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The Function of Allogrooming in Domestic Cats (*Felis silvestris catus*); a Study in a Group of Cats Living in Confinement[1]

Ruud van den BOS
Anthrozoology Institute, Dept. Biology,
University of Southampton, Southampton, UK;
Dept. of Ethics, History and Alternatives of Animal Experiments,
University of Leiden, Leiden, the Netherlands

Abstract — Grooming interactions (n=83) occurring in a group of non free-ranging adult neutered male (n=14) and female (n=11) domestic cats (*Felis silvestris catus*) were analysed. Grooming was not induced by the proximity (distance <=0.5 m) of another animal. Grooming was in general directed at the head-neck area. Higher ranking animals groomed lower ranking animals more often than the other way round. Groomers tended to adopt 'higher' (standing, sitting upright) postures than groomees (sitting, lying). Agonistic behaviour occurred in 35% of interactions. Groomers showed offensive behaviour more often than groomees, most often after grooming a partner. Furthermore groomers often groomed themselves after grooming a partner. The degree of relatedness of animals did not affect the frequencies or durations of grooming. These results are consistent with the hypothesis that allogrooming in domestic cats may be a way of redirecting (potential) aggression in situations in which overt aggression is too costly.

Introduction

Depending on the distribution and abundance of food free-ranging domestic cats (*Felis silvestris catus*) live either solitary or in groups (reviews: Bradshaw, 1992; Bradshaw & Brown, 1992; Liberg & Sandell, 1988). Females with their dependent offspring form the core of groups, whereas males are only loosely attached to such groups and wander between them (Liberg & Sandell, 1988). Over the last decade there has been a growing interest in cat social behaviour under free-ranging conditions (e.g. Macdonald et al., 1987; Natoli & de Vito, 1991; Brown, 1993) partly because domestic cats have been considered to be good model animals to study factors and processes leading to group living as well as the way the social organization is formed and maintained in the family of felids (e.g. Macdonald et al., 1987; van den Bos & de Vries 1996). At the same time there has been a growing interest in cat social behaviour under non-free ranging conditions (i.e. confined cats; Podberscek et al., 1991; Brown, 1993; van den Bos & de Cock Buning, 1994a,b; Smith et al., 1994; van den Bos, 1995a,b, 1996; van den Bos & de Vries, 1996) partly because of animal welfare related questions and partly because confined animals allow for studying aspects of social organization in more detail (e.g. van den Bos & de Cock Buning, 1994a,b; van den Bos & de Vries, 1996).

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[1] The data were previously presented at the 29th International Congress of the International Society for Applied Ethology (van den Bos, R. (1995) Allogrooming in domestic cats in confinement, Proceedings of the 29th International Congress of the International Society for Applied Ethology, S.M. Rutter et al. (Eds.), pp. 109-110)

[2] *Author's address*: Ruud van den Bos PhD; Institute of Evolutionary and Ecological Sciences, Section Theoretical Biology, University of Leiden, P.O. Box 9516, 2300 RA Leiden, the Netherlands

One important issue which has been addressed is conflict regulation in group-living conditions (Natoli & de Vito, 1991; van den Bos & de Cock Buning, 1994a). Cats appear to lack formal dominance hierarchies: none of their affiliative behavioural patterns shows a unique one-way distribution with respect to rank-orders based on the outcome of aggressive encounters (van den Bos & de Cock Buning, 1994a,b; van den Bos, 1995a,b). Still, allogrooming, i.e. grooming a conspecific, appears to be an important behavioural pattern in conflict-regulation, that is it appears to play a role in forming and maintaining stability of groups (van den Bos & de Cock Buning, 1994a; van den Bos & de Vries, 1996).

The following has been specifically revealed with respect to allogrooming between adults: (i) allogrooming occurs regardless of sex (male/female), sexual status (intact/neutered) or living conditions (free-ranging/non free-ranging); (ii) the distribution of allogrooming bouts in pairs is asymmetric; (iii) the flow of allogrooming is downrank; (iv) animals receive more bouts of grooming from animals from whom they also receive more bouts of offensive behaviour; (v) allogrooming is associated with behavioural patterns expressing confidence and which are more likely to be shown by high-ranking animals, such as social sniffing and sniffing rear; (vi) proximity scores of pairs and frequencies of allogrooming in pairs correlate positively; (vii) in groups, mean grooming rate (bouts/h/pair) and density (cats/sqm) correlate positively, while mean agonistic interaction rate (interactions/h/pair) and density correlate negatively, i.e. the higher the density the less aggression and the more allogrooming occurs (Brown, 1993; van den Bos & de Cock Buning, 1994a,b; van den Bos, 1995a,b; van den Bos & de Vries, 1996; van den Bos et al. unpublished data).

The asymmetrical distribution of grooming in pairs and the effect of rank order exclude the possibility that grooming solely serves a hygienic function as has been observed in impala's (Hart & Hart, 1992; Mooring & Hart, 1993). Furthermore the rank order effect excludes the possibility that grooming serves as a way of getting access to and establish relationships with individuals with whom it may be advantageous to affiliate like high ranking individuals — which may give support in future conflicts — as has been repeatedly observed in primates (see e.g. Wilson, 1975; Seyfarth, 1976, 1977, 1980; Goosen, 1980; Hemelrijk, 1990; Hemelrijk & Ek, 1991; Spruijt et al., 1992).

As hypothesized in a previous paper (van den Bos & de Cock Buning, 1994a) allogrooming may be a way of reducing tension between animals which are living near one another. This study addresses this possibility by careful observation and analysis of grooming interactions.

Materials and Methods

Animals & Study Area

The study colony existed since 1988. Cats (European short hairs) were purchased from different breeders and brought together while juvenile. Males were neutered at an age of 6–12 months, females at an age of 12–25 months. The coefficients of relatedness ranged from 0 to 0.632. These coefficients were calculated from breeders' information on which males sired which females (see Brown, 1993 for details on the genealogy of this colony). Males were generally stockier and heavier than females (weight ratio male to female: 1.3; ranges: male: 5–8 kg, female: 4–5.5 kg). At the start of this study eleven females and fourteen males were present. During the study, after 9 sessions, one female was removed from the colony, leaving ten females for the remainder of sessions.

This colony has been studied earlier (March–June 1991; reported in Brown, 1993). The behavioural characteristics of the animals as well as the rank orders for males and females are therefore well documented. Cats were classified into three ranking categories (high, middle and low) based on informal observations by Brown (1993) and formal analysis of the flow of agonistic behaviour (data in Brown, 1993; cf. van den Bos & de Cock Buning, 1994a).

The group's living quarters consisted of an indoor and outdoor enclosure. The indoor enclosure consisted of two rooms (A: 23 sqm; B: 28

sqm) and a corridor (length: 10.8 m; width: 1.3 m; area: 14 sqm) connecting rooms A and B and leading to the outside enclosure. Room A contained shelfs with beds in which cats could sleep, lie, sit etc.. This room also contained litter trays (bedding: wood shavings). Room B contained cages in which cats could lie, sit etc.. The corridor contained a pole with shelfs on which cats could lie, sit etc. as well as a box in which cats could hide. The outside enclosure (96 sqm) contained several elements on which cats could sit, lie (pole with shelfs) or in which they could hide (boxes). Furthermore it contained logs for cats to scratch on. The floor of the outside enclosure was made of tiles (29 × 29 cm). The population density was 0.16 cat/sqm.

Cats had free access to the outside enclosure during working hours (08.00–17:00 h). They remained in the inside enclosure at night. Cats were kept on a 12–12 h day-night cycle with lights on from 08:00–20:00 h. They were fed dry (SDS; U.K.) and wet food (Whiskas (R)) once daily in the afternoon (after observations took place; see below). Water was available throughout the day in bowls present at various places in the enclosure. Temperature in the inside enclosure was maintained at 21 degrees Celsius; temperature in the outside enclosure varied according to weather conditions.

Observational Regimen

For each recording session cats were moved to the outside enclosure if the weather allowed so. Only during dry weather recording sessions were initiated. Furthermore the floor and the elements on which cats could sit etc. had to be dry. Two litter trays were provided during recording in case cats needed to urinate or defecate. Observations were always made between 11:00 and 15:00 h. The observer was present in the enclosure and recorded the behaviour of the cats using a video camera recorder with zoomlens (Philips Explorer Autofocus CCD VKR6850). Previous observations showed that cats behave somewhat more aggressive and less affiliative towards one another when an observer is present in the enclosure (Brown, 1993). Therefore, in order to avoid too much interference with their behaviour, the cats were familiarized with the presence of an observer during two 1-hour sessions before actual observations started (cf. van den Bos & de Cock Buning, 1994a). During these sessions and throughout the observations the observer did not interact with the cats. The observer recorded all ongoing behaviour from one spot in the enclosure. The camera was focussed on the area most frequently visited by the cats (about one third of the enclosure). Several rehabituation sessions were included when recording sessions were separated too far apart in time (see below). Recording was spread out over a period of 6 months. Sessions were interspersed with recording sessions in room A. The latter sessions were initiated on days different from those in the outside enclosure (van den Bos, in preparation). The temperature in the outside enclosure was determined after each recording session using an ordinary thermometer to assess the effect of temperature on grooming rate (see Troisi & Schino, 1986).

Interactions

An interaction was considered to have started when a cat clearly and unambiguously approached another cat — approach: moving clearly towards another cat — or invited another cat for an interaction by e.g. rolling in front of another cat. The cat which started the interaction (approaching another cat or rolling in front of another cat) was labelled the initiator, its partner the recipient. If cats started to groom one another while sitting or lying close together (no approach or invitation) the cat which delivered the first bout of grooming was called the initiator.

The distance between the cats at the start of the interaction was split into two categories: start from within 0.5 m (proximity: a cat's body length; van den Bos & de Cock Buning, 1994a) and start from a distance of more than 0.5 m.

During the interaction four behavioural patterns of the initiator and recipient were recorded (Table 1A) using the programme 'The Observer' (v2.0; Noldus Information Technology, Wageningen, the Netherlands). One extra category of behaviour was added, i.e. 'other be-

Table 1. Ethogram used in this study (after van den Bos & de Cock Buning, 1994a; UK Cat Behaviour Working Group, 1991). In parentheses the abbreviations which are used in the tables are shown.

(A): BEHAVIOURS

Behaviour	Description
allogrooming (GC)	licking the fur of another cat;
autogrooming (GS)	cat licking its own fur (including wiping head region with paw after licking paw);
Offensive behaviour (OF)	combination of the following elements: (slowly) approaching another cat (lowered head); running in pursuit of another cat, erect ears swiveled to point back on the head; hairs on back and tail erected; lashing tail; panting, salivating; cuffing, growling, yowling; narrowing of the pupils (including mounting);
Defensive behaviour (DE)	combination of the following elements: lowering of hindquarters; piloerection; flattening of the ears to the head such that they tend to flush with the top of the head; hissing, spitting; growling; rolling on the dorsum to expose claws; cuffing; dilation of the pupils (including fleeing);

(B) POSTURES

Posture	Description
standing (STA)	standing on all four;
sitting upright (SITUP)	sitting on hindpaws with outstretched forepaws; the weight of the body is shifted towards hindquarters;
sitting (SIT)	sitting on hindpaws and frontpaws; forepaws may be tucked underneath body or stretched out in front of the animal; the weight of the body is supported by front- and hindquarters;
lying (LYI)	lying on the side, back etc.; the weight of the body is supported by the body rather than the paws;

haviour', which contained all other behaviours. Furthermore postures of the groomer and groomee (Table 1B) while bouts of grooming were exchanged were recorded.

An interaction was considered to have ended if one of the (or both) cats moved away or fled (distance: >0.5 m). If cats remained together (distance: <= 0.5 m; proximity) the interaction was considered to have ended if none of the behavioural patterns of Table 1A was shown by the cats for a period of 60 s.

A bout of allogrooming was defined as a series of licking spells not interrupted by another behaviour, like looking round, watch other cats, licking the perioral region, unclearly directed nibblings to the fur of the other cat or a clear short pause (cf. van den Bos & de Cock Buning, 1994a). The same principle applies to the definition of bouts of autogrooming, offensive behaviour and defensive behaviour.

Data Analysis and Statistics

For each allogrooming bout it was determined whether it was directed to the head-neck area, the shoulder-chest area or the abdomen area (see insert of Fig. 1 for the body-areas).

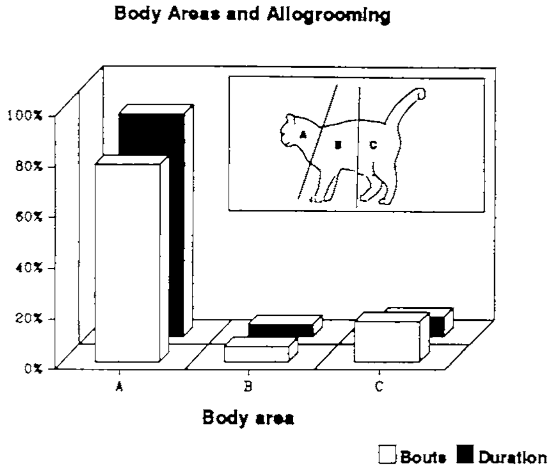

Fig. 1. Distribution of the number of bouts of allogrooming and of total duration of allogrooming across different body-areas; Insert: Areas into which the cat's body was split for analysis: A: head-neck area; B: shoulder-chest area; C: abdomen area.

Postures of the groomer and groomee were analysed by preparing a matrix containing postures for the groomer (rows) and the groomee (columns). The matrix was analysed using a Chi-square test (Sokal & Rohlf, 1981).

For each interaction the members of the interacting pair were denoted. Interactions were labelled unidirectional if only one animal groomed, otherwise bidirectional. Interactions between the same individuals, i.e. the same pair, were added to obtain one score (frequency, duration) per behavioural pattern per member of a pair. Thus for each member of a pair one score per behavioural pattern (frequency, duration) was obtained, whether the animal had been an initiator or a recipient in an interaction.

Scores (frequency, duration) per behavioural pattern per individual were totalled, i.e. for each individual one score (frequency, duration) per behavioural pattern was obtained, irrespective with whom the individual had interacted with as an initiator or as a recipient.

The number of interacting male-male (MM), male-female (MF) and female-female (FF) pairs was related to the maximal possible number of pairs for each category (MM,MF or FF pairs). For the final number of different grooming pairs an expected distribution was calculated based on the maximal number of pairs per category. The observed distribution and the expected distribution were subsequently compared using a Chi-square Goodness-of-Fit test (Sokal & Rohlf, 1981). Subsequently, means+SE's for the different behaviours of the MM, MF and FF pairs were calculated. Differences between males and female in MF pairs were analysed using paired t-tests.

To assess the effects of kinship, for each pair the overall scores of the different behavioural patterns (frequency, duration) were correlated with the coefficient of relatedness using Spearman rank correlation tests (Sokal & Rohlf 1981). Furthermore pairs were classified according to whether the animals were highly ($r => 0.25$), intermediately ($0.125 <= r < 0.25$) or distantly ($r < 0.125$) related. Differences in frequencies and durations of behavioural patterns between different categories were analysed using one-way Analysis of Variance (ANOVA).

Throughout the Results section MEAN+SE is reported unless otherwise stated. Reported p-values are two-tailed unless otherwise stated. p-Values equal to or smaller than 0.05 were considered to indicate statistical significant differences.

RESULTS

Interactions: General Aspects

In total n=28 sessions were recorded on video tape (23h45min) over a 6 month period. Ninety-two interactions were taped (3.9+0.4 interactions/h), but nine interactions (9.8%) could not be analysed, because interactions were only partly on screen and because other animals prevented reliable recording. No correlation existed between the temperature in the outside enclosure and the number of grooming interactions per h (rS=0.05, n=25, ns).

Most often (n=78 interactions; 94%) interactions (duration: 103.9+15.7s, n=83; range 5.7–945.4s) started with one animal approaching or inviting another animal; only 5 interactions (6%) started with animals sitting or lying together (distance: <=0.5 m). In 89.7% of the approaches/invitations animals were more than 0.5 m apart before the interaction started. Accordingly in total 84.3% (n=70) of interactions started while animals were more than 0.5 m apart.

The majority of interactions (91.6%) was unidirectional. In case of bidirectional interactions the distribution of grooming in terms of bouts (correlation coefficient: r=0.28, df=5, ns) as well as duration (r=−0.02, df=5, ns) deviated from symmetry (r=1).

Allogrooming was most often directed to the (dorsal part of the) head-neck area both in terms of number of bouts and duration (Fig. 1).

In the majority of cases (n=58 interactions; 69.9%) interactions ended with one animal moving away (>0.5 m); in only a small number of interactions (n=15; 18.1%) animals remained within 0.5 m of one another. Ten interactions (12%) ended with the flight of an animal.

Interactions: Behavioural patterns

Groomers were often standing (43.6%) or sitting upright (45.1%) whereas groomees were often sitting (46.6%; Table 2). Due to the large number of cells containing values smaller than 5 (9/16: 56.3%) a Chi-square could not be properly run. Yet, it should be noted that the cells containing the combination standing/sitting (groomer/groomee; 23.3%) and sitting upright/sitting (18.8%) contained the highest values (Table 2).

In 34.9% of interactions agonistic behaviour (offensive or defensive behaviour) was recorded. If offensive behaviour was shown by either an initiator or recipient of an interaction (n=30 cases) it was more often shown by the groomer (70%; n=21 cases) than by the groomee (30%; n=9 cases). Bouts of offensive behaviour shown by the groomer (n=26 bouts) were more often preceded (80.8%; n=21 bouts) than followed (19.2%; n=5 bouts) by bouts of allogrooming when both occurred. Bouts of defensive behaviour (n=18 bouts) were more often preceded by bouts of offensive behaviour (83.3%; n=15 bouts) than by bouts of allogrooming (16.7%; n=3 bouts) when both occurred.

A strong positive correlation between the number of allogrooming and autogrooming bouts as well as between their durations was found for both initiators (r=0.63, df=81, P<0.001 and r=0.42, df=81, P<0.001 respectively) and recipients (r=0.47, df=81, P<0.001 and r=0.14, df=81, n.s. respectively). These same correlations held when allogrooming and autogrooming scores of recipients and initiators were summed to the scores for different individuals (n=21 individuals: r=0.92, df=19, P<0.001 and r=0.87, df=19, P<0.001 respectively). Bouts of allogrooming (n=83 bouts) more were often followed (60.2%) than preceded (39.8%) by bouts of autogrooming when both occurred.

Pairs: Males and Females

In total, 37 different pairs were observed to groom (13.4% of all possible pairs; Table 3). The overall grooming rate was: 0.28+0.07 bouts/pair/h. The distribution of allogrooming across pairs was asymmetric whether in terms of frequencies of grooming bouts (Fig. 2A) or total duration of grooming (Fig. 2B).

The 37 pairs showed 83 interactions. Most interactions consisted of males interacting with one another: MM: 54 (65.1%), MF: 26 (31.3%) and FF: 3 (3.6%). In the 26 MF interactions,

Table 2. Occurrences of combinations of postures of groomer (rows) and groomee (columns) while bouts of grooming were delivered. Tot: totals for rows or columns. For abbreviations of behaviours see Table 1.

	STA	SITUP	SIT	LYI	Tot
STA	12	11	31	4	58
SITUP	13	16	25	6	60
SIT	0	1	2	2	5
LYI	2	0	4	4	10
Tot	27	28	62	16	133

Table 3. Total number of different pairs interacting (n=37). Since in the majority of sessions (67.9%) 10 rather than 11 females were present the values were calculated using the smaller number of females leading to a slight overestimation of the contribution of females. %tot: number of pairs expressed as percentage of total number of pairs (n=37); %class: observed number of pairs per class expressed as percentage of the total number of pairs per class (MM: n=91 pairs; MF: n=140 pairs; FF: n=45 pairs); int/pair: number of interactions per pair.

class	observed (%tot)	expected (%tot)	%class	int/pair
MM	18 (48.6)	12 (33.0)	19.8	3.0+0.7
MF	16 (43.2)	19 (50.7)	11.4	1.6+0.3
FF	3 (8.1)	6 (16.3)	6.7	1.0+0.0

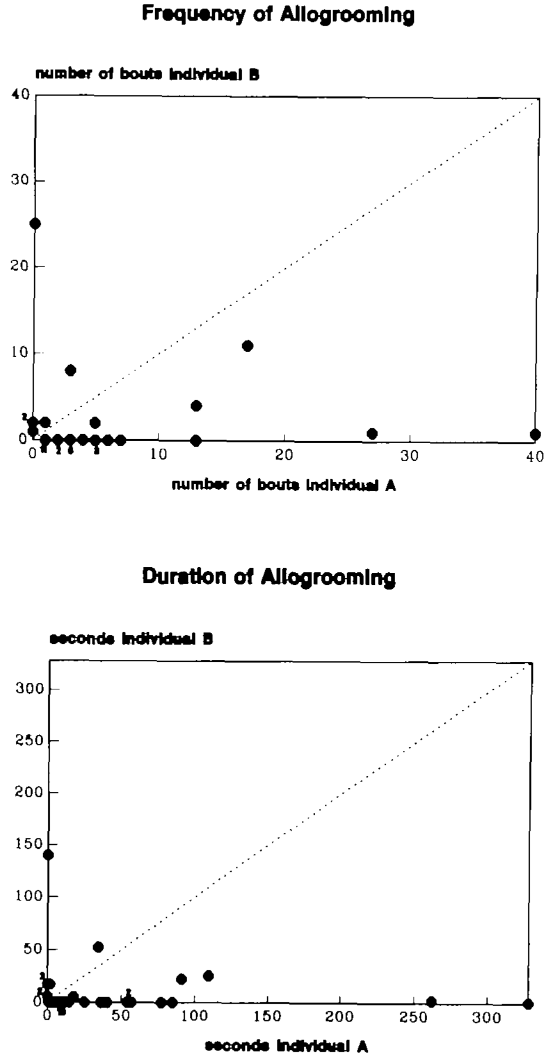

Fig. 2. Relationships between frequencies (panel A) and durations (panel B) of allogrooming of different members (individuals A and B) of pairs (n=37 in total) in which allogrooming occurred. The labels A and B were arbitrarily assigned to members of pairs. Although this prohibits calculating correlation coefficients properly (any change in A and B leads to different results) the distributions in panels A and B (for which correlation coefficients are: frequency: r=0.04, df=35, ns; duration: r= −0,05, df=35, ns) make clear that there is no 1 : 1 distribution in pairs (shown by the dotted line under the angle of 45 degrees in both panels) no matter how the labels A and B are assigned to individuals. Some dots reflect more than one data-point. These are indicated in the panels.

males acted as initiator in 80.8% of cases (n=21), females in 19.2%. Males behaved accordingly as initiator in nearly all interactions (90.4%; n=75).

In the 26 MF interactions, males delivered all allogrooming bouts in 17 cases (65.4%), females in 6 cases (23.1%); both delivered bouts in 3 cases (11.5%). In MF pairs (n=16), males appeared to deliver more allogrooming bouts per interaction than females (3.0+0.9 vs 0.9+0.3).

In MF pairs (n=16), males groomed females more often in 62.5% of cases whereas the reverse was true in 37.5% (Chi-square Goodness-of-Fit, n.s.). Males tended to groom females

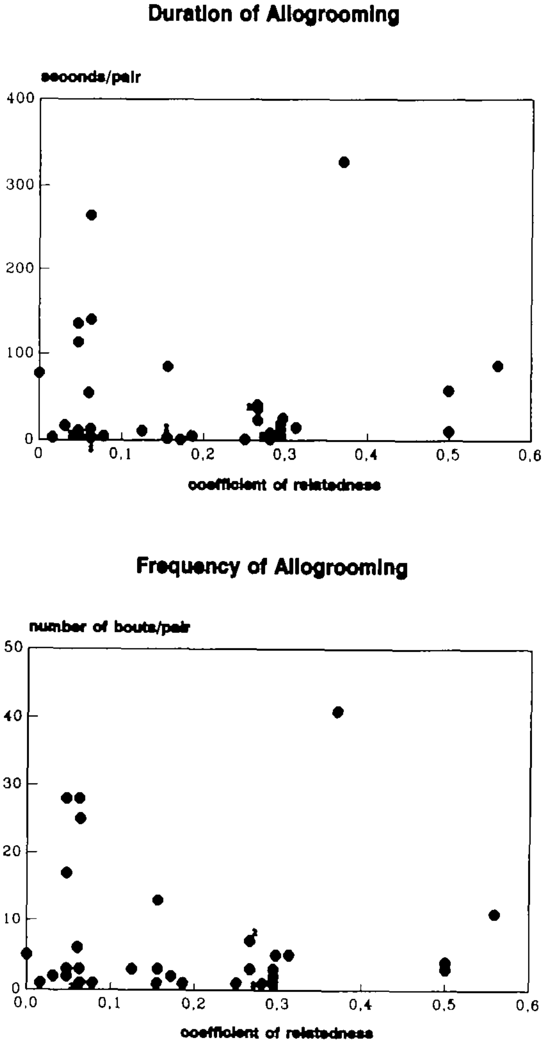

Fig. 3. Relationship between coefficient of relatedness (r) and frequency (panel A) and duration (panel B) of allogrooming in pairs (n=37). Some dots reflect more than one data-point. These are indicated in the panels.

longer than females males ($40.3+20.8$s vs $3.4+1.8$s; $t=1.777$, $df=15$, $P<0.10$); no other differences were observed.

Pairs: Rank Order

In MM pairs in which differences in rank existed ($n=12$ of $n=18$ pairs) higher ranking males groomed lower ranking males more often than the other way round in 75% of pairs ($n=9$ pairs). In two of three FF pairs in total in which a rank difference existed higher ranking females groomed lower ranking females more often than the other way round. Accordingly, higher ranking animals groomed lower ranking animals more often than the other way round in 78.6% of pairs ($n=11$); the reverse was true in 21.4% ($n=3$; $n=14$ pairs in total). This is significantly different from a 50–50% distribution (Chi-square Goodness-of-Fit: 4.571, $df=1$, $P<0.05$).

Pairs: Kinship

None of the behavioural patterns showed any correlation with the coefficient of relatedness, whether in terms of number of bouts or durations of patterns per pair (all rS, $P>0.05$). Fig. 3 shows the data for frequencies (panel A) and durations (panel B) of allogrooming. Analysing the data in terms of classes of relatedness (high, intermediate and distantly) showed the same picture (all one-way Anova's: $P>0.05$; not shown).

Discussion

General

This is the first detailed study on allogrooming in adult domestic cats in confinement. Until now allogrooming has been mentioned to occur among adults in confinement (Leyhausen, 1979; Podberscek et al., 1991; Brown, 1993; van den Bos & de Cock Buning, 1994a,b; Smith et al., 1994; van den Bos, 1995a,b; van den Bos & de Vries, 1996) but its function remained obscure.

In only a few pairs allogrooming was observed in this colony of females and males. Especially the number of female pairs (6.7%) appeared to be low compared to other studies (van den Bos & de Cock Buning, 1994a; van den Bos, 1995a: 53–95%). Although it has been shown that animals become less affiliative and more aggressive towards one another when an observer is present (Brown, 1993) this is unlikely to account for this low number. Brown (1993) observed cats in the outside enclosure using a closed video-circuitry in a situation in which the cats could freely move between the inside and outside enclosure. Recalculating her data showed that also under these conditions only a small number of pairs, i.e. 15.7%, was observed to groom in the outside enclosure (Brown, 1993; 157h of observation). The low number of pairs is also not due to observing animals in the outside enclosure per se: recordings (using a closed video-circuitry) of the animals in the inside enclosure (room A) revealed a low number of grooming pairs (5.8%; 22h55 min observation over a 4 month period, Van den Bos unpublished data). The low density (0.16 cat/sqm) under which the animals were living may however have been a contributing factor. For, previous studies showed a positive relationship between density (0.42–0.60 cat/sqm) and the number of grooming pairs in group living females in confinement (53–95%; van den Bos, 1995a,b), i.e. the lower the density the lower the number of grooming pairs.

Neutering may have been a contributing factor as well. For, it has been found that the sexual cycles in females affect the likelihood that females groom one another: females rub onto females while in oestrus and receive allogrooming in return during such interactions (van den Bos & de Cock Buning, 1994a). As to the males it should be noted that previous studies showed that intact confined males also groom one another (Podberscek et al., 1991; van den Bos & de Cock Buning, 1994b). Whether neutering facilitates the occurrence of grooming in males or not remains an open question as yet. It should be noted that for females and males the structure of allogrooming sequences does not appear to be affected by neutering (see Brown, 1993; van den Bos & de Vries, 1996).

Males appeared to be more active groomers than females, both among themselves and in male-female interactions. The latter observation will be discussed below within the context of different hypotheses on grooming. The former however seems to be surprising in view of the fact that males are normally wandering solitarily and hardly interact (Bradshaw, 1992; Bradshaw & Brown, 1992). As indicated above neutering per se does not seem to be a decisive factor. Rather it may be suggested that confinement per se, a situation in which animals are constantly near another and in which there are ample opportunities for males to interact may be a contributing factor (see below).

Despite the relatively low number of interacting pairs and the strong involvement of males the data allow along with those of previous studies to discriminate between different hypotheses on allogrooming in cats.

Allogrooming: Alternative Hypotheses

The present data confirm the notion that allogrooming is neither a hygienic behaviour nor a way of establishing relationships with animals with whom it may be advantageous to affiliate (see Introduction for references).

First, interactions were most often unidirectional, and if bidirectional highly asymmetric. This is furthermore reflected in the asymmetry in frequencies and durations of allogrooming in pairs (cf. van den Bos & de Cock Buning, 1994a). Secondly, differences existed with respect to the percentages of grooming pairs per sex class. Thirdly, higher ranking animals directed more grooming to lower ranking animals than the other way round (cf. van den Bos & de Cock Buning, 1994a). Fourthly, grooming was not affected by kinship.

Previously it has been hypothesized that allogrooming may be a way of reducing tension between animals which are living near one another (van den Bos & de Cock Buning, 1994a). Two different hypotheses may be formulated in this respect. First, allogrooming may serve as a way of redirecting (potential) aggression when overt aggression is too costly (Grant, 1963; Harrison, 1964; Wilson, 1975; Troisi et al., 1989; see also Spruijt et al., 1992; O'Brien, 1993; *hypothesis I*) and thereby reduce tension. Second, allogrooming may accelerate the decrease of the stress-response of individuals (expressed through behavioural (Aureli & van Schaik, 1991) and physiological (Terry, 1970; Boccia et al., 1989; cf. Feh & de Mazieres, 1993) signs); a stress-response which has arisen because of conflicts (cf. reconciliation; see Kappeler & van Schaik, 1992 for review) or the proximity of another animal (*hypothesis II*). Different predictions arise from these hypotheses. Following observations in birds (Harrison, 1964) under *hypothesis I* grooming is expected to be directed at the head-neck area since it is this area at which cats direct an attack onto others (Leyhausen, 1979). *Hypothesis II* does not predict a specific area in this respect. Under *hypothesis I* grooming may be accompanied by aggression during interactions (due to the balance between overt and redirection of aggression), while aggression is not expected to occur under *hypothesis II*. Furthermore following observations in rats (Grant, 1963) the frequency (and duration) of autogrooming (expressing the level of tension in cats as a result of the balance between overt and redirection of aggression (Maestripieri et al., 1992; Spruijt et al., 1992; Willemse et al., 1994; Willemse & Spruijt, 1995; van den Bos, 1996)) and the frequency (and duration) of allogrooming are expected to be positively correlated in individuals during interactions under *hypothesis I*. In contrast, under *hypothesis II* the frequency (and duration) of autogrooming, expressing the level of the stress-response due to conflict or proximity (Willemse et al., 1994; Willemse & Spruijt, 1995; van den Bos, 1996), are expected to be decreased in the groomee, since allogrooming reduces the level of the stress-response in the groomee (cf. Aureli & van Schaik, 1991; Spruijt et al., 1992); in fact a negative correlation may therefore be expected in individuals between the frequency (and duration) of autogrooming and the frequencey (and duration) of allogrooming received. Finally, following observations in birds (Harrison, 1964), rats (Grant, 1963) and primates (O'Brien, 1993) allogrooming is expected to flow downrank under *hypothesis I*, while this is expected to be rank-neutral or uprank under *hypothesis II*.

The question arises then as to what extent the data fit *hypothesis I* (redirecting (potential) aggression) or *hypothesis II* (reducing stress-response).

In line with previous observations (van den Bos & de Cock Buning, 1994a; van den Bos et al., unpublished data) it was found that offensive behaviour was more often displayed by the groomer — most often after grooming bouts — Moreover offensive behaviour appeared in the same factor as allogrooming when the individuals' behaviour was factor analysed (van den Bos, unpublished data). This seems to argue against *hypothesis II*. Furthermore, it was found that higher ranking animals were more likely to show allogrooming than lower ranking animals (cf. van den Bos & de Cock Buning, 1994a). Higher ranking cats are the more aggressive, lower ranking the more fearful animals (van den Bos & de Cock Buning, 1994a; van den Bos & de Vries, 1996). Together with the fact that males (being heavier and stockier) tended to show more grooming to females than the other way round in male-female pairs, it may in general be stated that the animal with the larger Resource Holding Potential (RHP; larger sized, heavier, and potentially more threatening animal) is more likely to show allogrooming than the animal with the smaller RHP (van den Bos & de Vries, 1996). The fact that the groomer often adopted a higher posture than the groomee while grooming (see also Fig. 1 in Macdonald et al., 1987; cf. Harrison, 1964) is consistent with this notion, i.e. the cat's higher or lower social status is reflected in its posture (see van Hooff & Wensing, 1987). These data argue in favour of *hypothesis I*. The observation that cats directed grooming most often towards the head-neck area also fits this hypothesis.

The fact that frequencies (as well as durations) of allogrooming and autogrooming were strongly positively correlated in individuals argues in favour of *hypothesis I*. If the occurrence of autogrooming is taken as a sign of tension in the groomer (Goosen, 1980; Troisi & Schino, 1987; cf. Willemse et al., 1994; Willemse & Spruijt, 1995; van den Bos, 1996; see also Maestripieri et al., 1992) the observation that autogrooming often followed allogrooming (cf. Grant, 1963) suggests that tension is gradually building up in the groomer during the interaction. This fits the forementioned observation that offensive behaviour occurs often after a groomer groomed its partner. Again this argues against *hypothesis II* but in favour of *hypothesis I*.

Previously, a positive correlation was observed between the frequency of grooming and proximity scores of pairs (van den Bos & de Cock Buning, 1994a; cf. 1994b). These data suggested that grooming and proximity are either expressing two sides of the same coin, i.e. both measures are expressing a mutual preference of animals, or that one induces the other (cf. Troisi et al., 1989). The analysis in the present study eliminated the problem of the previous study that grooming and proximity were not assessed independently. The present data show that allogrooming is neither induced by proximity nor induces proximity. This fits in with the notion that grooming pairs do not necessarily have higher proximity scores than non-grooming pairs (van den Bos & de Cock Buning, 1994a). Yet, it should be noted that in the inside enclosure (room A, in which cats normally sleep) allogrooming occurred more often when animals were already near one another for some time as well as remained near one another more often than in the outside enclosure (van den Bos unpublished data). Taken together these data suggest that allogrooming and proximity may rather independently express a mutual preference of cats for one another (two sides of the same coin) than that one induces the other (see Troisi et al., 1989). The immediate causation of grooming may therefore not be another cat's proximity with a resultant increase in tension, which is alleviated by allogrooming, but rather the mere presence of a cat with which the existence of a bond or social position (high and low rank) needs to be confirmed. These data argue against *hypothesis II*.

Overall the foregoing data strongly suggest that allogrooming between adult cats in confinement may be a form of redirecting (potential) aggression. A cost-benefit analysis for groomer and groomee suggests the following. The groomer would enjoy the benefit of not engaging in costly overt aggression in order to maintain its position, the groomee the benefit of not being attacked by its opponent (cf. O'Brien, 1993). In confinement such aggression regulating mechanisms may be important. This view is consistent with the observed positive correlation between the density of groups and the mean rate of grooming (bouts/h/pair) in these groups, and negative correlation between density and the mean rate of agonistic interactions (interaction/h/pair): with increasing densities there is a shift towards the expression of more grooming and less overt aggression (and less rigid rank orders; van den Bos, 1995a,b).

Allogrooming in free-ranging domestic cats

Although studies on confined non-breeding animals may not be conclusive with respect to the function of a behavioural pattern (see Krebs & Davies, 1993) such studies may allow to formulate a working hypothesis for the function of a behaviour, which can be subsequently tested under free-ranging and freely breeding conditions (see also van den Bos & de Vries, 1996).

If the hypothesis is forwarded that the function of allogrooming is to redirect (potential) aggression in cases where overt aggression is too costly and allows animals thereby to remain in one another's presence (cf. Harrison, 1964), it may be predicted that under free-ranging conditions this behavioural pattern would occur in groups under conditions in which it may be necessary to maintain bonds, e.g. in case of cooperative defense of resources or communal nursing and raising of kittens. Under free-ranging conditions related females with their dependent offspring form the core of groups (Bradshaw, 1992; Bradshaw & Brown, 1992). In line with the foregoing prediction grooming has been observed between (related) females (a mother and her two adult daughters), which defended their resources and cooperated in raising their young (Macdonald et al., 1987). Furthermore grooming occurred between these (related) females and a tom cat who appeared to be the breeding tom of this group. Although further data are lacking, the observation that in two colonies of free-ranging non-breeding (related and non-related) cats hardly any grooming occurred (Brown, 1993) seems consistent with this view.

Conclusion

All in all the data suggest that allogrooming in domestic cats may be a way of redirecting (potential) aggression when aggression is too costly, i.e. they suggest that allogrooming allows animals to remain to live in one another's presence and establish short-term and long-term bonds. Future studies are directed at whether this is a characteristic of species with facultative social structures like domestic cats (see introduction), and whether this function holds for other group-living felids, like lions and (male) cheetah's, as well.

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