Development of Social Behaviour in Four Litters of Dogs (Canis familiaris)

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Lund JD, Vestergaard KS: Development of social behaviour in four litters of dogs (Canis familaris). Acta vet. scand. 1998, 39, 183-193. – The development of social behaviour in 4 litters of dogs was observed without interfering with the puppies from birth to 8 weeks of age. Direct and continuous observation was combined with video recording. Three of the litters were observed during one session of 2 h once a week, and the fourth litter during one session of 40 min twice a week. Social interactions were divided into 1) investigation of litter mates (licking, sniffing or investigating orally), 2) social play, 3) and interactions in which agonistic elements (dominance postures, threats, bites or submission) were displayed. The different forms of social interactions appeared for the first time when the puppies were between 14 and 21 days of age. Social investigation appeared first and was followed by play and agonistic interactions. From week 5, differences between the puppies in the tendency to initiate social play and agonistic interactions emerged. Generally, within the litters individual differences were consistent over weeks 6-8 (positive correlations between weeks), whereas the tendency in the puppies during these weeks were negatively correlated with those of week 3 (play) or weeks 3 and 4 (agonistic interactions), indicating a rebound effect for both play and agonistic behaviour. No significant correlations, however, were found for social investigation. More often than expected males played or engaged in agonistic with other males, whereas these behaviours occurred less often than expected between females. Both males and females, however, preferred male partners for agonistic interactions. No sex differences were found in the direction of social investigation. Agonistic behaviour was often responded to by play and play was often responded to by agonistic behaviour, and the results indicated that before 8 weeks of age differences in social behaviour between the puppies were already established.

puppy; early development; social relationship.

Introduction

Until now, most studies of early behavioural development in dogs have been made on the basis of various tests (see *Scott & Fuller* 1965) and unfortunately very little information is available from puppies that were observed in their usual social environment. Such information, however, may be significant in order to obtain a more comprehensive understanding of develop-

mental aspects of social behaviour and of the social influences on the phenotype.

Social behaviour in dog puppies starts to develop from week 3 of life (the transitional period, *Markwell & Thorne* 1986), when the puppies begin to contact litter mates, and continues during the socialization period (weeks 4-10) when the puppies start to communicate with each other using many different postures, mim-

ics and forms of vocalization (Scott & Fuller 1965, Campbell 1975, Fox & Bekoff 1975, Fox 1978). In wolves the process of primary socialization is complete at the age of 14 weeks. After this age wolves are almost impossible to socialize to humans (Woolpy & Ginsburg 1967). In wolves a cub's social status may be determined by serious fighting as early as the 13th day of life (Mech 1970), and between 8 and 12 weeks of age both wolf cubs and dog pups develop a dominance hierarchy within the litter (Fox 1971). Therefore, there is evidence that the early social experience may be significant later in life both in dogs and wolves.

Although at an early age the puppies are able to perform the species specific elements of social behaviour, they have to learn the meaning of them by interacting with the litter mates and the bitch. Furthermore, they learn to control the intensity of their bites (Fox 1971). Out of all these interactions, gradually, some structure in the social relationships between the puppies emerge and individual behavioural profiles appear, probably as a result of genotype, the interactions between litter mates, and interactions between genotype and environment.

In this paper we examine the social interactions within the litter in order to study the developmental processes including those that may lead to individual behavioural profiles. Such profiles may, of course, also depend on genetics. Sex may be an additional influencing factor since some aspects of early social behaviour, for example the frequency or intensity of play, often differ between sexes in many mammals (e.g. Baldwin & Baldwin 1977, Warren & Holmes 1995). Sex and other individual characteristics may also influence the behavioural development of the dog in the human family during the secondary socialization period. For example sex and breed are known to influence the types of behavioural problems encountered by dogs in their human family (Lund et al. 1996).

We present results from weekly observations of social interactions between puppies during uninterrupted social activities in 4 litters studied from birth and until 8 weeks of age.

Materials and methods

Observed litters

Two litters of Siberian Huskies (H1-2), 1 litter of English Springer Spaniels (SS) and 1 litter of mixed breed (MB, Labrador Retriever × Alsatian/other breed) were studied from birth to the age of 8 weeks. Litter H1 was observed twice (40 min per session) a week and litters H2, SS and MB were observed during one continuous session of 2 h each week. In all litters the bitch was allowed to nurse the puppies during the time of observation. The puppies were naturally weaned by the bitch, but when the puppies were 3-4 weeks of age, the dam's milk was supplemented by food provisioned by the owner. The litters were observed in the afternoon between 12 am and 5 pm prior to the normal time of feeding by the owner in order to prevent disturbance of normal social behaviour. The individual litters were observed about the same time of the day during the period of observation.

The 2 litters of Siberian Huskies included 1 female + 2 males (H1) and 2 females + 3 males (H2), respectively. The litter of English Springer Spaniels included 4 females + 2 males, and the litter of mixed breeds included 5 females + 3 males. The litters were studied using continuous observation of all puppies. Direct observation was combined with video recording to allow later analysis - e.g. if several couples of puppies were interacting simultaneously. The 2 litters of Siberian Huskies were observed at 2 different kennels, where these dogs were bred and frequently used as sledge dogs. At birth the puppies were kept indoors, but at the age of 3-4 weeks, litter H1 (and the bitch) were transferred to an outdoor fenced area of 40

m² including a shelter for resting and sleeping, and litter H2 was transferred to a unheated enclosure of comparable size. The litter of *English Springer Spaniels* was observed at a small kennel (having this litter only) and was kept indoors for most of the time. However, from the age of 4 weeks the puppies had access to an outdoor fenced area of about 20 m² for the purpose of observation. The litter of mixed breeds was raised indoors by a private owner. The puppies were kept in a room of about 16 m².

Recorded behaviour

Social interactions were divided into 3 categories: 1) social investigation, 2) play and 3) agonistic interactions. During social investigation a puppy contacted a litter mate to lick, orally investigate or sniff its head, body, limbs and/or genitals. Play included chasing, tug-ofwar and prey-catching (slow approach and stiff legged jump) and prey-killing (grab and head shake) behaviour directed towards litter mates (Goodmann & Klinghammer 1985). Interacting dyads were formed if a puppy (the initiator) solicited play towards another. Sometimes a triad was formed by a third puppy actively joining a dyad. In these cases the third puppy was recorded as an initiator as well. All interactions which involved dominance postures (e.g. chin rest, mounting and stand over), threats (e.g. agonistic pucker, growl, growl bark and snap), bites or submission (active as well as passive) were classified as agonistic (Goodmann & Klinghammer 1985), even if the preceding behaviour seemed playful (see Discussion). Individuals that initiated dominant or aggressive behaviour towards a litter mate were classified as initiators, whereas individuals that reacted submissively to the initiator's behaviour were identified as recipients. Sometimes, however, recipients also showed aggressive behaviour in reaction to the agonistic behaviour of initiators.

Statistical analysis

Observed and expected proportions of the total number of interactions initiated and received were compared using a Z-test for a proportion (Kanji 1993). For all other statistical analysis the software package Statistical Analysis Systems version 6.04 (SAS Institute Inc. 1987) was used. Variation between the litters due to different rearing conditions and to dam, sire, and breed effects was summed as a litter effect. Correlations between interactions initiated and interactions received, and correlations in social activity between weeks of life were corrected for the litter effect by using a general linear model (PROC REG). The class variable of litter was recoded into 5 dummy variables (values 0.1) and the partial correlation coefficient for the corresponding variables of interest was calculated. The level of social interactions initiated by males and females was compared by an F-test using a general linear model (PROC GLM) and correcting for the influence of litter.

Results

General trends in development

During week 3, nearly 90% of the puppies had initiated social investigation, whereas only about 30% had initiated social play or directed agonistic behaviour towards litter mates. By week 6, however, all kinds of social interactions were observed in almost all puppies. Social investigation, therefore, appeared before social play as well as agonistic interactions (Fig. 1). Fig. 2 shows the frequency (number per puppy per h) of social and agonistic interactions as a function of age in the 4 litters. Generally, the frequency of the 3 types of social interactions increased with age, but in most cases the number of interactions suddenly dropped - especially in week 8. For all kinds of interactions the frequency was very high in litter H1 compared to the other litters. In all litters social investiga-

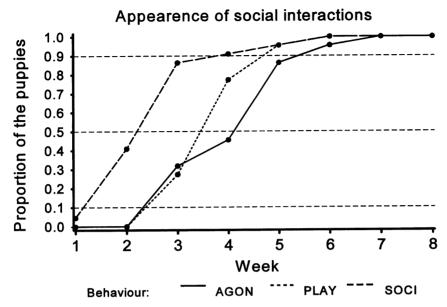


Figure 1. Appearance of social investigation (SOCI), social play (PLAY) and agonistic interactions (AGON). The figure shows the proportion of the puppies (N = 22) having initiated interactions with litter mates at a given age.

tion was shown for the first time when the puppies were between 14 and 21 days old. In litters H1, SS, and MB also social play and agonistic interactions appeared for the first time between 14 and 21 days of age, but the frequency was low. However, in litter H2 social play and agonistic interactions first appeared after 5 weeks.

The consistency of behaviour over time

The consistency of behavioural frequencies over the weeks of observation was examined by means of tests for autocorrelations between weeks from weeks 3 to 8. Social play was consistent over weeks 6-8 (positive correlation), whereas the frequencies during these weeks were negatively correlated with those of week 3 (Table 1). The correlations were significant between weeks 6 and 7 (positive correlation) and between weeks 3 and 6, and between weeks 3 and 7 (negative correlations). For agonistic interactions a similar pattern was found (Table 2).

The correlations were significant between weeks 5 and 8 and between weeks 7 and 8 (positive correlations), and between weeks 3 and 7 as well as between 4 and 7 (negative correlations). The correlations between week 6 and weeks 5, 7 and 8, however, were negative and non-significant. Therefore, for both play and agonistic behaviour the overall pattern was that the behaviour during the early weeks was negatively correlated with that of the late weeks, which were almost in all cases positively correlated with each other. Finally, no significant correlations were found for social investigation.

Effects of gender

In weeks 3 and 4, male puppies more often initiated social investigation of litter mates as compared to females (Table 3). In week 5, however, no difference was found. In weeks 6 and 8, females more often initiated social investigation than males. All these results, however,

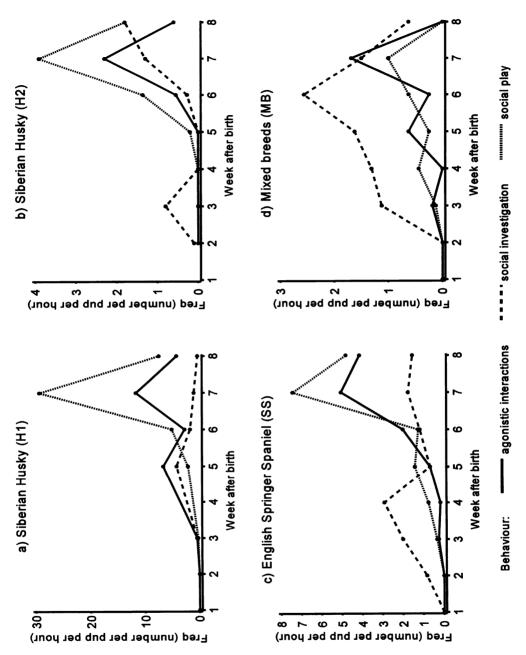


Figure 2. Social investigation (SOCI), social play (PLAY) and agonistic interactions (AGON) as a function of age in a + b) 2 litters of Siberian Huskies (H1 and H2), c) one litter of English Springer Spaniels (SS) and d) one litter of mixed breeds (MB). Frequency is presented as number of interactions per puppy per hour. Note the differences in the levels as indicated by the different scales on the y-axis.

Table 1. Auto correlation of social play in week 3-8 (4 litters, 22 puppies).

Week	3	4	5	6	7
4	-0.39				
5	-0.06	0.42			
6	-0.62**	0.06	-0.37		
7	-0.48*	0.03	0.03	0.55*	
8	-0.48	0.37	0.35	0.30	0.25

^{*} p<0.05; ** p<0.01.

Table 2. Auto correlation of agonistic interactions in week 3-8 (4 litters, 22 puppies).

Week	3	4	5	6	7
4	-0.29				
5	0.01	-0.13			
6	0.18	-0.42	-0.18		
7	-0.57*	-0.49*	0.08	-0.01	
8	-0.30	-0.44	0.77***	-0.28	0.48*

^{*} p<0.05; ** p<0.01.

Table 3. Level (relative to the litter mean¹) of social investigation (SOCI), social play (PLAY) and agonistic interactions (AGON) initiated by male (N = 10) and female (N = 12) puppies included in 4 litters.

Behaviour	Gender	Week					
		3	4	5	6	7	8
SOCI	M	1.31	1.29	1.00	0.60	1.07	0.89
	F	0.74	0.79	1.00	1.33	0.94	1.09
	р	_	_	_	-	_	-
PLAY	M	0.70	1.14	1.06	1.25	1.21	1.14
	F	1.25	0.90	0.95	0.79	0.83	0.88
	р	_	_		_	*	*
AGON	M	0.30	0.75	1.29	1.19	1.38	1.38
	F	1.58	1.18	0.76	0.84	0.68	0.68
	p	**	_	_	_	*	_

¹⁾ In case of litter mean = 0 the level was set to 1 for both males and females.

were not statistically significant. During week 3, females more often initiated social play, but the difference was non-significant. Thereafter males more often initiated social play than females, and in weeks 7 and 8 this was significant. In week 3, females as compared to males significantly more often initiated agonistic interactions. However, by week 5, the highest level was found in males, and the difference between males and females was significant in week 7. Table 4 shows the ratios of observed to expected number of interactions within and between males and females. Assuming equal distribution of interactions between the puppies within the individual litters the expected numbers were calculated on the basis of the possible

combinations of puppies of the same or different sex. The direction of social investigation was not significantly influenced by gender. However, both social play and agonistic interactions occurred significantly more often between males than expected. Between females these forms of interactions occurred significantly less often than expected. Furthermore, males initiated social play with females significantly more often, and females initiated agonistic interactions with males significantly less often than expected.

The observed (P) and the expected (P_0) proportions of male (M) and female (F) partners chosen by the puppies when initiating social interactions were compared for males and females

^{*} p<0.05; ** p<0.01 for difference between sexes (F-test).

Table 4. Social investigation (SOCI), social play (PLAY) and agonistic interactions (AGON) within males (M) or females (F) and between males and females. The direction of the interactions is indicated by arrows (initiator \rightarrow recipient). The interactions are expressed as the ratios of observed (N) to expected number (N₀), which equal the ratios of observed (P) to expected (P₀) proportions of the total number of observations (N₁).

Behaviour	Nt	Ratio (N/N ₀)				
		$F \rightarrow F$	$F \rightarrow M$	$M \rightarrow F$	$M \rightarrow M$	
SOCI	359	1.04	0.93	0.95	1.15	
PLAY	455	0.68***	0.86	1.15*	1.34***	
AGON	331	0.61***	0.83*	0.93	1.91***	

^{*} p<0.05; *** p<0.001 (H₀: P=P₀) Z-test for a proportion (Kanji 1993).

Table 5. Total number and range of the ratio of social investigation (SOCI), social play (PLAY) and agonistic interactions (AGON) initiated (I) and received (R) in the 4 litters of puppies.

T :	SOCI	SOCI		PLAY		AGON	
Litter	N	I/R-ratio	N	I/R-ratio	N	I/R-ratio	
———— Н1	28	0.46-1.83	154	0.66-1.58*	104	0.59-1.87***	
H2	54	0.50-1.75	64	0.47-1.38	31	0.17-3.00*	
SS	135	0.70-1.27	196	0.71-1.29	153	0.47-1.53	
MB	143	0.25-2.00***	41	0.50-2.00	41	0.57-1.67	

^{*} p<0.05; *** p<0.001; χ^2 -test (H₀: equal distribution of I and R within the litter).

separately. Males significantly preferred other males (P/P₀ = M_m = 1.47) to females (F_m = 0.71) when initiating agonistic interactions (p<0.001, M_m/F_m = 2.06, N_m = 203). Females, however, significantly avoided other females (P/P₀ = F_f = 0.75) preferring males (M_f = 1.26, p<0.004, F_f/F_m = 0.60, N_f = 128). Similarly, males preferred other males as play partners (M_m/F_m = 1.23, N_m = 272), whereas females tended to avoid other females (F_f/M_f = 0.75, N_f = 183). These preferences, however, were non-significant.

Individual differences within litters

For each of the 4 litters, Table 5 shows the total number of interactions as well as the range of the I/R-ratios (interactions initiated/interactions received) for the puppies within the litter. For agonistic interactions in litter, H1 and H2, the I/R-ratios were significantly different

(p<0.001 and p<0.05 respectively) from an equal distribution of the interactions between the individuals (equal distribution corresponds to I/R-ratios of 1 for all puppies). For social play in litter H1 and social investigation in litter MB, the I/R-ratios were significantly different (p<0.05 and p<0.001 respectively) from an equal distribution. All these results indicate that the puppies had developed individual characteristics in their social behaviour.

Relations between social behaviour categories Table 6 shows the correlations between social investigation, social play, and agonistic behaviour initiated and received. There was a negative and significant (p<0.05) correlation between social investigation initiated and received. A strong, positive and significant (p<0.001) correlation was found between playful interactions initiated and agonistic interac-

Interaction	SOCI-I	SOCI-R	PLAY-I	PLAY-R	AGON-I
SOCI-R	-0.56*				
PLAY-I	0.25	0.12			
PLAY-R	0.26	0.08	0.28		
AGON-I	0.03	0.11	0.57*	0.59**	
AGON-R	0.29	0.09	0.83***	-0.02	0.37

Table 6. Correlations between social investigation (SOCI), social play (PLAY) and agonistic behavior (AGON) initiated (I) and received (R). N = 22 puppies.

tions received. Additionally, positive and significant (p<0.01) correlations were found between playful interactions initiated and agonistic interactions initiated (p<0.05) and between agonistic interactions initiated and playful interactions received (p<0.01). Between playful interactions received and agonistic interactions received, however, no correlation was found.

Discussion

Scott & Fuller (1965) performed daily observations of puppies in their own environment within the litter and without interfering with them. They started their observation at birth and continued until the puppies were weaned at 10 weeks and further on to 16 weeks. All these careful observations led to an understanding about the development of a large amount of behavioural patterns in dogs. A quantitative analysis of social interactions between the puppies, however, was not made. Nor were the relations between the various categories of social behaviour analyzed. The general advantage of the present study is that it presents an analysis of social behaviour in undisturbed litters, and in spite of the large differences in environments in which the puppets were reared and of the use of a number of breeds many general trends in development and interaction patterns were revealed.

In our study the puppies seemed to actively contact litter mates from the age of 2–3 weeks. These early contacts were mainly in the form of social investigation, as also mentioned by *Scott & Fuller* (1965, page 104) but without quantitative evidence. *Scott & Fuller* also mentioned that at the same age similar investigation is directed towards humans. In our study the first signs of social play and interactions involving elements of agonistic behaviour were also seen at this age, but they clearly appeared later than social investigation. Of the play behaviour patterns *Scott & Fuller* (1965) only mention 'playful fighting', and, again, gave no quantitative description of its development.

At the age when the agonistic elements appeared they may not yet have been linked to the motivational systems controlling agonistic behaviour in adults. However, our study of autocorrelation over weeks showed that, in contrast to the frequencies of social investigation, the frequencies of agonistic interactions initiated by the individual puppies at weeks 5 and 7 were highly predictive for the frequency at week 8, and this may indicate the early emergency of differential behavioural profiles. Furthermore, the frequencies of social play initiated by the individual puppies at weeks 4-7 were positively correlated (although not significantly) with the frequency at week 8. This may indicate that from week 5, individual differences between

^{*} p<0.05; *** p<0.001.

the puppies in agonistic behaviour and in the tendency to initiate playful interactions were about to be established. The only exception to this pattern was the negative correlation between the frequencies of agonistic interactions between weeks 6 and 8; however, this correlation was not significant.

The autocorrelation analysis also revealed that, generally, the frequency of play during week 3 was negatively correlated with the frequency of play during the later weeks. This indicates that there was a rebound effect so that a low performance of play in week 3 was compensated for by more play during the later weeks and vice versa. Similar observations have been made on the play behaviour of a number of other mammal species, although more data are needed to confirm this phenomenon (Haas 1967, Müller-Schwarze 1971, see also Fagen 1981). Our autocorrelation analysis also indicates the existence of a similar rebound effect for agonistic behaviour during this period of life. For both play and agonistic behaviour, a rebound effect may represent a beneficial adaptation for a young animal in order to achieve a certain amount of physical exercise or experience (see Fagen 1981, page 280-318). The tendency for initiating social interactions seemed to develop differentially in males and females. Before week 5, males initiated social investigation more often and agonistic interaction less often than females. However, the situation was reversed by weeks 6 and 5 for the 2 forms of behaviour respectively. Both for social play and agonistic behaviour, the proportion of interactions between females was significantly lower, and the proportion of male interactions was significantly higher, than the expected proportion. Additionally, the proportion of male→female playful interactions was significantly higher and the proportion of female-male agonistic interactions significantly lower than expected. These results are similar to those from other studies in which a sex bias in infantile play has been found, for example in many group living primates (Baldwin & Baldwin 1977, Symons 1978) and in ground squirrels (Holmes 1995) in which male play is more frequent and/or more vigorous than female play. Aldis (1975, page 106), however, mentioned that play was not less frequent in female than in male domestic dogs, and, furthermore, Zimen (1972, page 228) suggested that in wolves play may be less frequent in male than in female cubs. None the less, our results are very clear and consistent for puppies reared in a variety of environments. Assuming that more play and/or play fighting results in better fighting skills, our results are also in agreement with those of Scott & Marston (1949), who found that in 36 out of 57 male-female relationships male puppies became dominant to females by the age of 15 weeks. Fagen (1981, page 371) suggested that sex differences in play fighting should be present only when fighting skills are differentially important in adult males and females, for example in intrasexual competition (Meaney & Stewart 1985). In accordance with the present results, Lund et al. (1996) found that male dogs had significantly higher probability of aggression towards the owner (which may reflect dominance problems) as well as aggression towards other dogs, as compared to females.

No dominance hierarchy between the puppies is expected to develop before the age of 8–12 weeks (Fox 1971). However, in the two litters of Siberian Huskies the I/R-ratios indicated individual differences in the number of agonistic interactions initiated compared to the number received. This might indicate that dominance relationships were about to be established. Playful interactions initiated were strongly correlated with agonistic interactions received. Similarly, playful interactions received was correlated with agonistic interactions initiated. The explanation may be that often aggressive ele-

ments were elicited in response to tough treatment by the litter mate during play, and it is indeed well known from many species that social play may be responded to by aggression (e.g. van Lawick-Goodall 1971, Ehrlich & Musicant 1977). Furthermore, in our puppies play may have been used as appeasement towards an aggressive litter mate. In both cases the direction of the interaction was reversed. Although during play agonistic elements may not be controlled by the motivational systems related to aggression, such interactions may have consequences for the relationships between the puppies. The 'aggressor' may learn that certain forms of behaviour will lead to submission or avoidance behaviour of litter mates. Furthermore, puppies subjected to tough treatment and associated aggressive elements during play may learn which litter mates to avoid. Therefore, the outcome of playful interactions may influence agonistic behaviour, and in puppies and in other young mammals a clear cut discrimination between play and agonistic interactions in functional terms may not be possible since play may often escalate into real fights (e.g. Symons 1978).

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Sammendrag

Udvikling af social adfærd i fire kuld hundehvalpe.

For at følge udviklingen af den sociale adfærd blev 4 kuld hundehvalpe observeret uden indgriben i deres hjemmemiljø fra fødslen til 8 ugers alderen. Tre af kuldene blev observeret kontinuerligt i 2 timer en gang hver uge, og det fjerde kuld i 40 min 2 gange om ugen. Samtidigt blev hvalpenes adfærd optaget på video. Den sociale adfærd blev inddelt i 1) undersøgelsesadfærd rettet mod kuldsøskende (slikken, snusen eller oral undersøgelse), 2) social leg samt 3)

interaktioner, der indeholdt agonistiske elementer så som dominanspositurer, trusler, bid eller underkastelse. De forskellige typer af social adfærd fremkom. da hvalpene var mellem 14 og 21 dage gamle. Social undersøgelsesadfærd sås først og blev fulgt af leg og agonistisk adfærd. Forskelle mellem hvalpene med hensyn til deres tendens til at indlede leg samt agonistiske interaktioner begyndte at udvikle sig i uge 5. Leg og agonistiske interaktioner mellem hanhvalpe forekom hyppigere end forventet. Derimod forekom disse adfærdsformer mindre hyppigt end forventet mellem hunhvalpe. Hos begge køn sås dog en præference for hanhvalpe som partnere i forbindelse med agonistiske interaktioner. I forbindelse med social undersøgelsesadfærd sås ingen kønsforskelle m.h.t retningen af interaktionerne mellem hvalpene. Generelt var de fundne forskelle mellem hvalpene med hensyn til deres tendens til at indlede leg samt agonistiske interaktioner konsistente (positiv korrelation) gennem uge 6-8. Derimod var frekvenserne gennem disse uger negativt korrelerede med frekvenserne i uge 3 (leg) eller uge 3 og 4 (agonistiske interaktioner), hvilket tyder på en rebound effekt for både leg og agonistisk adfærd. Tilsvarende signifikante korrelationer blev ikke fundet for social undersøgelsesadfærd. Agonistisk adfærd blev ofte besvaret med leg og leg blev ofte besvaret med agonistisk adfærd, og resultaterne tydede på, at forskelle mellem hvalpene med hensyn til deres sociale adfærd var udviklet før 8 ugers alderen.

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