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The ontogeny of social play and agonistic behaviour in selected canid species

Dorit Feddersen-Petersen

Abstract. The ontogeny of social play and agonistic behaviour in wolves (*Canis lupus lupus* L.), domestic dogs (poodles; *Canis lupus* f. fam.) and golden jackals (*Canis aureus* L.) during the first year of life was the subject of comparative investigation. Specific or domestication-induced variations in social play correspond to the phylogenetic (evolutionary) or domestication-induced differences in the social organization. Therefore, social play is defined in statu nascendi as specific group and communication behaviour. Qualitative and quantitative differences in the ontogeny of agonistic behaviour accord with specific differences in social play and are as well important for the development of hierarchies or species-typical social structures

Key words. Mammalia, Canidae, wolf, dog, jackal, ontogeny of social behaviour.

Introduction

Agonistic behaviour, the "competition" complex referring to fighting, threatening and submissive (e. g., immobility and passivity) and escape behaviour (Hinde 1971; Tembrock 1982; Wilson 1975) does not represent an independent functional system but is instead delegated to other functional goals. As such it serves the assertion of certain environmental demands.

The present study is an attempt to investigate those structures of agonistic behaviour as determined by mate requirements such as the biosocial mate (Tembrock 1982). Aggressive behaviour appears as a typical component of this behavioural complex in canids and may itself be the expression of several different intrinsic conditions or types of behavioural readiness (Hassenstein 1980). Aggressive behaviour is a component of communal social behaviour of many mammals such as the canids and is significant in the establishment of social hierarchies. In accordance with the suggestion of Tembrock (1982) the term "aggressive behaviour" is used in the following only in conjunction with the appearence of motor patterns directed against the physical well-being of conspecifics. It has to be stressed that aggression cannot be studied apart from the response that it evokes (Bekoff 1978; Eibl-Eibesfeldt 1967). So the interacting animals must be viewed as a social unit (Bekoff 1978).

Observations of social animals show that agonistic behaviour and behaviour involved in an establishment of contact (e. g., social play) are the basis for creation and maintenance of a social hierarchy, that is, dynamically balanced behaviour patterns for increasing or decreasing distance. Agonistic distance regulation involves distance increase on the one hand and, on the other, prevention of distance decrease and, as such, counteracts social play. In terms of motivation and function play activities represent various phenomena of varying quality because they include complex, diverse forms of behaviour. They deviate from other forms of behaviour in cer-

tain attributes (Tembrock 1958) and may be characterized on the descriptive level by identification criteria (Loizos 1966; Hinde & Stevenson 1969). An inventory of those behaviour forms shown during play is important as there still exists a deficiency of quantitative data. This deficiency is more than counterbalanced by an excess of unproven speculations.

Exact analysis of behaviour during the ontogeny of all group members is imperative as behavioural studies concerned solely with adult animals often lead to unqualified conclusions. Only through knowledge of the individual development of an animal its social status within the group and the appearence of agonistic behaviour may be determined causally.

Closely related wild canids such as wolves (*Canis lupus lupus* L.), coyotes (*Canis latrans* Say) and golden jackals (*Canis aureus* L.) exhibit under comparable captivity conditions, alongside conspicuous similarities, a number of interspecific dissimilarities in social behaviour and its ontogeny — with marked intraspecific variability (see Bekoff 1987). This applies as well for the comparison of domestic dogs (*Canis lupus*, f. fam.) of various breeds with their progenitor the wolf. As such, comparative study ot these animals offers excellent opportunities to record constants in regard to the development and significance of individual or species-typical behaviour particularities as well as those induced by domestication (including breed-typical behaviour).

It should be possible to define more precisely the significance of variability as well as similitaries in certain developmental phases for the species or the individual through long-term observation of as many individuals as possible the development of which is exactly known. This applies especially for the ontogeny of agonistic behaviour as well as for the development of social play each in regard to their mutual significance for the creation of hierarchies and/or a specific social structure. Statements on "different inborn developments of readiness to play" and "questions how far the ontogeny of social behaviour shows similarities and to what extent it is genetically determined" can hardly be answered by the example of play behaviour for 3 canid hybrids (cross breeds between dog and golden jackal) of one litter from 7—23 weeks of age (Willkomm 1991): firstly not only the small number of individuals but also the short space of observation time do not allow general statements and secondly especially hybrids show a very high individual variability with regard to many physiological and ethological processes in ontogeny which are hard to estimate (Feddersen 1978), and cannot be analysed "in order to find out whether the similar results are caused in social adaptation or genetically" in pups growing up together and developing in interdependence of each other.

Material and Methods

My data concerning the ontogeny of social behaviour originate from long-term studies of various wild canids, domestic dogs (poodles) and hybrids between wild and domestic dogs. In the course of 12 years a total of 159 canids (74 of these hand raised) were observed and videotaped regularly. The observations making up the present study are part of comparative behavioural ontogeny studies in wolves (n = 22), golden jackals (n = 12) and domestic dogs (poodles, n = 27). Only dyadic interactions were filmed and analysed by using the slow-motion and the single picture's mode, and of these, only those were selected in which the interacting animals were in complete view throughout the play-bout or the agonistic encounter or

other social behaviour patterns. This resulted in a total of 72 352 complete interactions being analysed both in nature and frequency (35 688 entries concerning the agonistic behaviour complex were evaluated as well as 22 796 bits of information concerning play behaviour).

All of the canids grew up and live in the animal garden in open air enclosures (20 x 15 m) at the Institut für Haustierkunde, University of Kiel, in groups of 5 to 13 individuals. The enclosures contain several rocks, trees and boxes which provide shelter and refuge from aggressive inmates. Observations were analysed on a daily basis from birth to the age of 12 months.

Canid groups: Wolves: three seperate litters concerning 5 (2, 3), 6 (3, 3) and 5 (3, 2) pups; jackals: two litters of 5 (3, 2) and 7 (3, 4) pups; poodles: three litters of 7 (4, 3), 6 (3, 3) and 7 (4, 3) pups; a mixed poodle-wolf group of 6 (3, 3) wolves (one litter) and 7 (3, 4) poodles (one litter). Each litter respectively grouping (poodle-wolf-group) was observed independently. Sex ratio within all litters happened to be nearly balanced, so conditions altogether were highly equivalent within each grouping and allowed comparison.

All litters were observed for approximately 1600 h between birth and 12 months of age. Observations were randomly scattered between 06.00 and 20.00 hours.

All animals were hand-reared and housed for the first two months of life in the 3 m x 4 m indoor pen of the enclosure. Wolves and poodles of the mixed group were hand-reared together being nearly of the same age.

Each litter was filmed independently under comparable conditions. Filming was carried out using a Panasonic time lapse video-recorder and a Sony video-camera, conducted from a higher placed hide which overlooked the whole enclosures.

The data described in this study are part of longitudinal studies, and were analysed with especial attention to age changes within the groups. If one takes the view that play is closely tied in with other behaviour patterns, then one might expect the process of sexual maturity, for example, to be reflected in the context of play behaviour. The identity and sex of each of the participants in play or in agonistic encounters were recorded. Sex-differences have been reported in other aspects of the canid behaviour. They have claimed that males generally play more than females in all groupings (Feddersen-Petersen in prep.) and individualities may be seen as differences in the developmental strategies that have been evolved conform to the sex roles typical of the species. These developmental strategies are not part of this study. The following criteria were used to differenciate playful from agonistic encounters and other social behaviour patterns.

Operational definition of play

Interactions selected for analysis were those which consisted principally of play signals, those as play-bow, "play-faces", play-approaches, withdrawals and communications in an exaggerated manner. Definition of exaggeration resulted by video-film analysis. Play contains many behaviour patterns which are also used in agonistic or predatory context, but shown in a special manner: The subjective impression of an exaggerated expression that is typical for the play situation results in a complex way: certain signals are shown in a "typical" intensity in a stereotyped way that brings about the impression of an exaggeration because of the context when combined with "neutral" signals (Feddersen-Petersen 1989). Play signals have been stereotyped into "typical intensities".

My results are not contradictory to those of Hill & Bekoff (1977) who found that motor acts were actually less exaggerated only in terms of duration and more stereotyped when performed during social play than during "serious" agonistic encounters. Compared to the amplitude of signals within a "serious" threatening e. g. of high intensity I could not find any difference. Further, there is a typical "play glance" which does not stare at the partner but overlook him slightly or is directed into the distance, and the conspicuous speed of changing expressions (expressions may be changed short-dated in very high frequency, and then shown strikingly slowly even to grown stiff in this pose leading to the rupture of the sequence). Furthermore, aggressive vocalizations are totally absent during play (Hill & Bekoff 1977) and play-vocalizations occur (Feddersen-Petersen in prep.). There are role reversals during play between animals of known ranks. So play soliticing actions are typical for play situations.

Non-playful social behaviour patterns

Agonistic encounters such as typical mimics, postures and vocalizations of offensive and defensive threatening in various intensities, behaviour patterns of attack and fighting, flight and "passive submission" (Schenkel 1967).

Other behaviour patterns

Movements of contact behaviour, "active submission" (Schenkel 1967), greeting, olfactory investigation of the partner and mating behaviour.

Behaviour patterns categorized as play behaviour, agonistic behaviour and other behaviour patterns were analysed in quality as in quantity without considering sex-differences.

Results and Discussion

Wolves

Juvenile wolves are characterized during the first year of life (and beyond) by pronounced play activities. In addition to the wellknown canid types of social play, e. g., contact and race games, which normally intergrade into one another and consist of very variable sequences, wolves display a further category. Indeed, these communication or mimic games make up a large part of the social plays (Feddersen-Petersen 1986, 1988). 19 % of all social behaviour patterns registered for the third month of live involve mutual communication of playfully expressed, exaggerated signals almost exclusively from the mimic area (fig. 1). If one considers the percentage of the social play forms mentioned (and solitary play) in the course of the first year as compared to all observed social behaviour patterns it becomes apparent that contact games (i. e. those games with body contact directed towards a social partner; Tembrock 1958; play behaviour within the contact field; Tembrock 1982) are the earliest type of play. To a large extent contact games may be termed bite and fight plays or play-fighting. For example, the participants attempt to softly bite each other, tug one another's fur or to fight with playful exaggeration (muzzle very widely opened, etc.). Transitions to "serious" conflicts are the exception and indeed if one partner were to bite overzealously, as an example, the interaction would be interrupted immediately. Very early bite games (2—5 weeks) involve almost exclusively mutual muzzle hugging or biting in ears, cheeks, limbs and tail. Subsequent to the eighth week biting is directed primarily towards the throat and shoulder areas increasingly combined with shake movements, embracement, pouncing and other elements of play-fighting. After the third month this type of contact play is carried out with pronounced role assumption and subsequent exchange: a puppy will first play, for example, the "underdog" by sending a few, limited body signals indicating social inferiority in a playful exaggerated manner while his partner plays the role of the social superior (fig. 2). The "social superior" may then switch roles and bring elements of "submission" (in the sense of Schenkel 1967) into the play (fig. 3). The playful exaggeration refers to the amplitude and speed of expressive movements or behaviour patterns (Feddersen-Petersen 1989, Feddersen-Petersen in prep.). Contact games with role exchange normally appear in combination with race games (i. e., all those games directed towards a social partner and involving mutual pursuit and a lack of body contact; Tembrock 1958; motion plays taking place within the near or the distant field; Tembrock 1982) in which the primary goal is the playful pursuit of one's

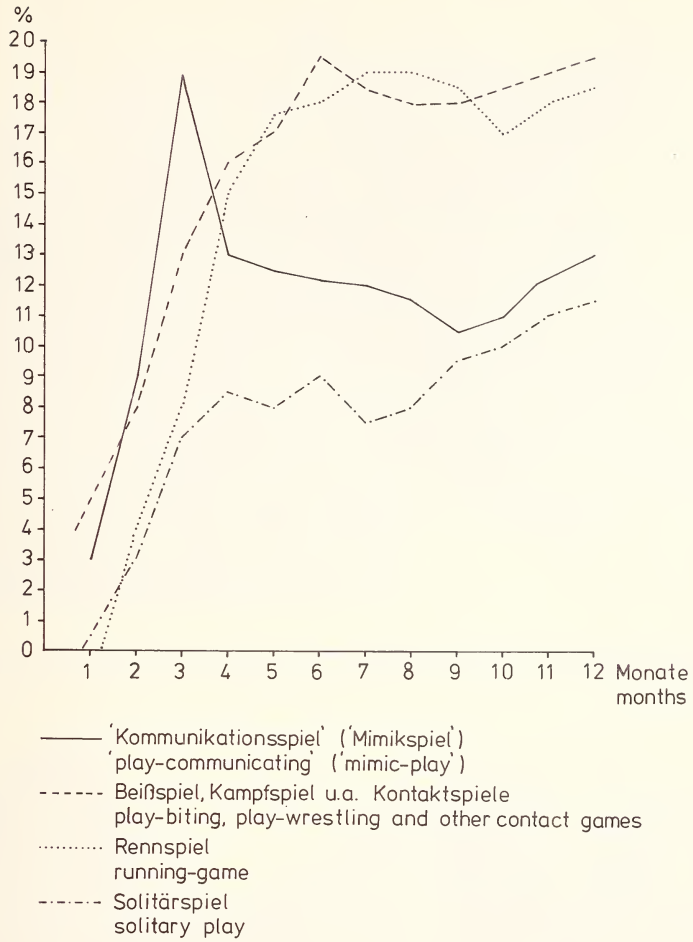


Fig. 1: Frequency of various forms of play during the first year of life in wolves (*Canis lupus lupus* L.), n = 16, as a percentage of all dyadic interactions observed.

opponent. Solitary play is much less common as compared to social games. Mimic games (i. e., all those partner-related games without body contact characterized by playfully exaggerated communication primarily in the mimic area and a paucity of body movement; Feddersen-Petersen 1988) may be observed in greatly increased frequency subsequent to the fourth week of life: normally only two animals participate and stand, sit or lie opposite to and communicate with one another. Signals from the entire mimical repertoire (a rich assortment of facial expressions displayed in at least 23 individual signals of highly different intensity) are at first (4—6 weeks) exaggeratedly expressed and answered individually (one play-signal per expression as a rule; fig. 4). Included are bizarre forms of muzzle-wrinkling or lip retraction, for instance. Later, after 7—8 weeks, signals are given in steadily increasing and increasing-

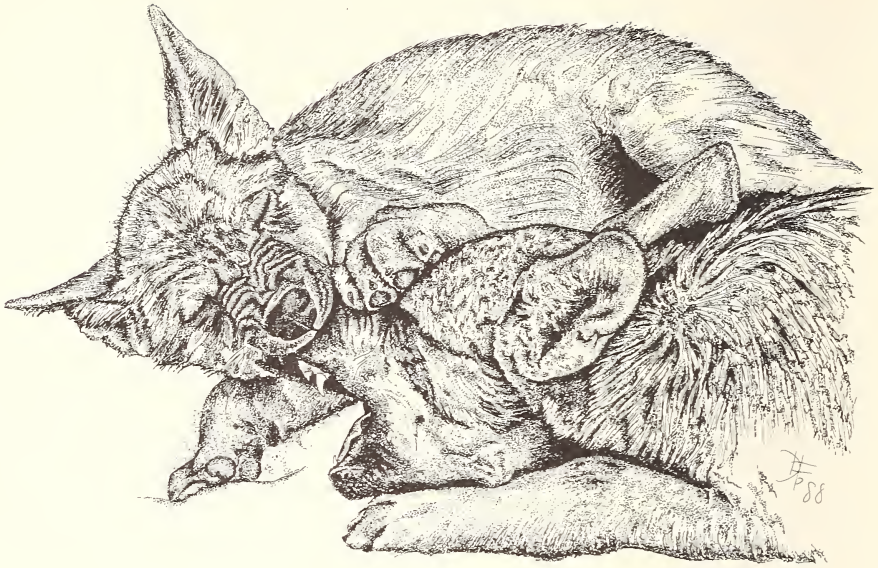


Fig. 2: "Muzzle-hugging" as a playful dominance gesture (play-fighting) in infant wolves.

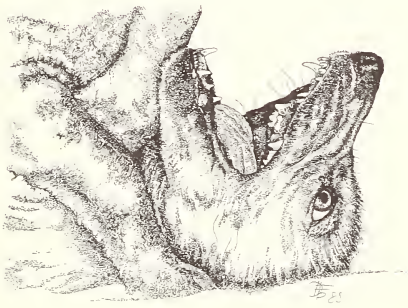


Fig. 3 (left): "Submission", playfully performed (play-fighting) in infant wolves.

Fig. 4 (right): Play-threatening, expressed solely by pronounced muzzle-wrinkling (mimic play) in wolf puppy 6 weeks old.

ly differing combinations (now one expression contains several play-signals as a rule; Feddersen-Petersen 1988). Emphasis must be given to the difficult attempt to replace the complex perception of mimical exaggeration by the quantification of a few characters, although the very high intensity of individual signals may be proven by film recordings.

Fig. 5: Play-threatening, expressed by widely opened mouth, muzzle-wrinkling and pronounced teeth-baring (mimic play) in wolf puppies 8 weeks of age.

Fig. 6: Defensive threatening in adult wolf.

For example, various forms of agonistic behaviour, "appeasement" and contact behaviour are played solely with motions and postures involving facial elements such as the muzzle, lips, eyes, forehead skin and the ears. Mimic playing, e. g., playful threat exaggeration (fig. 5) is always characterized by the high intensity of a limited number of specific signals, in this case by muzzle-wrinkling, teeth-baring and mouth-opening widely correlated with the absence of those additional signals present during expression of "genuine" threat (fig. 6). Indeed, the body posture is completely relaxed, the ears are placed "neutrally" (i. e., the posture present when the animal is not involved in any particular activity) and the opponent is not looked at directly but instead somewhat from the side (play-look). In this case, the opponent answers with play biting. Occasionally, mimic signals can be interrupted by a particularly successful play signal (e. g., head whipping) which certainly has a metacommunicative significance (in the sense of Bateson 1955). The playful mood remains even when play signals are expressed in an agonistic context. In addition, much seems to indicate that the entirety of playful expression can be answered differently dependent upon which signals are expressed first. This is apparently the case even when the signal combination is absolutely identical. Sequence-analytical studies should help reveal which function the action units may have within the sequences (Feddersen-Petersen in press).

Poodles

Poodles exhibit a maximum in play activity between the sixth week of life and approximately 6 months of age (fig. 7). By the latter time a relatively stable hierarchy has been established and from now on the games are coloured by a primarily aggressive tone or may even end in serious fights. Play-fighting (bite and fight games) predominates but decreases rather abruptly towards the eighth month and continually thereafter. In contrast to the wolves, poodles play a great deal less especially subsequent to the fifth or sixth month. Whereas wolves integrate primarily optical signals into the games, the "talkative" poodles develop bark-games (Zimen 1971), so-called acoustic communication games (Feddersen-Petersen 1986) which proceed relatively stereotypical and reach their maximum frequency in the fourth month of life. Poodles rarely imitate expressional motions in play while mimical communication games are lacking. Play soliciting actions (Bekoff 1972; 1974a) especially trampling, hopping or bowing (the front legs and shoulders touch the ground while the hind quarters remain standing), which are carried out with a minimum of variability, usually initiate play-fighting. Play in wolves appears much more complex for these reasons: the playful contacts are on a much higher level of complexity and play signals elicit much more differentiated answers; play-fighting leads to more counterattacks and various role reversals between attackers and defenders are the rule.

Comparison of the relative frequency of play by wolves and poodles (fig. 8) shows that wolves begin to play earlier and play frequency is almost always greater than the corresponding poodle norm. This does not change for the entirety of the first year. In contrast, poodle play contains increasingly more agonistic behaviour patterns subsequent to the sixth month.

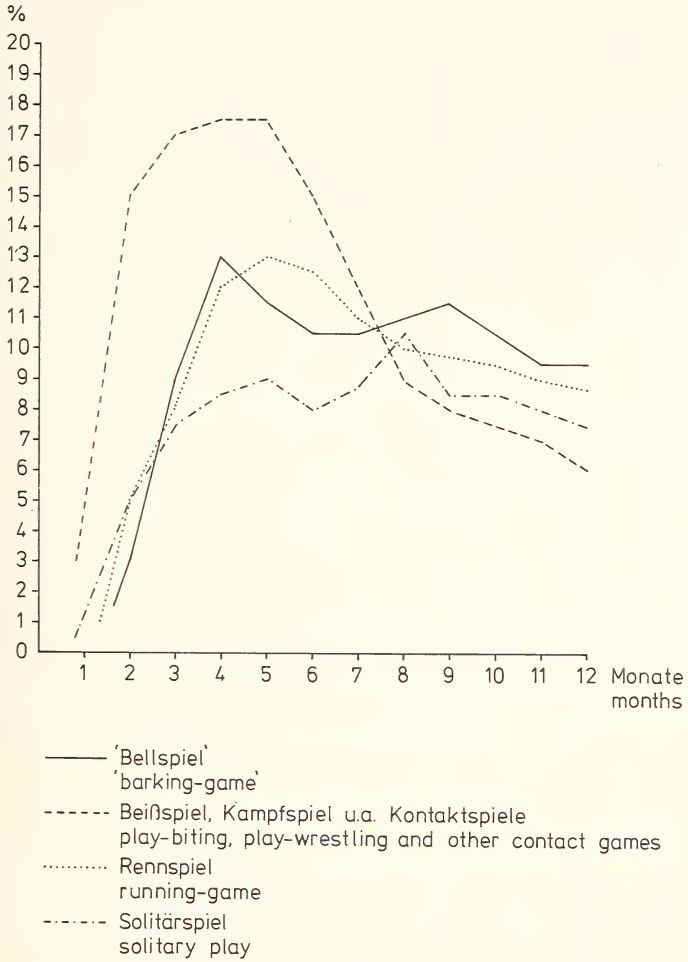


Fig. 7: Frequency of various forms of play in poodles (*Canis lupus*, f. familiaris) during the first year of life, n = 20, as a percentage of all dyadic interactions observed.

Agonistic interactions (fig. 9) appear earlier in the poodle groups than amongst the wolves. The frequency of such interactions increases among poodles in the course of the first year and accelerates thereafter. The frequency within the wolf group always lies under the corresponding poodle norm where it decreases in the course of the last third of the first year. An increase in aggression in the wolves first appeared after 22—23 months.

Agonistic behaviour among wolves living in a closed, naturally formed group (i. e., a group developed without human interference regarding community composition) is determined structurally by a high degree of ritualization. A number of signal motions are used to elucidate the dominance or subdominance of a certain animal during each contact with another member of the group in a specific situation. Conflicts

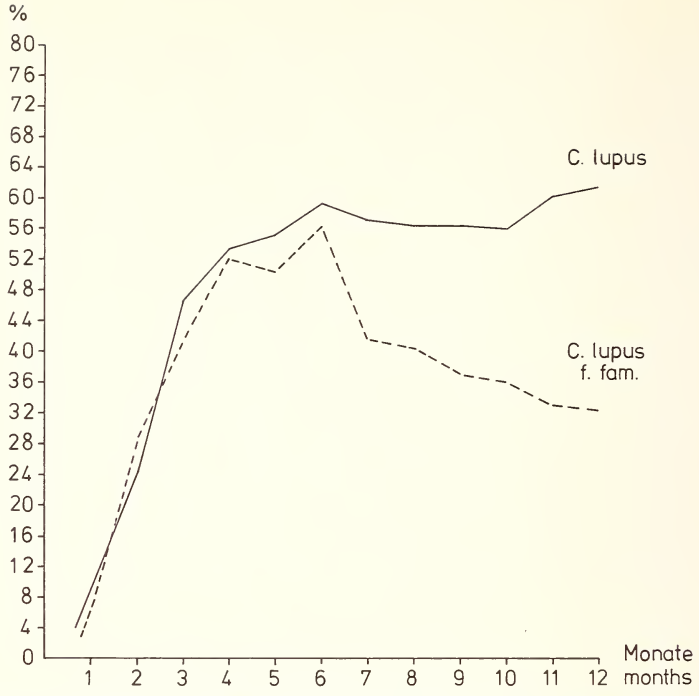


Fig. 8: Frequency of play in 16 wolves and 20 poodles during the first year of life as a percentage of all dyadic interactions observed.

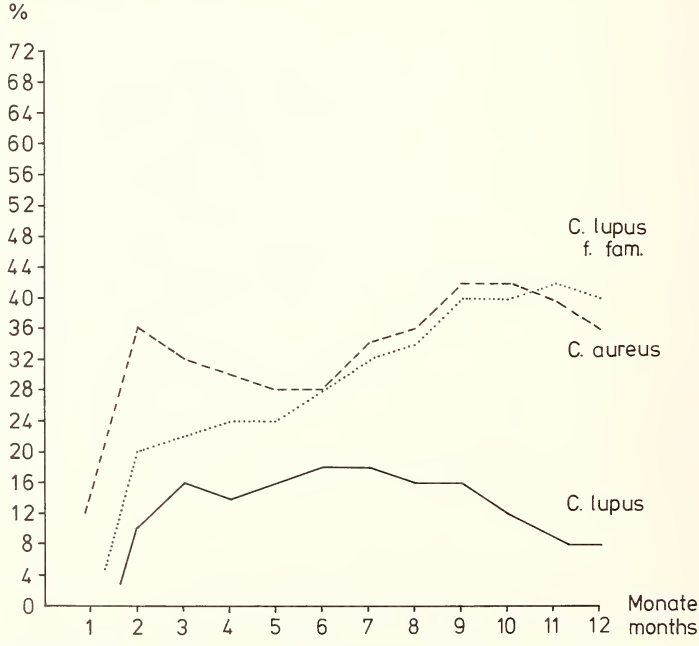


Fig. 9: Frequency of agonistic behaviour in 16 wolves, 20 poodles, 12 golden jackals (*Canis aureus* L.) during the first year of life as a percentage of all dyadic interactions observed.

in an agonistic context among wolves were seen during the observation period solely in form of ritualized fighting on a high level of complexity (Feddersen-Petersen in prep.). Poodles fight in a much less ritualized manner. An attack launched by a dominant poodle male escalated in 70 % of the observed cases to grabbing and bite-shaking regardless of the opponent's reaction. Group aggression (Hassenstein 1980) was often the result when all group members joined a collective attack on the threatened animal. The so-called "underdog" lacking in social rights is quite common in poodle-groupings these being characterized by the absence of a fine-tiered social hierarchy. The social distance between the high ranking animal or animals and the rest of the group is large.

Mixed poodle-wolf-groups

The relative frequency of play is further reduced in mixed poodle-wolf-groupings (the total lying under the poodle norm) and a further increase of agonistic behaviour patterns in poodles directed towards the wolves is the rule. The wolves, in contrast, show remarkably often appeasement behaviour toward the poodles and are "submissive". Poodles react in most cases aggressively in response to the wolves' attempts to play (fig. 10). This is particularly true in regard to mimical play signals typical in wolves. However, even summons to play such as playful throwing of oneself to the ground, jumping around, jumping on one another or playful attacks rarely lead to social play but are instead the prelude to social attacks by the poodles. In contrast, the wolves

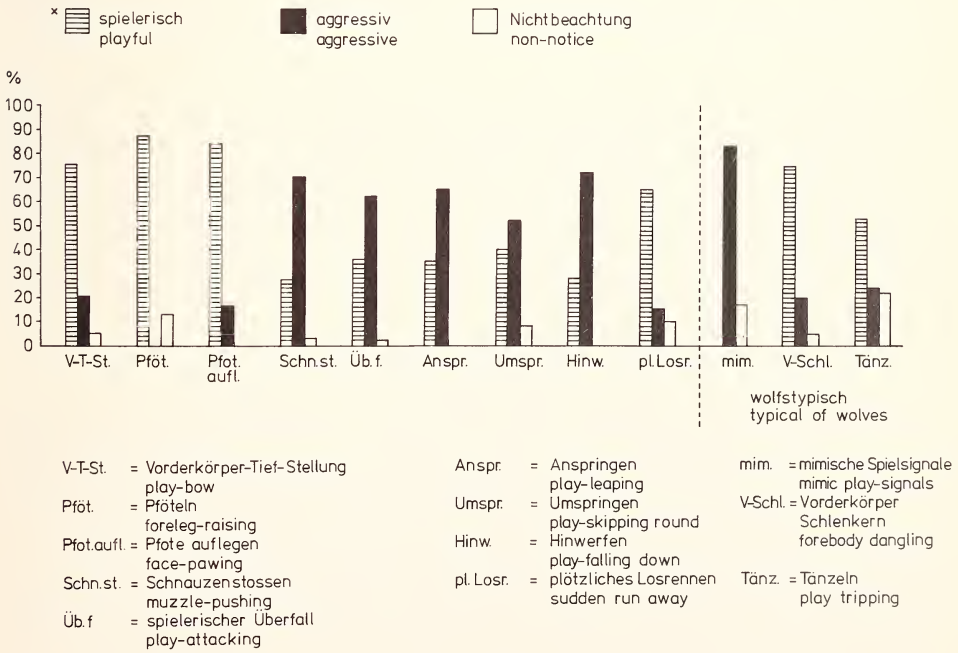
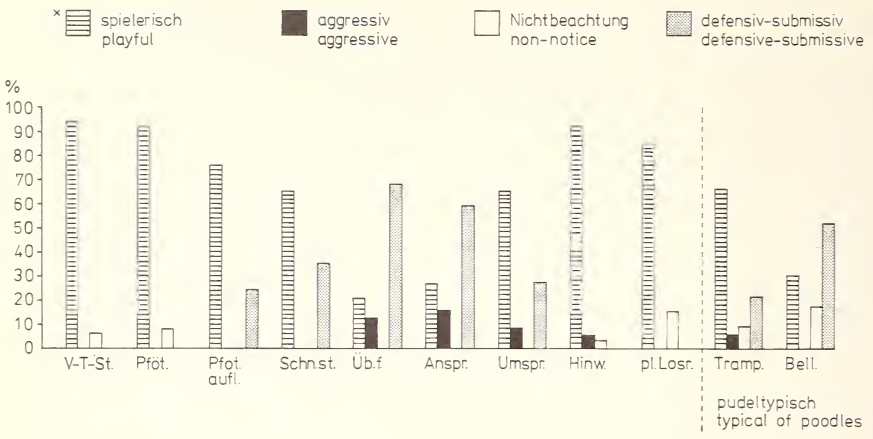


Fig. 10: Frequency of possible reactions of poodles, n = 7, to play signals given by wolves, n = 6, within a mixed poodle-wolf grouping (all animals between 0—12 months of age).



V-T-St. = Vorderkörper-Tief-Stellung
play-bow
Pföt. = Pfoteln
foreleg-raising
Pfot.aufl. = Pfote auflegen
face-pawing
Schn. st. = Schnauzenstossen
muzzle-pushing
Üb. f. = spielerischer Überfall
play-attacking

Anspr. = Anspringen
play-leaping
Umspr. = Umspringen
play-skipping round
Hinw. = Hinwerfen
play-falling down
pl. Losr. = plötzliches Losrennen
sudden run away

Tramp. = Trampeln
play-trampling
Bell. = 'Bellspiel'
'barking-games'

Fig. 11: Frequency of possible reactions of wolves, n = 6, to play signals given by poodles, n = 7, within a mixed poodle-wolf grouping (all animals between 0—12 months of age).

react much more often to play-signals shown by poodles (fig. 11) with play sequences or appeasement gestures and rarely with aggression (this applies as well for replies to typical poodle signals). The regularity of this behaviour has as a consequence that subsequent to the third or fourth month of life the male wolves are dominated by poodle males as expressed in priority during feeding and at favoured places, etc. This dominance causes that the wolves are at times greatly restricted in areas of their social behaviour.

Golden jackals

Pronounced aggression is present during the first 4—6 weeks of life in groups of pups (fig. 9). Bite and fight games, the sole form of social play in golden jackals, regularly escalate into unritualized conflicts including biting intended to harm. The frequency of agonistic behavioural patterns reaches its maximum at approximately 9 weeks. In this period 36 % of all registered behavioural patterns involve elements of attack and threatening behaviour, defense and escape. At 10 (12) weeks the aggression decreases in the group of pups. By this age the litters have established certain hierarchies and groupings or pairs have created spatially separated subgroups. Intragroup play frequency increases while intergroup cohabitation in a relatively restricted area is regulated by expressing ritualized threat motions (fig. 12). This takes

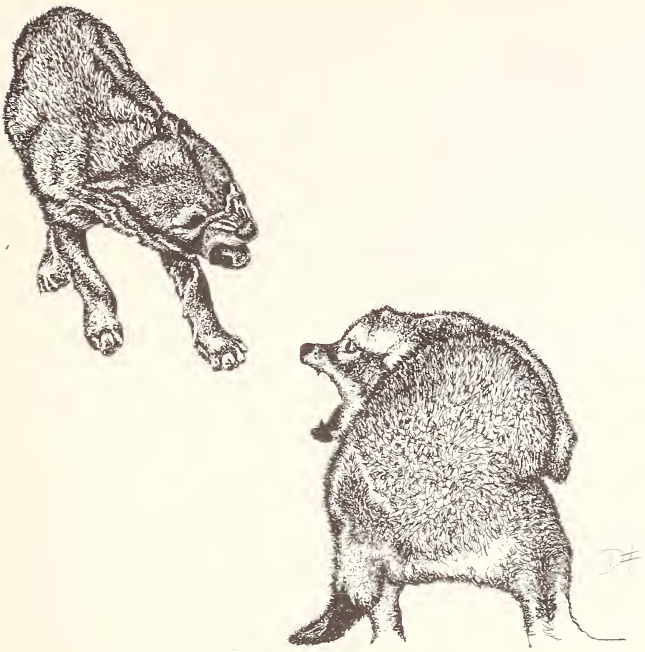


Fig. 12: Offensive and defensive threatening in golden jackals.

place without the occurrence of physically harmful conflicts. The frequency of play increases within the subgroups (fig. 13) and social games free of aggression take place up to the onset of the first estrus period. The expression elements of these games are restricted almost entirely to the agonistic context. Communication games are lacking. Wide mouth-opening (fig. 14) is shown as an intention motion (and only here) shortly before playful biting in the course of play-fighting and is not answered as a play-signal through mimical exaggeration. The relaxed, open-mouth face of golden jackals is always displayed during play-fighting as a prelude thereof.

If one considers the relative frequency of play forms in golden jackals (fig. 13) it becomes apparent that solitary play dominates over social plays up to the 3 months of age. The total amount of play is considerably less than that of wolves at a comparable age (fig. 15). The relative frequency of agonistic interactions lies considerably above the wolf and poodle norms (fig. 9) and is especially pronounced prior to the establishment of social groups (at approximately 9 weeks of age) and to the onset of the first estrus of jackals (February/March).

According to the results presented here qualitative and quantitative differences in social play forms and their ontogeny as well as the same type of differences in the development of agonistic behaviour in various wild canids and domestic dogs (poodles) correspond with species-typical or domestication-induced particularities in communication and social behaviour (Feddersen-Petersen 1986). Only wolves develop mimic-play in conjunction with their higher level of complexity in optical

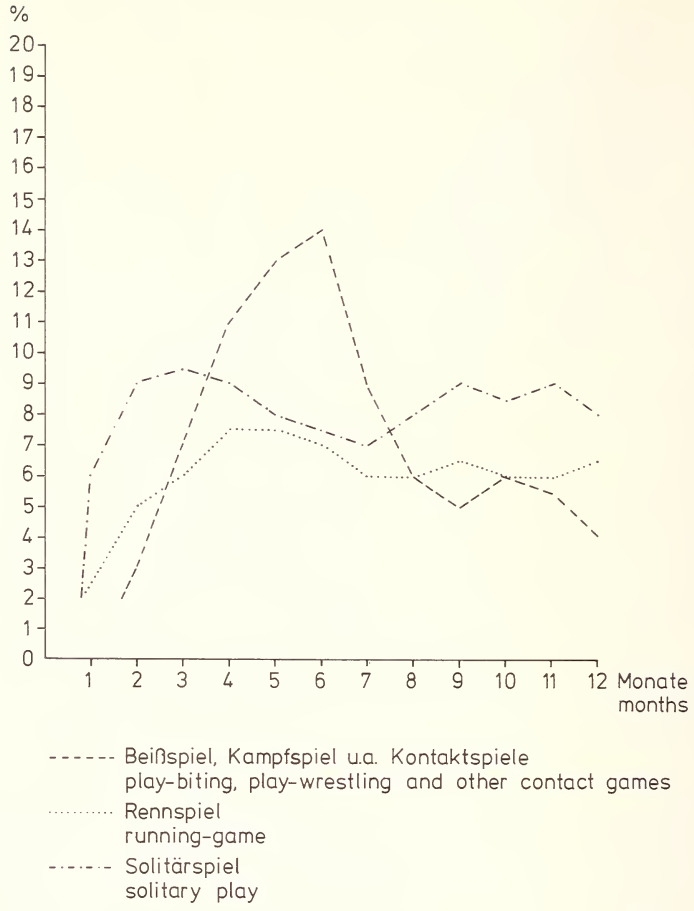


Fig. 13: Frequency of various forms of play in golden jackals, n = 12, during the first year of life as a percentage of all dyadic interactions observed.

communication and their finely graduated pack hierarchy (Mech 1970; Schenkel 1947, 1967). The mimic-play becomes progressively differentiated, graduated and subtile with increasing age. Within the framework of contact and race games, favoured body signals are employed and become themselves increasingly variable. The refinement of wolf communication in contrast to that of golden jackals becomes rapidly apparent in the course of ontogeny (wolves have a much larger number of expressive elements at their disposal with the help of which they may convey more complicated and graduated social communications (Feddersen 1987; Feddersen-Petersen 1986, 1988). Patterns are seen to occur in certain sequences or combinations of varying complexity and stereotypy and it follows that any behavioural element is potentially informative. Social games are obviously of great importance for the optimation of communicative sequences and the flexibility thereof. The play of poodles illustrates their relative coarsening in the optical area (Zimen 1971; Feddersen 1978)

Fig. 14: Wide-mouth-opening indicating the intention to playful biting (play-fighting) in golden jackals.

and their hypertrophizied bark tendency; acoustic communicative play and the infrequent appearance of optical expression structures in play correspond as such and "fit" in the relatively more simple pack organization of domestic dogs. The social games of golden jackals appear to be rather stereotypical through impoverishment in expressive elements while at the same time constructing fewer variable sequences. Such interspecific and intraspecific differences are to be seen highly genetically determined. The early ontogeny of rank-related fighting as well as certain partner preferences which reveal themselves, for instance, in mutual social play, are apparently responsible for the early segregation of young animals (see Bekoff 1974b). Accordingly, agonistic behaviour (together with territorial behaviour) provides important elements of the time-space succession (Tembrock 1982) between the members of a social unit by necessitating specific structures of social grouping and the creation of relatively typical role patterns. This is reflected in the tendency of golden jackals to subdivide larger groups and create subgroups whereas wolves and dogs create specific hierarchies. Thereby one may note that wolves first experience an extended phase of high play activity during which agonistic interactions are observed to take place primarily in a playful context. Aggression within the wolf groups is extremely rare during the first year of life. In social play young wolves develop a number of play motions by "rehearsing" signal sequences of varying composition. In the agonistic context a high degree of ritualization is established. The limited play period of domestic dogs (poodles) and the great amount of aggression in the latter part of the first year of life can most probably be correlated to their earlier achievement of sexual maturity. Althaus (1978) considered as an established fact a relative acceleration of the developmental processes (growth processes, sexual maturity, etc.) for various physiological as ethological parameters in domestic animals as compared to their wild progenitors. My results confirm this interpretation and stand in pronounced contradiction to the arguments of Zimen (1971, 1990) who states that poodles in contrast to wolves dispose of a lesser production of simulation-induced aggressive energy. Zimen (1971) interpretes this as a neotony in the sense that adult poodles behave like juvenile wolves. Especially for the ontogeny of agonistic behaviour confirmation of this thesis cannot be brought and this is further evidence that the term

"neotony" or the "persistence of juvenile characters" cannot be used. The unsuitability of the term in conjunction with morphological characters in domestic animals has long since been established (Starck 1962). As Starck (1962) stated this applies as well for behavioural studies as the claim cannot be made in domestication studies that a general principle of fetalisation is effective in the sense of a law of form genesis. Even the principle of the "retention of juvenile characters" in domestication cannot be upheld. Conspicuous is the large amount of agonistic behaviour displayed by a dog breed which under "normal" circumstances of cohabitation with humans is extremely willing to subordinate itself. Comparison with other dog breeds cannot be made as corresponding observations of ontogenies under comparable conditions are not available. As such, it is conceivable that differences may be considered breed-typical but are in reality merely the result of methodical differences in respect to observation, recording and evaluation. Comparative studies of the ontogeny of behaviour in German Shephards and Retrievers support the existence of breed-specific ontogenies (Feddersen-Petersen & Hoffmeister 1990).

In any case, it is evident that poodles fight primarily in an unritualized manner and this may be interpreted as domestication-induced changes in correlation with the reduction and coarsening of optical expression behaviour in this breed.

One last point is that apparently the ability of some dog breeds to live together as a group is rather limited as the result of the long-term selection pressure involved in cohabitation with man in his environment.

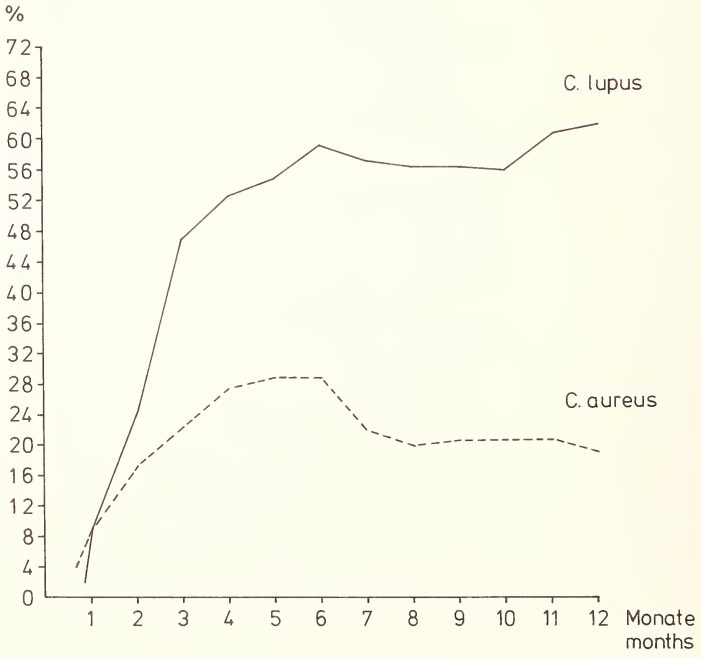


Fig. 15: Frequency of play in 16 wolves and 12 golden jackals during the first year of life as a percentage of all dyadic interactions observed.

Zusammenfassung

Die Ontogenese von Sozialspielen einerseits und agonistischem Verhalten andererseits wurde bei 16 Wölfen (3 Gruppen), 20 Pudeln (3 Gruppen) und 12 Goldschakalen (2 Gruppen) über den Zeitraum des ersten Lebensjahres vergleichend untersucht. Entsprechende Beobachtungen an einer gemischten Pudel-Wolf-Gruppe (7 Pudel/6 Wölfe) werden vorgestellt.

Artliche bzw. domestikationsbedingte Unterschiede im Sozialspiel (Entwicklung, Erweiterung und „Verfeinerung" von Spielsequenzen; Art der Spielformen, in denen diese Sequenzen auftreten; relative Häufigkeit einzelner Spielformen im Verlauf der ersten 12 Lebensmonate) korrespondieren im Gruppenvergleich unter weitgehend identisch gehaltenen Umweltbedingungen mit stammesgeschichtlichen bzw. domestikationsbedingten Verschiedenheiten im optischen und akustischen Ausdrucksverhalten, in der Kommunikation und im Sozialgefüge, weshalb Sozialspiele als spezifisches Gruppen- und Kommunikationsverhalten in statu nascendi definiert werden. So entwicklen allein die Wölfe mit ihrer differenzierten Mimik „mimische Kommunikationsspiele", die durch spielerisch „übertriebene" Kommunikation fast ausschließlich im mimischen Bereich gekennzeichnet sind, während die lautäußerungsfreudigen Pudel kaum optische Signale ins Spiel integrieren, vielmehr „akustische Kommunikationsspiele", die relativ stereotyp ablaufen, zeigen. Goldschakale spielen erst dann aggressionsfrei miteinander, wenn sich innerhalb der Gruppen gewisse Kleinsozietäten gebildet und räumlich abgesondert haben. Ihr Spiel ist relativ seltener als unter gleichaltrigen Wölfen zu beobachten, Solitärspiele dominieren, und die Sozialspiele sind relativ einfacher.

Qualitative und quantitative Unterschiede in der Ontogenese des agonistischen Verhaltens entsprechen diesen angeführten Verschiedenheiten in den Sozialspielen und werden ebenso in ihrer spezifischen Bedeutung für die Entstehung von Rangbeziehungen bzw. von artspezifischen Sozialstrukturen diskutiert.

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Dr. Dorit Feddersen-Petersen, Institut für Haustierkunde, Christian-Albrechts-Universität, Olshausenstr. 40, 2300 Kiel 1.