

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

(P. 96)

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 bicuspid) 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.

(P. 97)

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. *sep. ?*

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".