy displacements" (see below), witnessed to the storage of battle energies. These break loose at the slightest opposition, and are released at the weakest individuals of the society. In the development of such reactions, a close affinity with the taking of prey is indicated:

- a wolf of high status frightens a weakling in a "lying-in-wait position" and then perhaps pounces on the frightened one;
- a wolf of high status creeps up on a guileless weakling, falls upon him from behind and bites him in the neck;
- a wolf of high status attempts to grab a weakling, who is 'despairingly' defending himself, his excitement mounts steadily, and suddenly he

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pounces on his prey despite all opposition;
- several wolves of high status pounce on the
weakest wolf in the highest, sudden battle-like
excitement.

In these battle actions, however, an air of rejection and animosity, which is more or less clearly pronounced, comes to light, which nevertheless had another special significance in that in all of these actions the attackers belonged to another race of wolves than the prey. With certain definite exceptions, the attackers belonged to the larger race, the attacked individuals, however, were the repressed individuals of a smaller race of wolves.¹.

Often joint attacks by the large wolves were directed against one animal over a considerable period of time. This animal steadily lost the significance of environmental social partnership, was robbed of all social initiative and, in certain circumstances, with repeated attacks, became mortally wounded.

Despite rivalries and ravishing of the weaklings, the wolf pack continuously showed itself as an organic unit. This is evident above all when the whole pack atmosphere indicates friendly character - in chorus howlings, general "tenderness scenes", etc. - or when the whole pack presents a guarded front as a closed

¹. The concept of "race" is used here without claim to systematic correctness. (see III.B.)

society toward an "alien". Finally, sociability is shown as well in an "harmonious unity", in remaining quiet whilst awaiting food, on the whole in every situation and in the smallest detail - and last, but not least, the intra-social struggle.

The conditions of life in zoological gardens are marked by the absence of predation and by special circumstances in the avoidance of the enemy; these conditions alone, however, do not lead to the development of the above-mentioned social forces. The presence of both sexes in the society is of great importance as well, and also the size of the pack.

Rivalries (which occur exclusively with individuals of the same sex) only become violent when the society (P. 90) contains individuals of both sexes. If the total number of individuals continues to remain small, then all of the social disputes may be only rarely observed. The internal activity, then, is dominated by reaction to stimuli of the environment in the sense of tendency to flee; the wolves now appear shy.

On the other hand, as soon as the society controls a certain number of individuals, the manifestation of all individuals toward individuals from outside becomes more secure; "cool" observations, even threats to attack characterize their behaviour, with only rare indications of intimidated shyness and readiness to flee. When there

is added to the simulation to rivalries by the presence of both sexes, of which only one needs to be in majority, and to the suppression of escape-allied reaction against the outside world, resulting from "basic harmony of the collective security", an incapacity to actively oppose the outside world - predation, group battles -, then the conditions for maximum enhancement of the intra-social conditions have been fulfilled.

This would seem to indicate that reaction-specific energy in the basic behaviour mannerism of the wolf does not exist. The "displacement activity" (TINBERGEN, 1940), or perhaps better still "displacement attitude" has given up a characteristic quality in more primitive vertebrates; which is the deliberate jump from one "behaviour track" into another. The greatest variety of nuances and possible combinations in all socially (i.e. in expression behaviour) are characteristic perhaps generally of the most highly developed vertebrates, including the wolf.

III. PERIPHERAL EXPRESSION STRUCTURES AND NON-DELIBERATE EXPRESSION STRUCTURES

A. Scent Expression Structures

First, it should be stated again that we shall describe as peripheral structures those tendencies which do not indicate action or reaction, but which indicate an ever-present "form", which, however, owing

to showy elements are subject to certain expression reactions, or which require definite "presentation motions" in order to be effective as expression. The whole of the peripheral expression structures is the outer form, insofar as it is actually part of expression. The expression function of these structures may be optical or olfactory; in addition stimuli of the skin sensory organs come into play.

Here we are interested primarily in olfactory stimuli.

The scent expression functions of a macrosomate such as the wolf are possibly to a great extent outside of our direct experience. To a certain degree we can come to some conclusions by observing the "reception behaviour" of the social partner. Actually wolves will besnuffle one another repeatedly on particular parts of the body. This does not, however, occur as often with wolves as with domestic dogs, which meet on the street as strangers.

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One should not consider, however, that scent expression, respecting its reception, is the essential component of most "snuffling scenes". On the contrary, the behaviour of snuffling itself has an optical expression value of almost greater intensity and permeation than scent expression; insofar as scent itself is concerned - it is, however, an indication of social initiative, a sort of invasion into the partner's sphere. The

besnuffled individual governs this invasion on his part by expression accomplishments whose effectiveness for the most part is not a result of olfactory components. Thus, the scent expression is instilled in superior "scenes", and these themselves are instilled in many complex courses of social relation behaviour.

The most important olfactory controls in wolves are described in brief as follows; they must form the indices for scent expression structures.

An attitude of peacefulness and lack of tension is a prerequisite to smelling the fur of the neck, the nose, the sides of the head and the mouth area. All these forms of olfactory control have completely subordinate social significance.

By snuffling the sides of the neck, the tip of the nose reaches the skin through the fur, so that the nose is completely lost in the hairs. The snuffler usually moves the head very slightly at the same time, whereby the tip of the nose moves searchingly in the fur of the partner.

Besnuffling the tip of the nose and the sides of the head is observable incidentally among friendly males and among male and female before the rutting season (Fig. 48 & 50). In the latter case, it is undoubtedly a component part of the very complex preliminaries to pairing.

It seems likely to me that the smelling of the lip area (Fig. 1) represents a behaviourism that tells

the wolf whether his partner has received food a short while ago, so that the probed scent would not be an "endogenous expression", and in this connection the term, expression structure, could not be used. It often happens that after a short while the besnuffled one moves aside with an upward movement of the head.

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In this connection it should be mentioned that in peaceful attitude wolves in general are interested in any large foreign objects in the fur of the pack comrade. Bone splinters, mud clots, stuck-together hairs, etc. are obviously discovered optically at first and are then probed with the nose. In like manner, bite wounds are looked for "in strangers", these are checked and sometimes licked.

The actual centre of scent expression in wolves is the anal region. Moreover, with the exception of the head, it is the most important centre of optical expression. Expression and control of the anal region are of great variety and have an extraordinarily high expression value.¹ Moreover, with one exception, the

¹. During the period of observation, the effective scent organs of the anal region proved to be primarily the genitals and the anus, and less frequently the upper part of the tail base (compare Fig. 4 to 6). The last mentioned region is the seat of the actual scent gland, according to Young & Goldman (1944, p. 73). My observations do not allow definite conclusions respecting its function.

scent associated system takes on less importance in social significance than the optical-acoustical system. At the same time, it is surpassed by more complex, physically higher expression values.

Without simplifying the conditions too much, it may be stated that the presentation of the anal region - scent-wise and optically - as well as controlling the anal region indicates social rights. In the bitch, control is seldom observed and presentation may only be seen in the winter. Withdrawal of the anal part from control on the one hand and lack of "control initiative" on the other hand denotes subordinate males; further, in the pack- and rutting season it signifies subordinate females, and in addition, it denotes all females at other times in a more or less clear-cut manner.

The withdrawal of the anal part is accomplished by curving the spine downwards, bending the back legs and "pulling in" the tail (Fig. 2), and further, under certain circumstances, by sideways turning away of the hind body. During tense relations, there may be added to these motions, repulsion or defensive attack, (Fig. 3). If, on the contrary, a peaceful, "erotically" coloured harmony exists, then shyness and rejection in the behaviour of subordinate individuals does not exist. Presently, a behaviour of passive submission (passive subjugation; compare Fig. 4 and 5) makes its appearance,

or in singularly playful activity - sideways swaying of the hind body and lowered tail, upward tossing of the snout and weak hip movements - a positive interest and initiative on the part of ^{the} subordinate individual becomes evident (active subjugation; Fig. 6). The behaviours described here for brevity reasons as being signs of subordinate individuals apply also to a degree to females of superior status in the summer.

The opposite of withdrawal, being the presentation of the anal part, may, as mentioned, only be observed in superior males; in females, however, this may be observed only during the pack and rutting season.

In my observations it was not only the females, but also the males who not infrequently besnuffled one another in the anal region. This applies as well to community dog packs. This type of scent control appears to be greatly reduced by continuous living together in contrast to what may be observed in meetings between separately kept domestic dogs.

Besnuffling of the genitals is generally endured quite indifferently by dog wolves as well as domestic dogs; the social significance of anus control is much more pronounced. This is actually a very active expression of social initiative. Insecure individuals react immediately by withdrawing the anal part, and contrari-wise the superior wolf is denoted by "unembarrassed"

demonstration and control activity of his own (Fig. 7).

While presentations and withdrawals in dog wolves indicate only direct social significance, this is tied in inseparably with the sexual functions of the female; females make presentations only during the later mating season and even then only when they have assured themselves the top place in their social order. With raised tail, the rutting α -bitch moves in a feathery dance step, while whimpering or "singing" "tenderly" (Fig. 8). Meanwhile she moves her genitals in slow, minute, pendulum-like movements in a vertical direction. In exception to this, during the rutting season one could also observe a subordinate bitch release her genitals within the immediate vicinity of a dog wolf, holding her tail to the side in a downward curved position in accordance with her status.

The genital scent of rutting wolf bitches - as well as domestic dog bitches - has an extraordinary effect on aggressive males. The actual putting into action of this olfactory rutting expression is the most important privilege of an α -bitch, and indeed not only does this consist of exhibiting the anal part, but also in urinating in a spray-like manner (urine ceremony). The privilege of the male lead wolf, on the other hand,

is the demonstrative reception of this expression, i.e. smelling and licking of the genitals and urine of the bitch.

In accordance with what is known of the urine ceremony in free-living wolves and of this phenomenon in domestic dogs (SARRIS and UEXKÜLL, 1931), and what I was able to determine respecting wolves in captivity and domestic dogs, spray-like urinating by the males fulfills several different functions. It is not merely an olfactory expression phenomenon, but rather a "gesture", i.e. with optical expression effect. Its function fluctuates between:

- 1 Territory marking (with free-living wolves in summer and with separately-kept domestic dogs throughout the year);
- 2 "Making acquaintance" (as above);
- 3 "Pair formation and introduction to pairing (with wolves in winter);
- 4 "Legitimizing" the lead wolf (constantly with captured wolves held in packs but most evident in the winter; presumably too with free-living wolves in the winter. This function is also discernible in domestic dogs).

With both sexes it is clearly evident that along with the social aspect of the various forms of anal expression, the optical function always remains in the foreground.

A sequel to these expression studies - II - is necessary in order to provide a detailed description of sexual behaviour and the urine ceremony.

Dominance over the olfactory expression by the optical expression and the close relation of the latter to the social sphere, further the efficacy of control as a behaviour with an optical expression function, and finally the larger expression intensity of anus control as opposed to genital control among dog wolves, are typically characteristic in wolves of the phenomenon described as "anal expression". I had repeated opportunity to observe corresponding expression phenomena in smaller canines (jackal, fox, raccoon dog), in other types of predators (primarily felidae and bears) and finally, also, numerous other animals. I obtained the impression that relations among wolves differ from relations among other predators in ways and means which are very closely tied in with the high development of the social life of wolves. The following simplified comparison attempts to analyze these ideas precisely:

Normal case for various socially more primitive predators (= "primary step").

The olfactory anal expression of the female is entirely reproductive; presentation and withdrawal of the anal region have no expression value in themselves; i.e. they are without optical expression function.

In contrast to females, the urine ceremony is performed by males throughout the year. As a pure olfactory expression phenomenon, it is important in dividing an area (marking of territory). - In the rutting season this activity appears to be the sole function, or certainly the dominant one, even though the latter brings with it a striking increase in the urine activity of males.

The case of the wolf and domestic dogs (= "secondary step")

The - actually female - motions of presentation and withdrawal of the anal region become optically effective expression gestures of superior social significance, and they carry over into the expression display of males as parts of the social behaviour ceremony. Likewise, anal control becomes a gesture of social expression accomplishment of effective importance.

The established factors concerning presentation also apply to the urine ceremony: During the rutting season, spray-like urinating is an optically effective gesture of great social significance; it is a sign for the lead wolf respecting the α -bitch. With this in mind, the urine ceremony of the female is quite conservative, but it remains an important aspect of pair formation and pairing. The urine ceremony of the male, on the other hand, is useful only in marking territories during the solitary family phase. At other times its usefulness is in pair formation and social differentiation as a phenomenon of predominant optical expression value.

A glimpse of this so important phenomenon in mammals, anal expression and the source of its impression on wolves, might possibly be enlarged by complete, comparative, psychological research, possibly in the manner which was conducted by ANTONIUS (1937) on the phenomenon of the "horse-like appearance" of perissodactylous animals.

B. Optical Expression Structures¹.

Optical expression structures are much more easily grasped and are more readily observed by us than the olfactory, peripheral expression structures. Usually they show up in specific presentation motions with which they form a functional unity. Characteristically, they are most pronounced while the animals

¹.I can leave out an isolated description of the acoustical expression accomplishments of wolves, on the one hand, because detailed, suitable combinations may be found in SCHMID (1936, p. 25 & 56) and MENZEL (1937, p. 33) (in SCHMID under the devised title "Speech!"); and on the other hand because the majority of vocal sounds of wolves seem to be an "accompaniment" to deliberate expression actions. In connection with others, several vocal expressions will be mentioned later on.

are in winter fur and full development occurs during the winter social and sexual period.

As Figs. 10 and 11 should demonstrate, form and colouring of the body surface were quite different in the two previously mentioned races of wolves which were kept in captivity in Basle.² The larger form showed a more striking superficial appearance, and characteristically, its social behaviour was also more clear-cut. The human observer found the appearance of the smaller form to be mask-like in comparison to the larger form. The warden considered the smaller form to be more malicious and dangerous despite the fact that they were much more shy. In addition to their

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²·YOUNG AND GOLDMAN (1944, p. 389 ff.) differentiated between two species of American wolves: Canis lupus, the grey wolf which is spread out over most of the northern world, or simply wolf, and Canis niger, the (smaller) red wolf of the Mississippi Valley.

The larger Basle wolves were undoubtedly grey wolves; but the small form and the red wolf have many similarities. Regrettably, the origin of the Basle wolves could not be ascertained.

distrustful manner and continuous endeavour to find optical cover, their comparative poverty of expression and "locked-upness" of the wolf countenance added to this opinion (Fig. 11b).

In the following discourse I shall restrict myself mainly to sketching the most striking optically-effective expression occurrences and peripheral structures of the large race of wolves.

The most important optical- and acoustical expression centre of the wolf is the head. The interaction of the colouring of the face and function of the facial muscles and, also, the activity of eyes, ears and nose makes the snout, lips, eyes, forehead and ears the bearers of extremely important and variable expression phenomena. It is as difficult to comprehend it as it is to describe it. It is only possible here to consider a few of a large number of expression possibilities. At the same time I shall endeavour to elucidate the most important principles of facial expression.

Baring of the teeth belongs to the function of threat to attack and to defend. (In IV.B. it is mentioned again as a ritualistic motion of intent to bite.) Its indications are foreshortening of the snout, ^(wrinkling) folding of the neighbouring skin and raising the lips so that the front teeth (incisors, canines and bicuspids) become visible.

With insecurity in social behaviour, especially if a wolf of superior status threatens to attack, the corners of the mouth are pulled back and this is accompanied by soft, "sad" whimperings.

While baring the teeth, the mouth may be open in varying degrees. Enlargement of the mouth opening indicates increased intensity of battle excitement.

It is characteristic of the wolf that the three elementary behaviours of the nose-mouth area show up in varying degrees and with innumerable possibilities of combination. Figs. 12 to 19 illustrate some of them.

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In the whole facial expression an extraordinary role is played by the eye-forehead region. Besides many subordinate phenomena, forehead expression takes two main directions:

1. Contraction of the forehead in the middle and towards the snout base. The forehead appears swollen thereby, especially over the eyes. This forehead form is associated with the threat expression, resp. battle readiness.
2. "Pulling apart" of the forehead in the direction of: corner of the eyes - lower part of the ears - neck sides. With this "pull", the forehead becomes smooth, the brows disappear and the eyes become slit-like. This expression is evident with all types of insecurity and subjugation - with "fear of the enemy", inferiority in aggressiveness, passive or active subordination.

Doubtless, the eyes themselves largely contribute to expression. It was, however, impossible for me, owing to technical reasons, to make special observations of pupil reactions. Making allowance for this then, it is the security, and contrariwise, insecurity of the glance of an individual that has above everything else the highest expression value. High status ensures an "aim sure" glance. This activity of the eyes is tied in with the deliberate expression accomplishments and as such will be mentioned again later on. Fig. 20 to 25 illustrate possible eye-forehead expressions.

The last mentioned sketches indicate clearly that the expression of the forehead is coupled with ear placement. Ears that are pointed forward indicate social initiative; ears drawn backward and respectively kept close to the head indicate all of the possibilities of insecurity - restraint in social differences, resignation, fear of enemies - in battle attitude, the ear cavities are somewhat inverted, and in defence against an enemy (the zoo keeper) the ear lobes are dropped to the side.

The expression phenomena sketched heretofore are devoted to facial expression. It is impossible to go into all the different variations and combinations of individual facial characteristics. However, in order not to exclude facial expression altogether, I have attempted in Figs. 26 a to h to illustrate at least four quite different possibilities in "caricature".

Of course, facial expression is not an isolated independent unit of expression. It is built into the total expression structure. This shows up most strikingly in the connection between ear placement and head posture. In head posture - exactly as ^{with} the glance - orientation in respect to the social partner plays an important role; direction has high ranking significance in these expression phenomena. Hence, head posture is a part of the level of deliberate expression actions which, as high ranking behaviour patterns, preempt non-deliberate expression occurrences and peripheral structures.

With regard to an outlined description of several possibilities of head posture and ear position, it should be expressly noted that they arbitrarily define limited segments of the total body posture (compare, also, Figs. 22 to 38!), and, again, the latter is only a temporal excerpt of deliberate actions, an excerpt to be sure, which is detached from "true" actions by an especially dynamic characteristic - namely the "building up" of the flow of movement towards its taking shape in the form of an "action".

As peripheral optical expressions, special mention should be made of the rump colouring and the structure of the back fur. The milky to light brown ground colour seems to be tipped with black because of the black

coloration of the tips of the guard hairs (in the larger race). The shading effect varies with the local hair length and is strongly influenced by activity of the hair bristle muscles and body posture. The shoulder and withers hairs are longer than the hairs of the middle back. Should the back hairs be raised in battle excitement or while giving demonstrations - phenomena which are absent in repressed or frightened animals - a very striking back line is evident (Figs. 28 a and b).

We have already acknowledged that the anal region is the most important expression centre and we have established that its - doubtless more primitive - olfactory expression function is equally preempted by the - higher - optical expression function.

In optical regard the tail is the most dynamic (compare hereto: MENZEL, 1937, p. 30). Its function of covering up, and, contrari-wise, placing-on-exhibit of the olfactory-optical "anal face", and its sexual and social significance has already been mentioned (Figs. 29 a & b). We became acquainted with the extent of width variations respecting holding the tail and, like- wise, "tail height"; a great variety of transition steps may be observed in keeping the tail raised and in keeping it pulled in.

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The self-assured wolf does not carry his tail

high¹. under conditions with no social tension (e.g. drinking, observing the environs), rather, it is raised at the base and from there it hangs loosely (Fig. 30f), or it may hang from the base with the upper half forming a concave curve (Fig. 30d). On the

¹.As deviations in relation to wolves, two circumstances respecting certain species of domestic dogs are striking:

1. The development of tails which are curled upwards.
2. The very frequent holding high of curly as well as wolf-like tails from the base up.

These deviations cannot altogether be accepted as being merely outward organic constructions. Especially with holding high of the tail base, the leading role might more frequently be played by such central factors as - endocrinological, certainly also, psychological. To my knowledge, in domestic dogs in general, the tail, at least at the base, is pressed downward with fear of the enemy and during severe social limitations, and in addition, it hangs loosely in a depressed condition following unsuccessful social attempts.

The infrequency of enemy experiences and rare deep-rooted social suppression while under the protection of man may well be considered to be a part of environment in the above mentioned phenomenon. Doubtless, however, constitution is also of great significance. In support of this, several varieties of coursing dogs may be mentioned: Even under the best of keeping conditions, some coursing dogs are inclined to pull in their tails, and this phenomenon must be viewed as having some connection with constitutional physical properties (social sensibility, inclination to social passiveness).

other hand, with social differences as well as during friendly scenes, the superior individual distinguishes himself by high carriage of the tail. The shape of the tail indicates certain attitude-conditioned differences. With threatening, for instance, it may be described as being actually "notched". Fig. 30 illustrates several cases of tail carriage and tail shape.

With wolves as well as domestic dogs sideways sweeping and circling tail movements occur. Liberal swinging of the tail in a sideways manner (wagging) with a free movement signifies friendly relations with individuals of every status, with respect to tail elevation. Individuals of low status frequently conduct these swinging motions with lightly pulled in tail and movement of the whole hindquarters. In periods of great liveliness and playful attitudes, this friendly wagging may end with tail circling.

Very abrupt and quick sideways wagging with an outstretched tail, or with the end of the lowered tail, may occasionally occur in battle attitudes; it reminds one, especially in the latter form, of the tail movements of foxes and cats (Fig. 31).

When wolves of highest status meet, the vertical tail is at times in trembling motion. "This tension-trembling" gives the impression of being energy laden and is actually also an expression of the highest social potential.

Finally, in mock attacks, which take the form of pushing past one another with snarls and threats to bite, a type of beating of the tail towards the body of the individual being attacked is not uncommon (Fig. 32). This motion is similar to the "balance or steering motion" which may be seen in dogs and wolves at the instant of sudden veering away from their directional motion. Whether these tail motions, as the above-mentioned beating of the tail, could be diverted from "ritualized" (see IV.B.) (preliminaries) introduction towards a direct attack remains to be established.

In order to illustrate the link between the previously described optical expression elements more or less clearly, the pencil sketches Figs. 33 to 38 show ear position, head carriage, backline and tail combined. It becomes immediately evident here that these are only the showy elements of the whole body carriage. This itself, however, is deliberate and is related to a social partner or an environmental component - which is generally true for the higher, more comprehensive expressive accomplishments of the wolf. Already the momentary aspect of total expression achieves the characteristic of "self-representation", and this characteristic becomes particularly impressive when one regards the scenes of social ceremony in their temporal extent and the whole life behaviour in general with all its social conditions.

Again, it should be expressly confirmed that the elementary optical expression structure in wolves does not provide for a certain number of clearly isolated possibilities of form - as one might assume because of the very limited choice of sketches - but rather an absolute wealth of nuances, displacements and combinations.

IV. DELIBERATE EXPRESSION ACTIONS

A. The role of deliberate expression

Deliberate expression actions have already been mentioned incidentally as being the highest, most inclusive level of expression phenomena. They are motions which are part of the "animal personality", which may be seen both inwardly and outwardly, not merely automatic reaction mechanisms and limited organ-groups of the body surface.

The whole subject of deliberate expression in wolves has many aspects and is difficult to grasp. It is easiest to fix the limits of certain courses of behaviour which are distinguished by their locked-upness and by their more or less established behaviour-course forms. It would not do to describe them as "instinctive actions" within the meaning of LORENZ (1935, 1937 a and b); their behaviour course as well

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as investment with subordinate expression phenomena is far too interlocked, i.e. rich in variety. (As indicated in the introduction, the behaviour of birds, which is the research area preferred by LORENZ, is very much simpler and easier to understand than the behaviour of mammals.)

Obviously, the indefiniteness of deliberate expression actions in wolves is nothing else than their diverse orientation - in respect to direction, quality and intensity - to changing social conditions.

In his expression actions the wolf actively tests his social partner all over - and thus his partner's reactions - and so he lives up to the limits of his own social behaviour freedom.

This self-orientation to the partner is especially evident with all status altercations and arguments over rights.

The fitting in of socially significant action to social situations may, under certain circumstances, be carried to the extent that one cannot limit any, even of the more or less continuous and closed behaviours or conducts. Naturally, however, every behaviour element is "truly wolfish" and the total accomplishment is never "orientation reaction" alone.

If we compare these findings with those which have become known for fishes, reptiles and birds, we obtain the impression that social conditioning or the social structure of behaviour in wolves is associated with the "decomposing" of instinctive behaviours. Therewith - it seems to me - the true character of this - and perhaps all - "higher" behaviour patterns is indicated; they are given direction by a higher, i.e. more capable of adaptation, psychical organization. Behaviour is not merely opened up by "key stimuli" and runs its course in accordance with inborn behaviour laws, rather it consistently actively adapts itself to momentary situations - naturally within the framework of inborn possibilities. (The ambiguous definition of "intelligent action" should be avoided).

It may be assumed that in wolves the highly developed (P. 102) psychical "apparatus" of adaptation does not merely become a function within the social life, but quite generally it raises the standard of life of the individual and the species decisively.

In the following description of the more important phenomena of deliberate expression, the established courses of behaviour will not be covered. There are, nevertheless, a few behaviour actions which have fewer variations in wolves as well; but they are not socially

significant, i.e., wholly subordinate in expression function and they give the impression of being rudiments. For examples may be mentioned: - scraping after urinating, circling around before lying down in cold weather. Contrasted with these, are the quickly changing, predominantly optical-acoustical expression actions of living-together in close proximity, which are the actions which will especially concern us here. Here, the behaviour forms are not firmly established in detail; and yet in certain situations they are movements which may be recognized repeatedly, and they are distinguished by a certain similarity or relationship of form, of dynamics and of subordinate expression.

Possibly one comes closest to the truth when one speaks of "attitudes" and their related "form groups".

We now direct our attention to these form groups of expression and the characteristic form relations which exist between them and other behaviour patterns of the species.

B. The form groups of the deliberate expression

So to speak, a pure demonstration of the occurrence of orientation is found in reception behaviour, primarily in looking, but then too in snuffling, and to a certain degree also in listening. We have already accepted

smelling and looking as controls, as invasions into the sphere of the social partner, and as social prerogatives. Generally, the look of the subordinate wolf is unsure and he avoids the stare of the wolf of higher status; his ears are laid back in a "resigned position", and he does not venture into the olfactory-optical control of the anal part of his partner. In the presence of a male of higher status, weaker males do not even possess the privilege of genital checking of a female.

Every steady, penetrating control, in particular the looking control, brings forth a feeling of restriction in wolves of low status (Fig. 39); where there is very little status difference on the other hand, this control is rejected by "protest" (Fig. 40).

The sensory organ which registers all control activity of the partner is the eye; the control of social behaviour itself is optical. Here, it is evident again how much the higher optical expression behaviour also controls the social life of the larger race of wolves. In confirmation of this, communication between humans and dogs proves this relatively easily.

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Freedom and restriction of the sensory activity may be observed with every mood. The activity of the sensory organs cannot therefore be divided into form groups. That applies, on the other hand, to the greatest variety of forms of demonstration.

Demonstrational actions are partly reduced to their intention movements, partly to being gestures of distorted battle behaviour, which vary in many different ways and which primarily show the characteristics of the courses of behaviour which correspond to social status. In general, the demonstrations of superior wolves show up in the dominance of carriage - postures indicating introduction to attack, hence, "threat postures"; whereas in subordinate wolves hasty courses of behaviour movements, especially biting behaviours - "snapping" - are more common. In high status wolves, hair bristling and very variable vocal tones accompany the gestures. Both of these actions rarely occur, as it were, in low status wolves, rather a short, shrill note of pain or fright is evident if they do not venture to oppose a superior attacker who has suddenly overcome them. Demonstrations, however, are not always evident on this low energy step; and there is evidence of all possible transition steps before actual battle. To the threat posture and to snapping there are ^{also} now/added the behaviours of jumping at, pushing against, "circling" and actual biting. A description of these latter phenomena is only satisfactory if the interplay of accomplishments of the partaking wolves is given its full value.

This type of consideration will be applied to the proposed sequel to this work - II.

In order to avoid repetition, only the "bite-threat posture", "defensive snapping" and "surprise-attack threat" will be described first of all.

The "bite-threat posture" is preparatory to biting, which is "ritualized" (TINBERGEN, 1940) into an impressive grimace. In superiors, the body shows an impressive or threatening posture, tense trembling of the tail as well as of the stretched out legs and bristling of the back hairs increases the threatening character. The eyes stare and the ears are raised up and turned outward slightly. The focal point of expression, however, is in the baring of the teeth. It is accompanied - only in high status wolves - by continuous rumbling growls, which sometimes with rhythmic thrusting of the tongue between the teeth slightly fluctuate in tonal colour. The whole expression behaviour in high status wolves creates the impression of highest explosive readiness (Fig. 41).

Already in the body carriage a slight subordination shows up in a curve of the back and a tendency towards holding the head backwards; in addition, also a downward curve of the tail with raised base, laying back of the ears and uncertain eyes are in evidence.

With deeply subordinate wolves the characteristics of threatening are absent - with exception of baring of teeth - they curve their legs, duck their heads, curve the tail base downwards ("pull in", compare Fig. 2), do not raise the back hairs and do not growl. The threat posture is replaced by a purely defensive posture, and "self-inflation" is replaced by "self-deflation".

The less a wolf is able to cope with a situation and the more the defensive character dominates the threatening character, the more quickly and frequently an "explosion" occurs following the readiness posture.

Its basis is the motion of snapping. Only in very great battle excitement does actual biting occur, and then only on the part of the individual with the initiative. Much more frequently an empty snapping motion occurs. This is always a part of the defense mechanism, at times more within the meaning of protest or rebellion, and at other times more within the definition of self defence. I am therefore designating this conduct as "defensive snapping".

If in the altercation a wolf growls and bristles, then his defensive snapping has the character of protest; if these preliminaries are not present, then his snapping likewise is purely defensive.

Protest-snapping is accompanied by very sharp barking - battle barking. The more secure a wolf feels in the face of his rival, the more tense will be the bite-threat action which precedes the protest-snapping, and the more close towards the body of the opponent the snapping action will be carried out.

Defensive snapping of deeply subordinate individuals occurs without barking; instead the jaws are brought together with a loud clap (Fig. 35c). This gesture is carried out at a great distance (up to cir. 10 metres) and in quick repetition. In contrast to protest-snapping it does not take a precise direction. This contrast indicates that the characteristic of deliberate control exhibits intensity steps, and in wolves at least - the intensity of expression is dependent on these steps.

In particular circumstances, chiefly for repression of the weakest individuals, and more rarely for repression of subjugated former rivals, a posture of jump readiness - "surprise attack threat" - may be observed as a threat posture in high status wolves. Often, it has the property of waiting-in-ambush in (optical) cover - and leads incidentally also in fact to an unexpected sudden attack -, often, however, this gesture is quite openly accepted as an actual threatening posture, and it quite obviously

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frightens low status individuals (Fig. 42 to 44). Here, too, a threat may be followed by jumping at.

(As has already been mentioned, there will be a later discussion on jumping at, circling and biting).

It is a widespread phenomenon among vertebrate animals that expression behaviour, which must be described as preliminaries to battle (demonstration), are "distorted" battle actions. In wolves, too, the distortion media are, - limitation to the intention movements and ritualization (TINBERGEN, 1940). The latter has an extraordinary wealth of possibilities and governs the status characteristic of behaviour.

A type of contrast to the form group of demonstrations are the "erotic" expression actions - playfully caressing and flattering. As far as dynamics and subordinate expression are concerned, these appear as a single form group, however, with respect to action itself, they have a double 'origin'; they stem from sexual behaviour and the relation of the infant to the mother ("infantilism"). This again is not exclusively a characteristic of wolves, but rather of many mammals.

The fact that preliminaries to pairing could be "distorted" copulation actions indicates the same form of expression development that we have been able to establish for demonstrations. A totally different possibility is laid bare if "distorted" sucking becomes an expression of sexual readiness or of friendly attitude.

Here, it is a case of phenomena related to displacement activity (TINBERGEN, 1940). Of course, in carrying over this concept to the accomplishments of wolves, one should not overlook the special structure of their deliberate expression actions.

First, the "riding up" of the bitch should be mentioned as an expression of "erotic" mood. The bitch carries out this behaviour in a wholly playful, indefinite manner and only with the male to whom she is attracted. Often, too, the action is reduced to the preliminaries (Fig. 45 a and b). The same behaviour plays a completely different role in the interrelationship of males, and accordingly is an indication of a completely different mood.

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R. and R. MENZEL (1937) report on domestic dogs that the "milk step" or "first pawing towards the mother" of pups develops into "bepawing", which is a part of the playful, friendly approach. This also applies to wolves; but the gesture disappears with getting older.

Much more frequently transformed sucking motions may be observed, which are part of the behaviour pattern of "humility" or "active submission" as well as preliminaries to mating.

The former follow, with laid-back ears, a licking of the face and gentle snout bunting against the lips of the dominated one (Fig. 46a and b), or finally as a gentle grabbing of his snout accompanied by "tender"

whimpering. The anal part of the submissive individual is covered up under all circumstances, however the tip of the tail does not necessarily need to be pulled in. Often he "wags" sideways with his whole hindquarters. This lively action, accompanied by a weakly curbed forward movement, and above all the deliberate snout motions, creates the impression of definite initiative, which, because of its behaviour is called "active submission". Naturally, transitions occur as between "passive, "shyly active" and "obtrusively active" submissions; these may be found generally among the most varied expression forms of wolves (one should compare also Fig. 4 to 6.)

The described action of snout bunting with laid-back ears is also carried out "empty" by subordinate individuals, if in a peaceful mood a superior wolf observes them from a considerable distance, (Fig. 47). This is a weakening of the deliberate expression action similar to the relatively indefinite behaviour that we found in the defensive snapping of subordinate individuals.

Incidentally, it should be mentioned that in rare cases, also, among individuals of almost equal status, such as high ranking males, "tenderness actions" are exchanged, which have a certain similarity with the expression accomplishments discussed here. The "snout tenderness action", to be sure, is reduced to snuffling and rubbing of the sides of the head; rarely in this connection was a pressing together of heads observed (Fig. 48 and 49).

In the mating preludes quite a variety of "snout tenderness" forms may be observed, which, moreover, are closely related in a functional and formal way to the previously mentioned behaviour of mutual besnuffling of the nose and the sides of the head (Fig. 50a). At the outset of the rutting period, contact forms between head and head - besnuffling each other, head rubbing, snout bunting, grabbing of the snout of the other (Fig. 50b) - predominate; during the actual rut, on the contrary, the contact is between the snout of the male and the genitals of the female in the form of snuffling and licking (Fig. 51), or again the male touches the back of the bitch with his snout (Fig. 52). The ^("connection") "relationship" of this behaviour with that of "snout tenderness" and that of riding up is unmistakable (one should compare Fig. 45).

To these forms of direct contact between sexual partners there is added the indirect relationship over the excrements. The change in the forms of interrelationship of the sexual partners during the course of the winter may perhaps be described as a transition from an oral to a genital contact.

In the observed packs, and indeed only while they were in peaceful mood and then only with about a quarter of the individuals - males and females - a behaviour showed up, which could possibly be interpreted as a

distorted infantile behaviour. This is the - close up - standing across the forequarters of a recumbent, resting partner (Fig. 53). Occasionally, the recumbent animal will lick the genitals of the animal standing over him (Fig. 54). If this does not occur, the persistence of the latter is less than in the other case.

Especially as "standing across" may be observed only among very intimate individuals, I believe that one must consider it as a distorted relationship of the whelp to the mother and is actually an offering of the genitals, which release the tongue massage of the mother.

The riding-up action as a preliminary to pairing has already been related and indicated that the action among males cannot be viewed as an intention motion of sexual significance. Of course it may be added that homosexual relations could also be observed in wolves, much more rarely however than in domestic dogs. (I could confirm the attempt towards homosexual relations in only two males of the small, subordinate race of wolves). Generally, however, the riding-up action of the dog wolf (P. 108) is a kind of deliberate action demonstration. This is reminiscent of the findings of LORENZ (1939, p. 280) concerning formation of pairs in fishes and birds

after the "labyrinth fish type". To be sure, with wolves - as moreover also with various monkeys - the riding-up action is not only the expression of superiority over the passive partner, but coincidentally it is the demonstration of social prerogatives over the whole society.

If the action is directed mainly towards the jumped-upon individual, then it may occasionally be accompanied by "symbolical" biting of that individual's neck (Fig. 55); however, frequently it remains in the state of an intention movement (Fig. 56). In contrast to this, a scene is sketched in Fig. 57 in which the riding-up wolf bares his teeth at the actual addressee over the back of the jumped-upon individual.

As transformed forms of original sexual activity, which became expression actions with social significance, anal controls and anal presentation and, respectively, anal withdrawal should also be brought to mind.

All of these expression actions are in no way locked-up in appearance, or ^(precisely) exactly established courses of behaviour. WÖRNER (1940), during an investigation of monkeys arrived at the conclusion that excitement, expression and understanding are part of an inclusive, firmly-established framework, which has significant free play room along with the firm, inheritance-dependent disposition characteristics.

With free play, secondary principles, which are determined by inward and outward factors, may result. This witness to the lack of establishment of the expression phenomena in certain monkeys is very worthwhile.

In the form elements of expression, to be sure, WÖRNER sees inherited abilities, which remain locked up to broader understanding, excepting for the physiognomical-dynamic similarity with thought-out behaviour. Although he acknowledges their limitation in numbers and the variable occurrence of some of them in plastic areas of expression behaviour courses; apparently, however, he is not aware of the fact that the action forms of expression in general may be ascribed to deflected motions, - or "distortion products" of behaviour without expression functions - arising out of battle action, sexual behaviour, food intake of the infant, etc. The following types of distortion were already mentioned:

- (a) Limitation to behaviour components with intentional character;
- (b) Ritualization, i.e. shaping (through subordinate expression phenomena) in the sense of showy impression.

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These expression values now may either, -

a* be preliminaries to "source accomplishments", or

b* show up as displacement-activity phenomena with completely different functional relationships. (Whether or not TINBERGEN'S expression of "behaviour aroused from without" should be modified for wolves is debatable.)

The previously described expression behaviours and actions have now been set up in table form which also designate "origin" and function. The suggestion of function is given in a completely inadequate manner so far as causal analysis is concerned. In the whole behaviour structure of wolves, it is however hardly possible to suggest the effect of an expression phenomenon in the sense of a solution. (within the meaning) As already mentioned actual behaviour is conditioned by a very complex social situation; here again, not only do numbers of individuals but also "personality values" play a decisive role.

We may take from the accompanying table that propagation is guided by a ramified expression system, which is related to inwardly and outwardly stimulated expression accomplishments. However, the "chief customer" of expression actions is obviously social life. Even pair formation and pairing is subordinate to social relations and they have a social expression function along with their expression values.

It is not an exaggeration to say that in wolves the whole behaviour storehouse - which is unconsciously enriched with the aid of reduction to intention movements,

ritualization and manifold possibilities of variation and combination - is opened up, by the (modified) displacement principle, for social expression, or in itself possesses an expression function. The expression phenomena described heretofore may be used as a temporary guide in this connection.

The described results of the investigation bring to mind an historical development process, namely the higher development of the social life - and with it also the enrichment of expression - in the course of life of the wolf. Associated with enrichment of expression, I believe I may also deduct that there is a tendency towards "degradation" (and also "symbolization"; compare ANTONIUS, 1939) of the individual expression accomplishments; a decline in the ever-increasing hierarchy of expression values. In my opinion, the behaviours of baring of teeth, snapping, anal presentation and anal withdrawal, anal control, snout thrusting, etc., may be so considered; as original deliberate actions, namely, those, which, by the progressive process of expression-created "distortion", have broken away from their origins and have become little more than deliberate behaviours with very general expression functions. The superior expression action gave way

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*P. 110 is the table.

to mere "decoration", i.e. to a subordinate level of expression, and this change indicated both the specialization of and for the expression function.

The previously listed form groups of deliberate expression actions are not in any sense altogether complete. Recently several striking cases were brought out, primarily with a view to a closer understanding of the deliberate expression actions of the wolf. In any investigation, even if it is only more or less inclusive, the interplay of expression accomplishments in the environment of wolves, in particular within the society, must be considered as a matter of course. Here, for the first time, at the highest level of expression, the actual "social actions" can really become effective.

In this paper, a description of the social relationship ceremonies in their broadest meaning has not been given, it shall, however, form the main consideration of the already mentioned sequel (II) of this expression study.

V. SUMMARY

It is hoped that this paper will be an introduction to and the start of an orderly description of observed expression phenomena of wolves in captivity.

First, it was necessary to develop the bases of this order and to establish the limits of an area which seemed to be blurred. On the basis of several years of continuous observation and occupation with this subject, the functional limitation of expression came to the fore as being the most useful: expression as a function of living together!

So considered, expression must have the closest possible relation to species-typical sociological laws. Following a sketchy biological survey, it is therefore attempted to understand functionally the expression accomplishment beginning with the structure of the society. Here it is worthwhile to bring out the fact that social relationships leave an imprint on life conduct in all its aspects, and that the form of life of each individual itself adds to the shaping of the social situation, and thus has expression functions.

If the limits of expression are extended thus far, then the hierarchial structure of the sum total of expression should not be overlooked. The superior "social actions" following the introduction of the "animal personality", in the other extreme, (serve as a contrast to) oppose phenomena which may be seen as mere "decoration" in order to sharpen the effect of expression. Deviation (P. 112)

from these extremes is impossible. Hence, it is not desirable to reserve the designation of "expression" for those subordinate phenomena which were given closer study under olfactory and optical expression. We are concerned with a co-ordinated hierarchy of expression values.

In this hierarchy the deliberate, psychological, "primitive" olfactory tendencies are, of course, partly of great significance (for propagation purposes), but at the same time they are overshadowed by higher optical expression accomplishments of actual social relationships. The subordination of propagation to the social sphere is in harmony with this theory.

By delving into the higher levels of expression, we come upon the deliberate expression actions. These expression actions indicate their characteristic as being real actions primarily in that they follow the introduction of "personality" and fit into the momentary social situation at all times. They do not in any way conform to a rigid form of behaviour course.

The study of these forms indicates that they are comprised of a limited number of species-typical "original forms". The manifold capabilities of interposing these forms and of combination and of transformation, create an expression system on these bases with seemingly unlimited possibilities of nuance.

Consideration of this whole expression phenomenon brings up the question of its historical development progress. The creation of expression is part of the higher development of social life. First, it indicates an enrichment of expression by including ever-increasing areas of life into the social sphere, and later it indicates a reversal to the more exclusive expression phenomenon. This functional specialization, which may also be called "symbolization", is also a "degradation" of the functional hierarchy of expression values.

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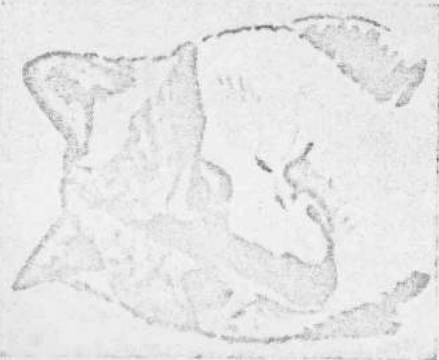


Fig. 11. a Gesicht eines Wolfes der grossen Rasse. Vor allem durch ihr Gesicht, daneben aber auch durch ihr Verhalten, wirkt die kleine Rasse gegenüber der grossen maskenhaft-ausdrucksvoll-jämperloslich.



Fig. 12. Normales Aussehen eines rassetreuen Wolfes.



Fig. 13. Drohung. Der Ausdruck zeigt die Prämienstellung.

Fig. 14.

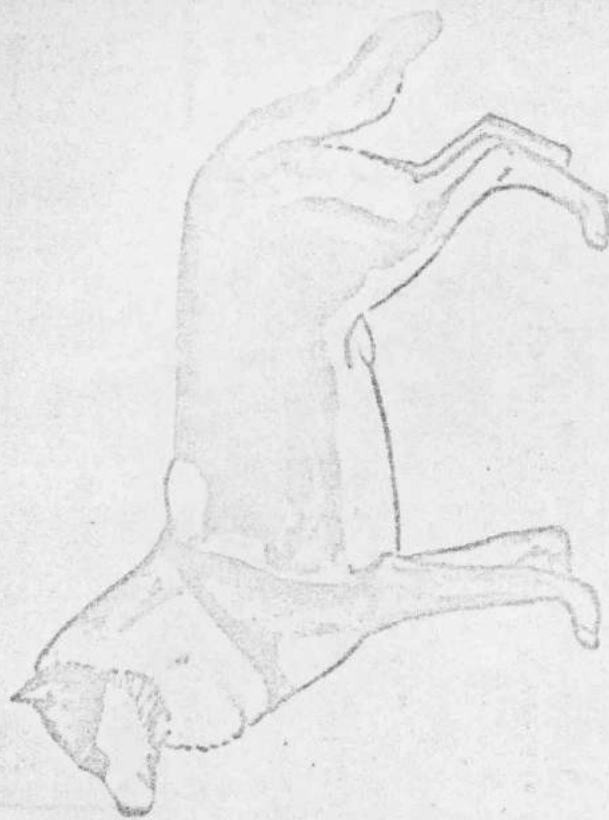


Fig. 10. a Vertreter der grossen Rasse
b Vertreter der kleinen Rasse
c zeigt die maskiertere Gestalt und die kontrastreichere Färbung der grossen Rasse.



Fig. 20. Letzter Wolf: Blick sicher, Kopfhaltung und Ohrenstellung dergleichen.



Fig. 21. Wolf mittlerer Höhe: Blick nicht sicher, leichter „Ruckwärts-Zug“ in der engesend. Ohren mit Ruckwärts-



Fig. 22. Drohung: Man verzi. Fig. 13 und 14. Blick stark, Pupillen gross, zeigen die Brauen gelblich.



Fig. 23. Angstliche Erregung.



Fig. 24. Flachbiter (Cervulus): Ausdr. nicht gebländert (Sinn: Jern). Fig. 25) ist zu erkennen, dass er sich nicht um soziale Unsicherheit handelt.

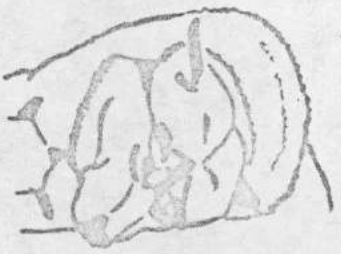


Fig. 25. Argwohn und Abwärtendenz (ähnlich Fig. 19).



Fig. 1. Drohung — Zahnefleischen, senken und Brauen gewinkelt, Leberheit — Mundwinkel nicht abgezogen. Reichmassigkeit der Erregung — Kiefer fast geschlossen.



Fig. 2. Drohung — Zahnefleischen, sich stark erregte Erregung — Mund stark geöffnet. Leichtere Unsicherheit — Mundwinkel etwas zurückgezogen, Stirn schwach gewinkelt und Ohren zurückgezogen.



Fig. 3. Drohung sehr schwach — adrenergen nur andeutend. Unsicherheit — verd. Fig. 14 schwachen der Erregung — Mund mittelstark geöffnet.



Fig. 4. Drohung schwach Unsicherheit gering.



Fig. 5. Angstliche Erregung, Schwertschwanz-Situation.



Fig. 6. Feind vorwärts — Ohren gewinkelt, Unsicherheit. Abwärts gerichtete — Brauen gezogen. Argwohn — Ohren vorwärts und rückwärts gezogen, Mundwinkel leicht zurückgezogen.

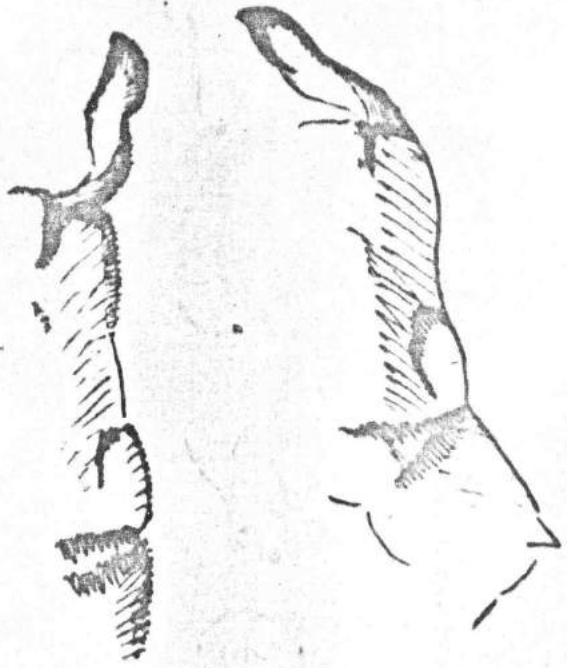
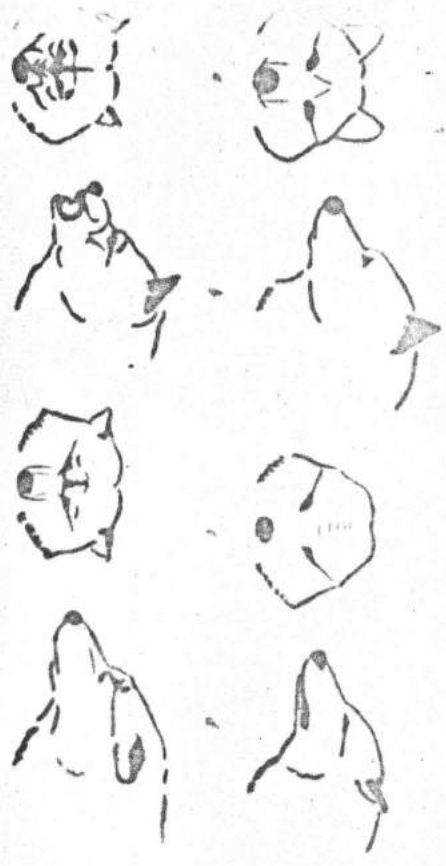


Fig. 28. Ausdruckswerte der Rückenlinie durch die Eitelhaarfärbung und des Haarstrahlens a Rückenlinie normal; b Rückenhaare ge-



Fig. 29. Das „Analgesicht“ des Wolfs. a Normalhaltung, Schwanz b Analgesicht des Überläsers im sozialen Verkehr.



26. Möglichkeiten des Gesichtsausdrucks in Karikaturform. a und b Normalgesicht eines Kanjohren; c und d Anglichkeit; e und f Drohung; g und h Argwohn



27. Zusammenhang von Kopfausdruck und Körperhaltung bei der Ohrstellung und Körperhaltung dargestellt an Möglichkeiten a Kanjohren normal; b Vorderkörper normal; c Imforten von vergl. Fig. 50a und 61; d aktives Entwerfen von vergl. Fig. 36a und e Abwärtswendung von vergl. Fig. 37; f Aktive Vorwärtsbewegung von vergl. Fig. 37; g Spreizstellung von vergl. Fig. 37; h Aktive Vorwärtsbewegung von vergl. Fig. 37; i Aktive Vorwärtsbewegung von vergl. Fig. 37; j Aktive Vorwärtsbewegung von vergl. Fig. 37

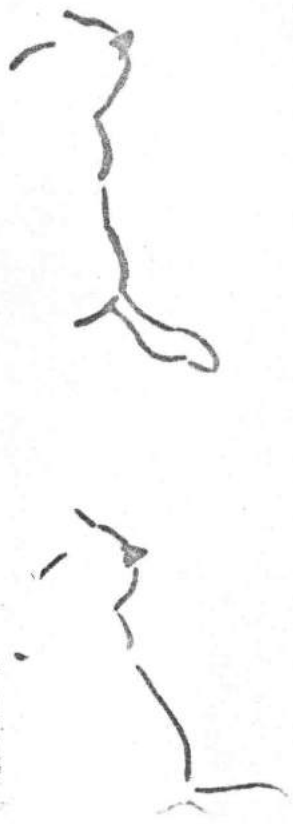


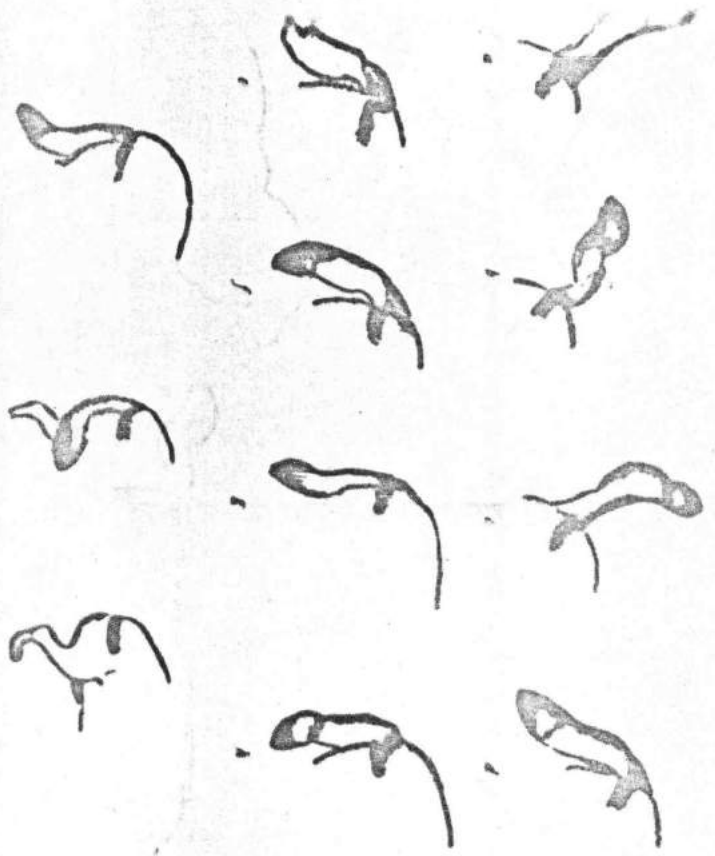
Fig. 33^a Formen freundlicher Lebhaftigkeit: *a* Impassieren, aufforderung (Rückwärtendenz; gespöckliche Flüchtbereitschaft).



Fig. 34 Drohstellungen, gekennzeichnet durch Sträuben der Rückenhaare. Heben der Schwanzwurzel *a* sichere Drohung; *b* unsichere Drohung; Drohung und Abwehr.



Fig. 35 Abwehr mit „Zusammenziehen“ des Körpers, *a* sehr gekrümmte häufig bei unterlegenen Weibchen; *b* beharrliche Abwehr, „Trotz“; *c* „Notwehrschlagen“.



36 Zur Ausdrucksfunktion des Schwanzes, *a* Selbstsicherheit; *b* sichere Drohung; *c* (mit seitlichem Wedeln) Impassierhaltung; *d* (nahehaltung (Situation ohne soziale Spannung); *e* nicht ganz sichere Drohung; *f* (nahehaltung (ähnlich *d*), besonders häufig beim Fressen und Beißen; *g* - wie Stimmung; *h* zwischen Drohung und Abwehr (vgl. Fig. 34 b); *i* (mit seitlichem Wedeln) aktive Unterwerfung; *k* und *l* starke Hemmung.



37 Wedeln mit dem Schwanzende in Kampfstimmung.



Fig. 38 „Schwanzschlagen“ im Auftritt.



Fig. 30. Gehemtheit eines Rangstiefern auf Blick. Man die Ohrenhaltung und die Rückwärtstendenz des Gehemnten.

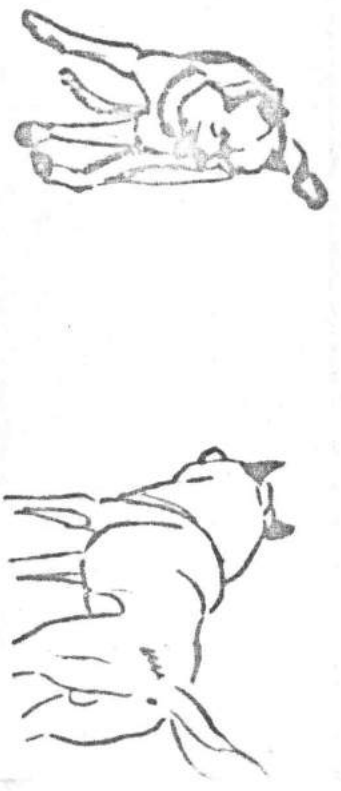


Fig. 30. Ranghoher „protestiert“ gegen optische Kontrolle.

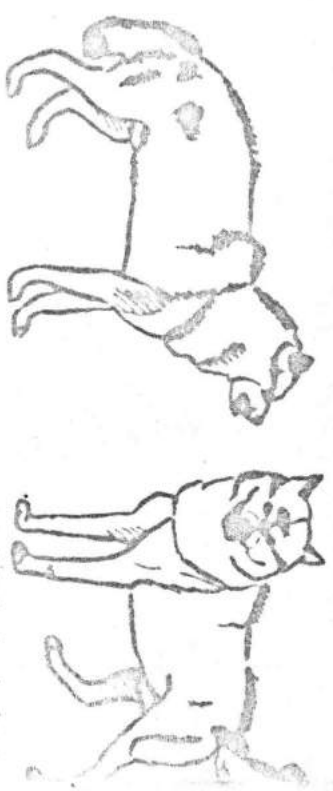


Fig. 31. Die „Beissdrohstellung“. Der Wolf links ist leicht in Rückwärtstendenz in Kopf- und Ohrenhaltung. Kucken nach unten gekippt. Schwanz gesenkt.



Im Feindeskreis: a Argwohn mit Abwehrkomponente; b geduckte Bewegung (Fluchbestreben); c wie b, aber mit Beobachtung, ev. hinter Deckung.

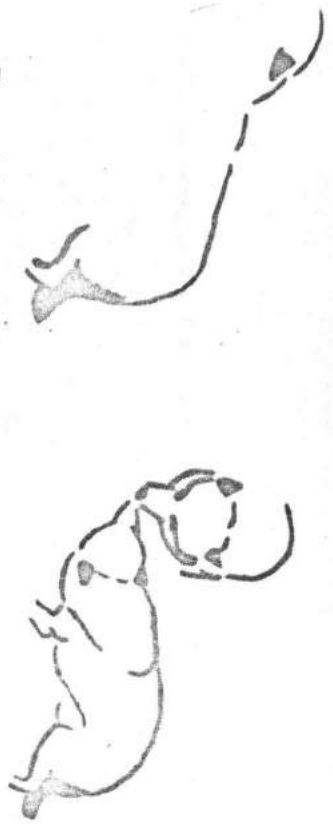


Fig. 37. Aktive Unterwerfung (verg! Fig. 46 a und b).



Fig. 38. Chorheulen

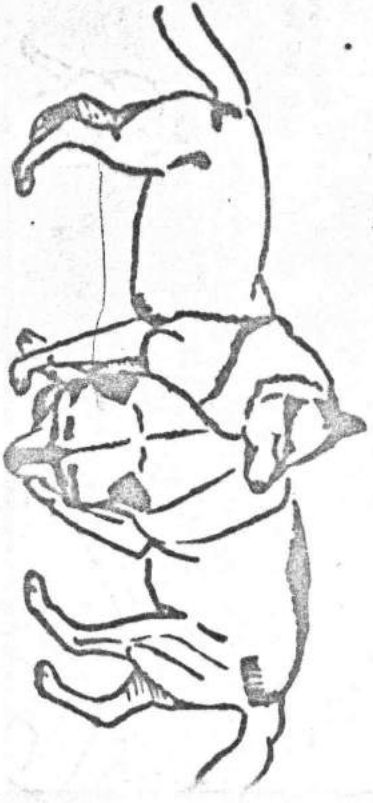


Fig. 45. Intentionsbewegungen der Wölfin zum „Aufsitzen“ allein intuitiv „arriviert“ die Wölfin einen ihr sympathischen ruhenden Ranghohe, aber nicht ranghöchste Mannchen weisen diese „Vertraulichkeitsbewegungen“ mit grösserer Aufmerksamkeit gegenüber dem Leitwolf zurück. Leitwolf leckt am ehen spritzweise abgegebene Harn der Wölfin. Nach diesen Bewegungen und einer Runde federnden Lautes „interessiert“ sich diese Wölfin für die Bewegungen und spielerisch-lebhaft „zärtlich“ zugleich.



Fig. 46. „Schauanzärtlichkeit“ im Sinne der aktiven „Anpassung“ a die Haltung des Tierchen ist „streng“, aber doch in der „Anpassung“ b die Haltung des Tierchen ist „gütlich“, an der Schwanz des Tierchen ist die Haltung des Tierchen gesteuert. Von passiv bis zu „frecher“ Aufdringlichkeit sind alle Übergänge zu finden.



Formen der Überfallsdrohung a Diese Haltung kommt auch vor; b Drohung, die im Verlaufe von Auseinandersetzungen auf kurze Distanz (ca. 1 m) angenommen wird (vergl. Fig. 3).



Fig. 47. Überfallsdrohung zwischen rivalisierenden Weibchen.



48. Hanghafter Rude ansteigt einen rangtieferen durch „Lauerstellung“.



Fig. 51. Der Leitwolf leckt das Genitale der Spitzwew (Vgl. Text zu Fig. 52)



Fig. 52. „Schauzenschulterstossen“ während der engeren Bräu im Treit, bald im Schritt, bald das Genitale der Wölfin leckend, bald mit „zenschulterstossen“ folgt der Leitwolf — ev. in Begleitung eines weiteren Ruden — dem Weibchen unaufrichtig. Unterbrechungen bilden das Harzer Ruden — dem Weibchen unaufrichtig. Unterbrechungen bilden das Harzer Ruden — dem Weibchen unaufrichtig, seltener auch „Eifersuchen und Angriffe auf Rivale, bezw. Rivallinnen, seltener auch „Eifersuchen“ seitens der Wölfin.



Fig. 53. „Quersteher“ zwischen vertauschten Ruden



Fig. 54. Der Leitwolf (das Genitale des „quert“ der Weibchen. Die ist hier anstehend beid-



Schnauzenstossen als Distanzgebärde. Es ist immer mit Rückwärtsziehen der Ohren und „Glattziehen“ des Gesichts (vgl. Fig. 23) verbunden.



Freundliche Annäherung zweier ranghoher Ruden.

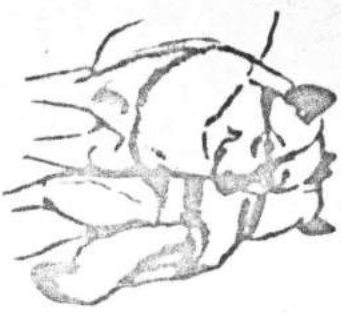
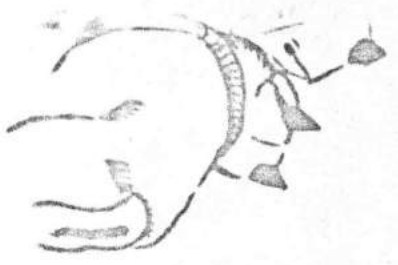


Fig. 55. Zärtliches Reiben der Körperseiten zwischen Ruden.



„Schauverträglichkeit“ als Parallelschreitbewegung. Zwei Weibchen (Schauverträglichkeit). Zu solchen Zusammenkünften es im Herbst zur Zeit des „Feststellungsjahrs“ kommt aber immer wieder zwischen ranghohen Weibchen und unpaarigen, aber zu „abgesetzten“ Weibchen & zärtliche Annäherung des Weibchens. Insofern ist die Bildung des Rudens.



Aufreiten mit Drohung
Nackebiss als Überlegen-
monstration. Der Besprungene
er eingeschüchtert, wird aber nun
am Gegenstoß reagieren. (Beide
Individuen knurren stark.)



Fig. 56. Intentionsbewegung
zum Aufreiten zwischen Rüden.
Deutlich sind die leicht drohende Hal-
tung des initiativen und die Unsicher-
heit des passiven Wolfs zu erkennen.



57. Aufreiten als Demonstration an die Adresse eines
Rüden. Das Knurren des Besprungenen ist nicht einleuchtig gerichtet. „Konfron-
tation“ bis zu 4 Männchen, die alle knurren und die Zähne fletschen, sind nicht
An der präzisen Adressiertheit der Besardung ist die Überlegenheit zu erkennen.
wird nie gemeinsam angegriffen, solange er überlegenes Aufreiten bewahrt.

AUSTRUCKS-STUDIEN AN WOLFEN
(Expression-Studies of Wolves)

by

R. Schenkel

A

Translation of the
Illustrations

Behaviour, vol. 1:81-129

TABLE OF EXPRESSION FORMS AND ACTIONS, INCLUDING THEIR ORIGINS AND FUNCTIONS

ORIGIN	EXPRESSION ACCOMPLISHMENT	FUNCTION	ORIGINS AND SUPPORTING
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1. Expression behaviour courses, which are preliminaries to source accomplishments:

Biting	1x Baring of teeth	Threat to attack as well as to defend.	
	2x Opening the mouth wide	Threat to attack as well as to defend.	
	3x Snapping	Threat "protest" - or defense character.	
	Springing at	4x (Bite-) threat position	Threat only applies to superior individuals
		5x Unexpected attack threat	Threat only applies to superior individuals
		6x Uncompleted springing at	Threat to intimidate as well as to defend.
	Mating	7x Fixed stare	Threat the "control lock" is the most reduced form of encroachment.
8x Anal presentation by the ♀		Part of the rutting ceremony.	with respect to the total expression function see below: 18x and 19x.	
9x Intention motion of the ♂ to ride up on the ♀		Part of the rutting ceremony.	"	

.....(continued)

2. Expression behaviour courses with displacement activity characteristics:

Food Intake of the Whelp,

(a) Milkstep

10x "Bepawing"

Pleasure accented relationship.

(b) Sucking behaviour

11x Snout bumping against the lips

Licking of the face
Grabbing of the snout

Expression of submission, of friendly attitude, and part of the rutting ceremony.

In the relationships between man and dogs the human hand often replaces the face (in some cases, as with dachshunds, also the foot) as the receiver of these gestures.

(?)

12x Licking of the genitals of the rutting ♀ (by the ♂)

Part of the rutting ceremony.

Along with social privilege, hence (status-demonstration).

(?)

13x Licking the urine of the rutting ♀ (by the ♂)

Part of the rutting ceremony.

(compare 14x).

(?)

14x (Compare 12x) general anal control.

Demonstrative expression of social initiative.

Posture of release of the whelp for cleansing by the mother (?).

15x "Diagonal standing" over a recumbent animal.

Expression of infantile-"erotic" mood.

16x Spray urinating of the ♂ in summer.

Marking of territory and making acquaintance. (status-demonstration).

17x of the ♂ and ♀ in the winter.

Part of the rutting ceremony.

"

18x Anal presentation (General) Expression of security.

19x Riding up beneath ♂

Status demonstration

With a distinctly aggressive character.

Mating (compare 7x, 8x)

ILLUSTRATIONS

- Fig. 1. Smelling at the corner of the mouth. This type of "relation-assumption" is of subordinating social significance.
- Fig. 2. Withdrawing the anal portion. The gesture is a sign of inhibition and social inferiority. This withdrawal is seriously hindered by intense excretion, and in extreme cases, there follows, in addition, emptying of the intestine; less often, emptying of the bladder.
- Fig. 3. Withdrawal of the anal portion by turning away the posterior part of the body. A slight defensive motion of the head. (The superior wolf is recognizably in control of the initiative and the presentation of the anal portion.)
- Fig. 4. The passive act of "throwing oneself down." This is assumed particularly by youngsters and females; the latter before the start of flocking in the company of males. The gesture qualifies with all passivity as a certain obtrusiveness: it presents itself, for example, as a "way of begging for food."
- Fig. 5. The passive throwing down oneself with an indication of activity: activity of the sense organ, raising of the muzzle, and readiness for locomotion.
- Fig. 6. First step of the "active throwing down" (compare with Fig. 46 a & b).
- Fig. 7. An anastomosis meeting of higher rank. Presentation of the anal parts and control activity are signs of social initiative. (This sort of encounter is very unusual among animals commonly considered.)
- Fig. 8. Presenting a female (α) wolf in heat, in a "dance step."
- Fig. 9. Presentation of a suppressed female wolf during heat.
- Fig. 10. a) An example of the large strain. b) An example of the small breed. One observes the striking form and the contrasting coloring of the large strain.
- Fig. 11. a) The face of a wolf of the large breed; b) the small strain. Above all, in the face and also in the behavior, the small type is opposite to the "impersonal" one with the mask-like expression.
- Fig. 12. The "right angle" expression of a high ranking wolf.

- Fig. 13. A threat--the frontal view shows the nasal bulges and those of the eyebrows.
- Fig. 14. Threat--the snarl and the convolutions of the bridge of the nose and the eyebrows. Certainty--the corner of the mouth is not pulled back. The uniformity of the excitation--the jaw is almost closed.
- Fig. 15. Threat--the snarl. Mounting excitement--the mouth firmly opened. Slight uncertainty--corner of the mouth somewhat drawn back, forehead slightly raised, and the ears "pinned" back.
- Fig. 16. A very weak threat--only a suggested snarl. Uncertainty-- Compare with Fig. 14. Increase of excitement--the mouth opened with moderate force.
- Fig. 17. Weak threat; great uncertainty.
- Fig. 18. Anxiety; "cry of pain" situation.
- Fig. 19. Enemy "vis-a-vis"--ears directed sideways. Component of defense--brows raised. Uncertainty, suspicion--ears gently folded and directed posteriorly, corner of the mouth slightly drawn back.
- Fig. 20. "Leader Wolf." Confident glance; the holding of the head and placement of the ears are also confident.
- Fig. 21. Wolf of a middle rank. It is certainly not of "regal" appearance; a gentle "backward pull" in the region of the brows; ears with posterior tendency.
- Fig. 22. Threat. Compare with Figs. 13 & 14. A staring look; pupils large, raised toward the brows.
- Fig. 23. Uneasy submission.
- Fig. 24. Readiness for flight. One should notice, from the rough forehead (compare Fig. 23), that it does not pertain to a social uncertainty.
- Fig. 25. Suspicion and a tendency toward defense. (similar to Fig. 19)
- Fig. 26. Possibility of a facial expression in the form of a caricature. a & b) Normal face of a high rank; c & d) anxiety; e & f) threat; g & h) suspicion.
- Fig. 27. Correlation between "head expression" and holding of the body, with reference to placement and position of the ears, based on several possibilities. a) Normal high rank;

b) normal suppressed; c) imposing (compare with Fig. 50 a & b);
d) active throwing down of oneself (compare with Fig. 46 a & b);
e) threat to spring (compare with Fig. 42 thru 44);
f) self-defense advance (compare with Fig. 35 c); g) invitation to sport (playful readiness to flee); h) uncertain and weak defense.

Fig. 28. The expressive value of lines on the back through the effects of hair color and ruffling the fur. a) Lines of the back normal; b) hair ruffled.

Fig. 29. The "anal face" of the wolf. a) Normal position, tail hanging; b) anal face of the wolf pondering in social intercourse.

Fig. 30. Concerning the expressive function of the tail.
a) Self confidence in social intercourse; b) certain threat;
c) imposing attitude (with sideways brushing); d) normal attitude (situation without social pressure); e) a not-entirely-certain threat; f) normal attitude (similar to "d"), particularly common during eating and observing; g) depressed mood; h) between threat and defense (see Fig. 34 b); i) actively casting oneself down (with sideways brushing); k & l) strong restraint.

Fig. 31. Wagging the tail end when in the mood for combat.

Fig. 32. "Knocking the tail" in step.

Fig. 33. Types of a more friendly liveliness. a) To impress; b) a challenge to sport (a posterior tendency: readiness to play).

Fig. 34. Threatening attitude, characterized by ruffling up the hair on the back and raising the "root" of the tail.
a) Certain threat; b) uncertain threat, between threat and defense.

Fig. 35. Defense with a "pulling together" of the body.
a) A very obstructed defense, often used by inferior females;
b) stubborn defense, "defiance"; c) snapping in self-defense.

Fig. 36. In enemy territory. a) Suspicion with a defensive component; b) a humbled progression (a tendency toward flight); c) like "b", but with observation, perhaps behind cover.

Fig. 37. Active throwing down of oneself (compare with Fig. 46 a & b).

Fig. 38. Howling in a pack ("choir howling").

- Fig. 39. Rapid obstruction of a high ranking animal. One should notice the position of the ears and the posterior tendency of the wolf which is stopped.
- Fig. 40. A ranking animal "protesting" against optical control.
- Fig. 41. The "placement of a threatening bite." The wolf on the left is slightly inferior: the tendency to draw the head and ears back, the back curved from below, tail lowered.
- Fig. 42. Ways of threatening attack. a) This attitude occurs even in play; b) threatening position, which, during a dispute, is assumed at a short distance (about 1 meter). (Compare with Fig. 3.)
- Fig. 43. A threat of attack between rival females.
- Fig. 44. A superior male frightens a high ranking animal by "lying in wait."
- Fig. 45. A movement of intention of the female wolf to "ride."
a) Alone in the initiative, the female wolf "animates" one of her congenial resting males. The ranking wolf, but not the highest ranking male, usually declines this "intimacy" with resentment and with his attention toward the directing wolf. b) The guiding wolf even licks the squirt of released urine of the female wolf. After the raking movement and a round of springing runs, the wolfess is interested in the effect of her behavior. Her movements are playfully brisk and at the same time, delicate.
- Fig. 46. "Muzzle tenderness" in the sense of actively throwing oneself beneath another. a) The attitude of the superior is "stiff," but gently evasive. The most active form of the "stiffness" is shown when the superior seizes (claws) the muzzle of the other. b) The superior is in rather good spirits, but evasive. In compliance, the initiative of the ranking animal appears increased. One can find all transitions, from a passive humility to "bold" obtrusiveness.
- Fig. 47. Using the thrust of the nose as a gesture of distance. It is always combined with strong backward movements of the ears and a "smoothing" of the face (compare with Fig. 23).
- Fig. 48. Friendly approach of two ranking males.
- Fig. 49. Tender rubbing of the sides of the heads, between males.
- Fig. 50. "Muzzle tenderness" as the manifestation of pair formation. a) The female appears uncertain (holding the tail). Such a meeting comes in the fall, at the time of the "change of phase"; however, even further into the winter between individual ranking males and suppressed, but not entirely "frigid" females. b) Tender activity of the female, imposing attitude of the male.

Fig. 51. The directing wolf licks the genitalia of the "pointing" wolfess. (Compare with text of Fig. 52).

Fig. 52. "Nose-to-shoulder pushing" during heat. First pressing, then stepping, later licking the genitalia of the wolfess, then the directing wolf follows with the "nose-to-shoulder pushing" of the female—eventually in the presence of a male of higher rank. Urination and the attack upon rivals cause interruptions; there's also "jealousy" on the part of the wolfess with respect to rival females.

Fig. 53. A "diagonal position" between intimate males.

Fig. 54. The directing wolf licks the genitalia of the wolfess, who is standing diagonally, The initiating one here is approaching laterally.

Fig. 55. Riding (with a threat to bite the neck, as a demonstration of superiority). The springing one is indeed timid; it will, however, react with a push. (Both individuals give out intense growls.)

Fig. 56. A movement of intention to "ride" between males. The gently threatening attitude of the initiating one and the uncertainty of the passive wolf should be clearly recognized.

Fig. 57. Riding as a demonstration of the direction of a third animal. The growling of the middle wolf is not clearly "regulated." "Confronting" (up to four males, all of which growl and show their teeth) occurs quite often. The superior wolf is often recognized as the precise "director" of the gesture, and the male will, in general, never attack as long as he confirms his appearance of superiority.



Schnappeln im Mund
soll diese Form der Bezeichnung
als von unterworfenster sozialer
Bedeutung

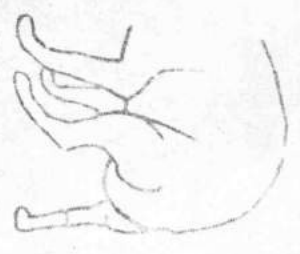


Fig. 2 Entziehen der Anal-
faktion. Die Eingänge der Zehen
der vorderen und sozialen Hinter-
extremität bei oberer Abstrichung ist
die Fortbewegung schwer zu ermitteln. In
extremen Fällen erfolgt zusätzlich
Darmselbstentleerung.



1. Entziehen der Analpartie durch Wegdrehen des
Oberkörpers, leichte Abwehrbewegung des Kopfes. (Bei oberlegene Wolf
ist an der Kontrollimpulsvorteil und dem Erreichen der Analyse erkennbar.)

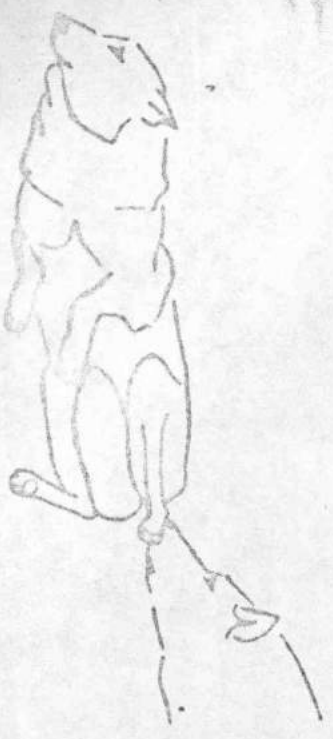


Fig. 5. Passive U-
wertung mit
Zeichen der
vorderen Abwehr-
Stellung. (Soll
beiden Lokomotion
schiff.)

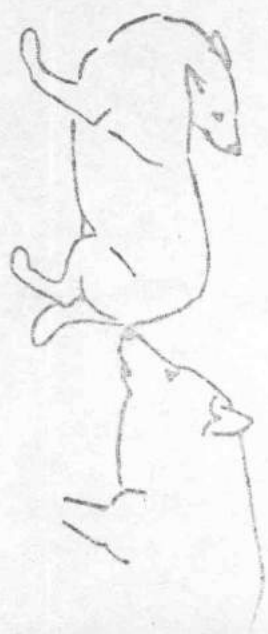


Fig. 6. Vorstufe
der aktiven
Unterwer-
fung* (Man vergl.
Fig. 46 a und b.)

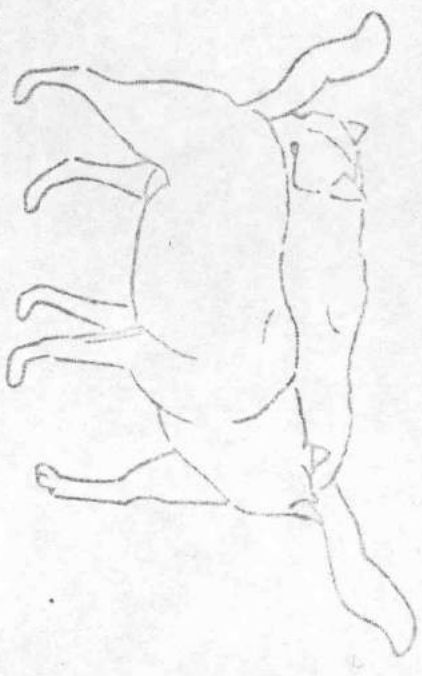


Fig. 7. Zusammengeführten Kniehöcker. Präsentation der Anal-
Kontrollaktivität sind Zeichen der sozialen Initiative. (Diese Form der Bezei-
gung ist bei reinen sozialen Verhalten Tieren sehr selten.)



Fig. 8. Präsentierende Brunfel-
tuge. a. Wolf im Laufs-
schritt.



Fig. 9. Präsentieren
unterdrückten Wollens
beim Revier.

1. Massive Unterwerfung. Diese Haltung wird besonders
bei den Wölfen, die zusammen von mehreren
Wölfen (bei Revier) beobachtet werden.