

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 ^(superior) 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).

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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 (P. 105) 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

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 unmistakeable (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.