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Social relations and individual coping reactions in a captive group of Central American Agoutis *(Dasyprocta punctata)*

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Abstract

Studied a captive group of Central American agoutis *(Dasyprocta punctata)*, consisting of 20 animals. The study focusses on relationships and individual coping reactions of six females, living together in unusually close proximity without all of them realizing an exclusive pair-bond to a male. Group structure centred on the pair-bond between the adult male and the oldest female (F1). F1 and her adult daughter (F3) were mutually attached. Another adult daughter of F1 (F2) displayed excessive maternal behaviour towards own and other young. F2, an introduced adult female (F4) and subadult daughters of F1 and F2 showed no enduring social attachment. For the non-attached females the frequencies of some agonistic and arousal-indicating behavioural elements were correlated with their monthly indices of retreat in relation to specific females indicating specific activations of aggression accompanied by specific levels and states of arousal. The hypothesis is proposed, that the females developed the different individual reactions by activating portions of their behavioural and motivational programmes, occasionally in excess, in coping with their specific situation to such an extent, that stress could be held low or moderate and regular breeding remained possible.

Introduction

Agoutis (*Dasyprocta* sp.), which are described in the field as living as monogamous pairs in defended areas (Smythe 1978; Dubost 1988) can, in captivity, be held in larger groups in which several females breed regularly without the possibility for all of them to develop an exclusive attachment to a male.

Bowlby (1969) regarded attachment as a behavioural system with its own form of internal organisation. Attachment in ethology is understood as the result of a process within the attached individuals, which activates specific possibilities of the behavioural programme and promotes an internal state of security (cf. Wickler 1976; Hendrichs 1978; Bischof 1985). It seems useful to differentiate between the transient mother-young attachment and the long-lasting bonds between adult animals (Bischof 1985; Hendrichs 1988). Depending on the qualities of social bonds, agoutis can activate different behavioural patterns and systems in regulating social situations and internal states (Korz and Hendrichs 1989). A central variable of internal dynamic is arousal, which can be differentiated at the levels of general arousal and specific states of arousal. Arousal can be correlated with qualities and frequencies of specific behavioural elements, e.g. scent-marking or autogrooming (cf. Ralls 1971; Eisenberg and Kleiman 1972). Specific behavioural indicators and correlations for the agouti are described by Korz and Hendrichs (1989). In group-housed females of the closely related acouchi *(Myoprocta pratti)* Kleiman (1972) found comparable results: positive correlations between frequencies of autogrooming and chasing as well as food-burying and higher frequencies of autogrooming in group-living than in isolated females; she discusses this as an outcome of social stress. Social stress can be regarded as a consequence of escalated and long-lasting arousal through frequent social perceptions (Hendrichs 1978).

In a territorial and monogamous species, pair-bond and territorial ownership are related to dominance (cf. Kleiman 1977), social bonds reducing aggression between bonded animals and often increasing aggression towards conspecifics (cf. Eisenberg 1966). Aggression in the sense of agonistic behaviour, however, is not necessarily correlated with the dominance state of an animal (Rowell 1974; Hand 1986; Francis 1988).

Thus, the primary aim of the present study was to characterise the specific social and dominance relations of the females in the observed group and to assess, in which way the individual females adjust to living together in a situation without exclusive use of space, in unusually close proximity to other females and especially most of them without realizing an exclusive pair-bond to a male. Besides contributing to a better understanding of the behavioural qualities of the agouti, such studies can further our knowledge on mechanisms and functions of social attachment.

Material and methods

Animals

Central American agoutis, descendants of animals captured in Guatemala, have been bred at the University of Bielefeld, Department of Ethology since 1974. From April 1985 to December 1986 one group of 20 animals was observed, quantitative behavioural data were recorded from June 1985 to July 1986. At the beginning of observation the group consisted of 1 adult male (M1, 10 years old), 4 adult females (cf. Fig. 1), 2 subadult females (F12, F31 each one year old), 1 subadult male (removed at 9. 8. 1985), 1 male and 3 female young. F1 is the mother of F31, F3 and F2; F2 is the mother of F12. F4 was born in another group and introduced to the group in 1982; she died in November 1986. M1 is the father of F1, F2, F3, F31, F12 and of all young. He belongs to the first generation born in Bielefeld and died in February 1986. The six adult and subadult females were the subject of the present study. Females have a post-partum-estrus lasting a few hours; the estrus cycle has a length of 34–36 days (cf. Weir 1971 for *Dasyprocta aguti*, own observation). Pregnancy lasts about 115–120 days. The one or two pups are well developed and begin to feed on their own at an age of two weeks, although they can suckle up to an age of three months. Sexual maturity is achieved at an age of six months. With four to five months of age immature animals were chased by adults (particularly by their mothers) for two to three months; thereafter the frequencies of chasing decreased.

The animals were kept in an outdoor enclosure of 9.00 m × 4.65 m, subdivided by wire-mesh into four parallel compartments of identical size connected by passages 0.75 m in width. Three of the compartments were each connected with a wooden sleeping cabin (1.10 m × 1.75 m) outside the enclosure; the fourth compartment had a smaller cabin (0.80 m × 0.70 m). The ground consisted of gravel covered with sand. The enclosure contained two wooden chests and branches. The ambient temperature varied from +30 °C to −10 °C. In winter the enclosure was protected against snow and coldness by partly transparent canvas; the larger sleeping cabins contained heat-lamps. The animals were fed corn, rolled oats, fresh vegetables, fruits and leaves once a day (dry food and water ad libitum). Three of the sections had a food-bowl, only two of them water-bowls.

Data recording and analysis

The behaviour of all animals was recorded by written entries in one-minute intervals as scan samples at those times of day (6–12 a.m., 17–21 p.m.) when all animals of the group were active. The analysis takes into account 150 hours of behavioural protocols. An index of retreat was computed for each two females based on the ratio $RI = R^+ / R^+ + R^-$ (R^+: number of retreats displayed by female A in reaction to a specific female B, R^-: number of retreats shown by female B in reaction to female A). Numbers of retreats are based on all recorded encounters between females ending with a retreat of one or both. The higher this index (ranging from 0–1) is for one of the two females, the clearer her superiority is regarded to be in relation to the other. The level of significance for all statistical tests (cf. figure and table legends) is $< = 0.05$.

A preference was defined a) for males if a male directed more than twice as much courtship behaviour towards one specific female than he showed on average towards every female (cf. Sachser 1986 for guinea pigs), b) between females if a female directed more than twice as much contact behaviour towards one female as she showed on average towards every female.

The following behavioural elements were recorded: "Bury": The animal takes a piece of food in its mouth, digs a hole into the ground with its forefeet, places the piece of food in the hole and covers it

up, pressing the substrate with the forefeet. "Scrape": The animal scrapes the ground with its forefeet (can change into burying and vice versa). "Nibble-of-bodysides": The animal nibbles at its flanks. "Scratch": The animal scratches its flanks with its hind leg turning its body. "Lick": The animal raises a forefoot and licks it. "Tremble": Brief body-trembling with hair erected. "Scentmark": The animal

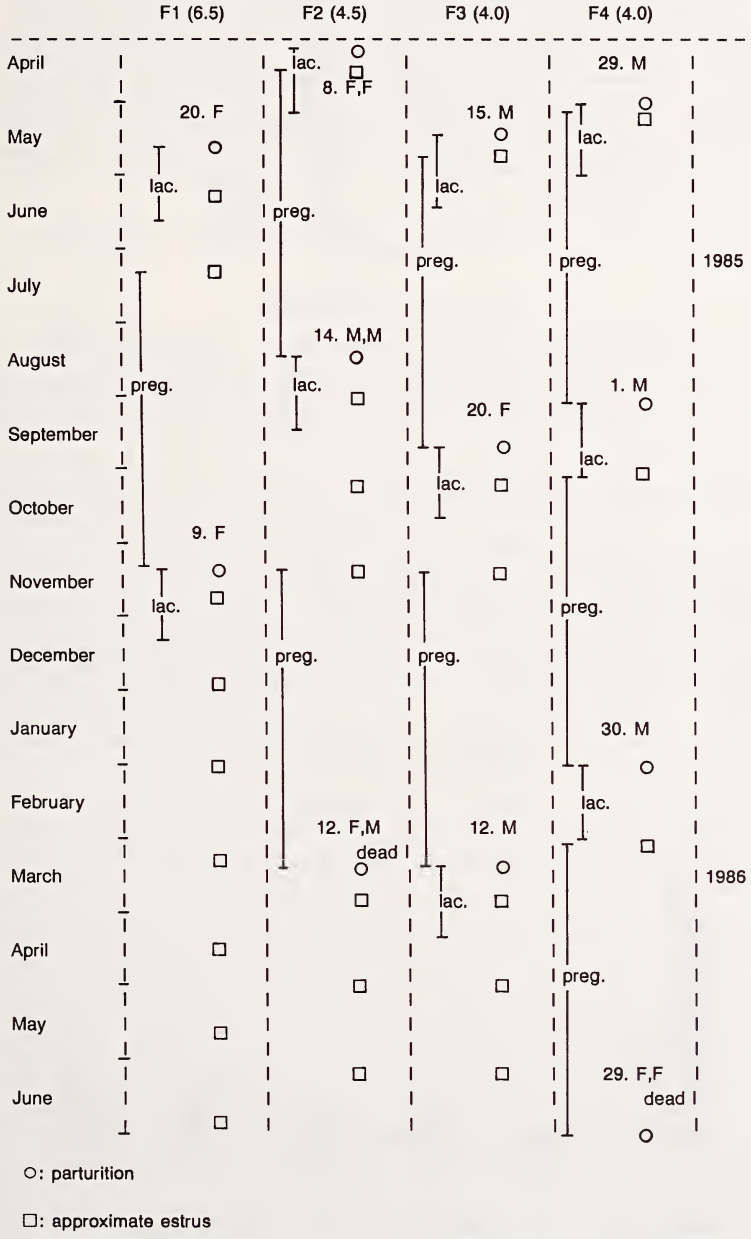

Fig. 1. Reproductive states of the adult females during period of observation. Numbers in brackets give the age of females (in years) at the beginning of data recording. Numbers give the dates of parturition (F = female young, M = male young), vertical lines label spaces of time, lac = lactation (period of regular suckling), preg = pregnancy

drags its anal glands over the ground leaving a secretion. "Chase": The animal runs after another one for at least two meters. "Joust": Standing opposite on their hind legs two animals drum on each other with their forelegs. This behaviour is often accompanied by raising the rump hair. "Head-thrust": The animal thrust its raised head at another. "Head-raise": Standing in front of or parallel to another animal at a distance of up to one meter the animal having raised its head stares at the other. "Bite-attempt": A biting movement in the direction of another animal while sitting, standing or quickly approaching. "Nuzzle": The animal nuzzles the corner of another's mouth (mostly when this one has a piece of food in its mouth). "Nibble": The animal sits at the side of another nibbling the region from ear to corner of the mouth of the other's head. "Sniff": The animal sniffs at parts of another's body. "Chin-raise": A male approaches a female with raised chin. "Drive": A male follows a female with raised chin for at least two meters. "Urine-spray": A male approaches a female, raises its body, and sprays a jet of urine in the direction of the female. "Follow": A male follows a female in a distance up to two meters. "Anal-licking": A female licks the anal region of a young. "Spit": A sound that females can display when a male approaches.

Results

Male-female relationships

M1 shows a preference for F1 (cf. Fig. 2). The amount of "Follow" is three times as high as the average amount towards every female. Referred to the adult females, "Nibble" occurred exclusively between M1 and F1 (the one "Nibble" towards F31 can be explained by the age of this female, "Nibble" occurring frequently between adult and young animals). On the whole M1 directed 50.2 % of the recorded behaviour towards F1. Fig. 1 gives the changes of some reproductive states of the four adult females from April 1985 to February 1986. Estrus of females (because of its short space of time) is difficult to observe directly, therefore the estrus-dates in Fig. 1 were computed proceeding from dates of parturitions with a scope of three days before and after the approximate dates of estrus. The frequency of "Nibble" M1 directed towards F1 was 0.80/h (18.6 h of observation) around estrus and 0.37/h (101.4 h of observation) out of estrus. Frequencies of courtship behaviour around estrus M1 directed towards F1 were 0.59/h, towards F2 0.00/h (7.7 h of observation), towards F3 0.81/h (3.7 h of observation) and towards F4 0.00/h (2.5 h of observation); frequencies out of estrus were 0.49/h towards F1, 0.09/h (112.3 h of observation) towards F2, 0.10/h (116.3 h of observation) towards F3 and 0.15/h (117.5 h of observation) towards F4. Fourteen days before and after parturitions, no remarkable

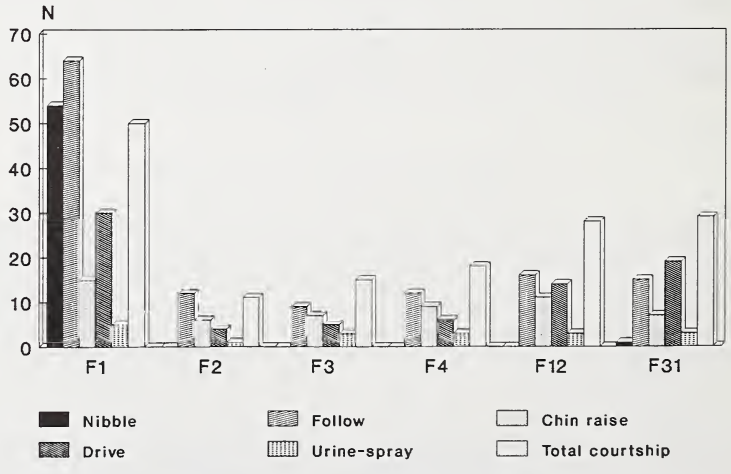

Fig. 2. Amounts of "Nibble", "Follow" and courtship behaviour that the male M1 directed towards the females from June 1985 to January 1986 (120 h of observation)

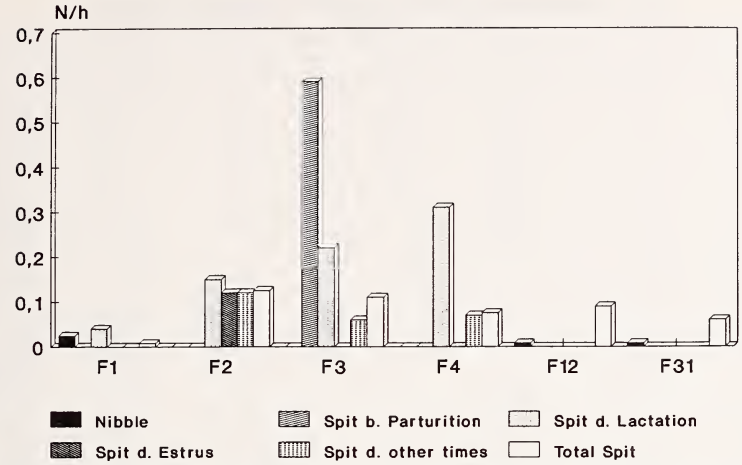

Fig. 3. Frequencies of "Nibble" and "Spit" that the females directed towards the male M1 from June 1985 to January 1986. b = before (14 days), d = during. N/h = average amount of behavioural element per hour

changes in frequencies of courtship behaviour appeared, but F1 was the only female courted by M1 in this period after parturition.

The frequency of the threat behaviour "Spit" directed to M1 is distinctly lower in F1 than in the other females (Fig. 3). "Spit" mainly occurred in periods of lactation with the exception of F3 which spat mostly in the fourteen days before parturition. The one "Spit" of F1 occurred shortly after parturition. F2, F3 and F4 also spat when they were not in a striking reproductive state. Agonistic behaviour of M1 towards females only occurred in few cases towards the subadult ones.

Female-female relationships

The amounts and distribution of agonistic (Table 1) and of contact behaviour (Table 2) show distinct differences between the females. Agonistic behaviour of F1 was mainly directed towards F2 and F12, that of F2 predominantly towards F1, the amounts directed towards the other females still being relatively high. F2 directed 40.3 % of her total amount of agonistic behaviour (268) towards F1, while F1 directed 52.9 % from a total of 202 towards F2. The main behavioural element which occurred between these females was "Joust". The main element of agonistic behaviour that F1 directed towards F12 was "Chase". F3 and F4 mostly directed agonistic behaviour towards F2 and F12. F12 showed agonistic behaviour, especially "Chase", mostly towards F2; F31 mostly towards F12. F2 displayed "Joust" more frequently (44.8 % from a total of 268) than any of the other females (F1 38.1 %, F3 11.3 %, F4 22.7 %, F12 25.2 % and F31 11.4 %) showing 66.6 % of this behaviour in 50 days following parturitions.

Preferences in directing contact behaviour are only recognisable between F1 and F3, and for F12 towards F1. Although following the definition, the amounts of contact behaviour shown by F2 towards F4 and by F4 and F31 towards F3 are too small to evaluate a preference. Between F3 and F1 "Nibble" occurred frequently and exclusively (with the exception of one "Nibble" of F1 towards F4). F2 and F12 did not display "Nibble" and among the other females, "Nibble" occurred infrequently. The distribution of agonistic and contact behaviour did not change after the death of M1.

Table 3 gives the monthly RIs for female pairs. The RIs of F2 towards any of the other

Table 1. **Amounts of agonistic behaviour between the females**

		F1	F2	F3	F4	F12	F31
F1	CH		14	0	2	33	2
	JO		61	0	9	5	2
	HT		3	0	0	4	0
	HR		15	1	3	13	3
	BA		14	1	1	13	3
Total			107	2	15	68	10: 202
F2	CH	4		4	6	10	6
	JO	67		7	22	15	9
	HT	4		1	3	2	2
	HR	20		10	7	8	13
	BA	13		10	5	13	7
Total		108		32	43	48	37: 268
F3	CH	0	3		0	11	0
	JO	0	7		2	0	0
	HT	1	3		1	2	0
	HR	0	10		0	11	2
	BA	3	5		1	17	0
Total		4	28		4	41	2: 79
F4	CH	1	27	0		5	1
	JO	8	21	1		5	0
	HT	0	10	0		2	0
	HR	1	25	0		10	1
	BA	3	8	0		20	5
Total		13	91	1		42	7: 154
F12	CH	0	37	0	0		1
	JO	2	16	0	4		5
	HT	0	3	0	0		1
	HR	0	18	0	2		1
	BA	1	11	1	1		3
Total		3	85	1	7		11: 107
F31	CH	0	1	0	6	60	
	JO	2	8	0	0	10	
	HT	0	1	0	0	6	
	HR	0	3	1	3	9	
	BA	0	5	2	13	46	
Total		2	18	3	22	131	: 176

CH = "Chase", JO = "Joust", HT = "Head-thrust", HR = "Head-raise", BA = "Bite-attempt". Amounts in 150 h of observation, behaviour of females on left side directed towards females above

females increased in August/September and in March/April, which were the months of parturition and lactation of F2 (cf. Fig. 1). In these periods her relations of superiority became unstable especially towards F1 and F3. Such a correlation is not found in the other females. Between estrus-dates and changes in RIs, no correlation is obvious in any female.

The monthly frequencies of "Chase", "Head-thrust" and "Bite-attempt" that F4 displayed towards F2 are positively correlated with her monthly RIs (cf. Table 4). The frequencies of "Bite-attempt" that F2 and F31 directed towards F12 and the frequencies of "Chase" F12 displayed towards F2 are correlated with their respective RIs. In the case of F2 the correlation depends on a rise in frequencies of agonistic behaviour and RIs towards F12 in the months of parturition and lactation. No significant correlations occur between frequencies of agonistic elements and RIs in F1 and F3 towards any other female. The frequencies of "Bury", "Scrape", "Nibble-of-bodysides", "Scratch", "Lick", "Tremble"

Table 2. **Amounts of contact behaviour between the females**

		F1	F2	F3	F4	F12	F31
F1	NU		0	20	1	3	0
	NI		0	5	1	0	0
	SN		1	1	0	1	3
Total			1	26	2	4	3: 36
F2	NU	0		0	3	0	0
	NI	0		0	0	0	0
	SN	1		2	1	0	0
Total		1		2	4	0	0: 7
F3	NU	34	0		0	0	2
	NI	11	0		0	0	0
	SN	12	1		1	1	1
Total		57	1		1	1	3: 63
F4	NU	1	0	5		0	0
	NI	1	0	0		0	0
	SN	2	2	1		0	0
Total		4	2	6		0	0: 12
F12	NU	13	2	7	2		0
	NI	0	0	0	0		0
	SN	3	4	1	4		1
Total		16	6	8	6		1: 37
F31	NU	5	3	7	0	0	
	NI	0	1	2	1	0	
	SN	0	0	0	0	0	
Total		5	4	9	1	0	: 19

NU = "Nuzzle", NI = "Nibble", SN = "Sniff". Amounts in 150 h of observation, behaviour of females on left side directed towards females above.

and "Scentmark" can be taken as indicators of arousal of the animals (cf. Korz and Hendrichs 1989). The higher the frequency the more the animal is aroused. By multivariate analysis (correspondence analysis) of occurring frequencies these behavioural elements are ordered along an "axis of intensity", decreasing from "Bury" to "Tremble", the elements indicating different states of arousal. Frequencies of the less intense behaviour "Lick", "Nibble-of-bodysides" and "Tremble" of F2 correlate with the RIs towards F1, F3 and F4 (cf. Table 5). Frequencies of the less intense behaviour "Lick" of F12 correlate with the RIs towards F2. Frequencies of "Lick", "Nibble-of-bodysides" and the more intense behaviour "Scrape" of F31 correlate with the RIs towards F12. All correlation coefficients of behaviour of F4 are negative, the high intense behaviour "Bury" significantly correlating with RIs towards F2. There are no significant correlations of behavioural elements in F1 and F3.

Female-young relationships

Concerning maternal behaviour towards own and other young (up to an age of six months) F2 was of marked individuality, the amount of "Anal-licking"/ young is more than thrice as high (6.75) as the second-highest frequency towards own young (2.00, F1) and nearly ten times as high (5.40) as the second-highest frequency towards other young (0.56, F4). The relatively high frequencies of "Anal-licking" in the subadult females F12 (1.20) and F31 (2.90) probably result from play-like behaviour; these females are inexperienced yet in raising their own young. The frequency of "Chase" (2.18) and "Bite-attempt" (5.55) that F2 displayed towards young other than her own is the lowest of all females, ranging from

Table 3. **Indices of retreat for the pairs of females**

	F1/F2	F2/F1	F1/F12	F12/F1	F2/F3	F3/F2	F2/F4
June	0.87	0.13	1.00	0.00	0.13	0.87	0.04
July	0.82	0.18	0.90	0.10	0.13	0.87	0.04
August	0.35	0.65	1.00	0.00	1.00	0.00	0.80
September	0.47	0.53	1.00	0.00	0.85	0.15	0.08
October	0.00	1.00	–	–	0.50	0.50	0.10
November	–	–	–	–	–	–	–
December	0.50	0.50	–	–	–	–	0.08
January	–	–	–	–	–	–	–
February	–	–	–	–	–	–	–
March	0.56	0.44	0.92	0.18	0.85	0.15	0.83
April	0.40	0.60	1.00	0.00	0.84	0.16	0.83
May	0.85	0.15	1.00	0.00	0.20	0.80	–
June	0.33	0.67	1.00	0.00	0.00	1.00	0.62

	F4/F2	F2/F12	F12/F2	F4/F12	F12/F4	F12/F31	F31/F12
June	0.96	0.61	0.39	1.00	0.00	0.04	0.96
July	0.96	0.00	1.00	1.00	0.00	0.00	1.00
August	0.20	0.60	0.40	0.80	0.20	0.10	0.90
September	0.92	0.50	0.50	–	–	0.00	1.00
October	0.90	0.37	0.63	–	–	0.00	1.00
November	–	0.00	1.00	–	–	0.00	1.00
December	0.92	0.00	1.00	1.00	0.00	–	–
January	–	–	–	–	–	–	–
February	–	–	–	1.00	0.00	–	–
March	0.17	0.43	0.57	–	–	0.00	1.00
April	0.17	0.09	0.91	0.25	0.75	0.00	1.00
May	–	0.00	1.00	–	–	0.00	1.00
June	0.38	0.00	1.00	–	–	0.00	1.00

The indices refer to the first specified female. For less than five retreats no index was computed (–). Pairs of females with less than six indices were not taken into account.

2.49 (F4) to 15.40 (F1) of "Chase" and from 5.78 (F4) to 8.63 (F12) of "Bite-attempt". In all females the frequencies of "Nibble" were higher towards own (F1: 7.50, F2: 8.25, F3: 4.00 and F4: 5.00) than towards other young (F1: 0.75, F2: 1.20, F3: 0.25 and F4: 1.70). Figure 4 shows the frequencies of all agonistic and contact behaviour that the females directed towards young. F2 displayed significantly more contact behaviour towards young other than her own than any of the other adult females, and she is the only female displaying more contact than agonistic behaviour towards other young. Towards own young F2 showed significantly more contact behaviour than F3 and F4 (Fig. 4). Regarding all young, F2 displayed significantly more contact behaviour (76.20/y) than F1 (47.20/y), $Chi^2 = 6.82$, $p < 0.01$); F3 (17.50/y, $Chi^2 = 36.77$, $p < 0.001$) and F4 (23.20/y, $Chi^2 = 28.26$, $p < 0.001$); (Chi^2-test, two-tailed, df = 1).

Discussion

The preference of M1 for F1 (cf. Fig. 2) and the nearly whole absence of threat behaviour of F1 towards M1 (cf. Fig. 3) point to a specific relationship. The exclusive occurrence of "Nibble" between M1 and F1 in addition indicates a pair-bond, not restricted to times of estrus. Lamprecht (1973) and Wickler (1976) demand the exclusive occurrence of at least one behaviour restriced to pair members. Smythe (1978) in the field observed mutual

Table 4. **Correlation coefficients for the monthly indices of retreat and frequencies of agonistic behavioural elements between the females**

	F1/F2 N = 10	F1/F12 N = 8	F2/F1 N = 10	F2/F3 N = 9	F2/F4 N = 9	F2/F12 N = 9
CH	0.21	−0.09	–	–	–	–
JO	−0.27	–	0.43	0.25	0.07	0.19
HT	0.05	–	–	–	–	–
HR	−0.07	−0.15	0.54	0.63	0.12	–
BA	0.15	0.26	0.27	0.51	0.25	0.78***
	F3/F2 N = 9	F4/F2 N = 9	F4/F12 N = 6	F12/F2 N = 11	F31/F12 N = 10	
CH	–	0.89***	−0.35	0.67**	0.06	
JO	−0.23	−0.11	–	−0.19	0.38	
HT	–	0.69*	–	–	0.21	
HR	0.52	0.21	0.48	0.50	0.33	
BA	0.43	0.75**	0.30	0.31	0.68*	

CH = "Chase", JO = "Joust", HT = "Head-thrust", HR = "Head-raise", BA = "Bite-attempt". Spearman-rank-correlation-test (two-tailed); *: $p < 0.05$, **: $p < 0.02$, ***: $p < 0.01$. For less than four monthly frequencies of behaviour other than zero no coefficient was computed. Coefficients refer to the first specified female. Frequency: average amount of behavioural element per hour.

Table 5. **Correlation coefficients for the monthly indices of retreat and frequencies of behavioural elements indicating arousal**

	F1/F2 N = 10	F1/F12 N = 8	F2/F1 N = 10	F2/F3 N = 9	F2/F4 N = 9	F2/F12 N = 9
BU	−0.20	0.20	0.26	0.42	−0.38	0.28
SP	−0.30	0.26	0.30	−0.36	−0.30	−0.27
SC	−0.08	0.15	0.30	0.06	0.37	0.20
NB	−0.26	0.07	0.43	0.69**	0.67*	0.25
LI	0.03	0.15	0.63*	0.10	0.50	−0.04
TR	−0.13	0.03	0.51	0.44	0.67*	0.01
SM	−0.16	0.32	−0.06	−0.17	−0.11	−0.23
	F3/F2 N = 9	F4/F2 N = 9	F4/F12 N = 6	F12/F2 N = 11	F31/F12 N = 10	
BU	0.48	−0.63 p = 0.06	−0.85***	−0.12	−0.33	
SP	0.42	−0.37	−0.33	0.56 p = 0.07	0.62 p = 0.05	
SC	−0.21	−0.19	−0.68	0.11	0.51	
NB	0.31	−0.59 p = 0.09	−0.51	0.53 p = 0.09	0.68***	
LI	0.41	−0.25	−0.33	0.69 p = 0.01	0.62 p = 0.05	
TR	−0.06	−0.19	−0.33	0.25	0.52	
SM	0.29	−0.19	−0.33	0.42	0.00	

BU = "Bury", SP = "Scrape", SC = "Scratch", NB = "Nibble-of-bodysides", LI = "Lick", TR = "Tremble", SM = "Scentmarking". Spearman-rank-correlation-test (two-tailed); *: $p < 0.05$, **: 0.04, ***: $p < 0.03$. Coefficients refer to the first specified female. Frequency: average amount of behavioural element per hour.

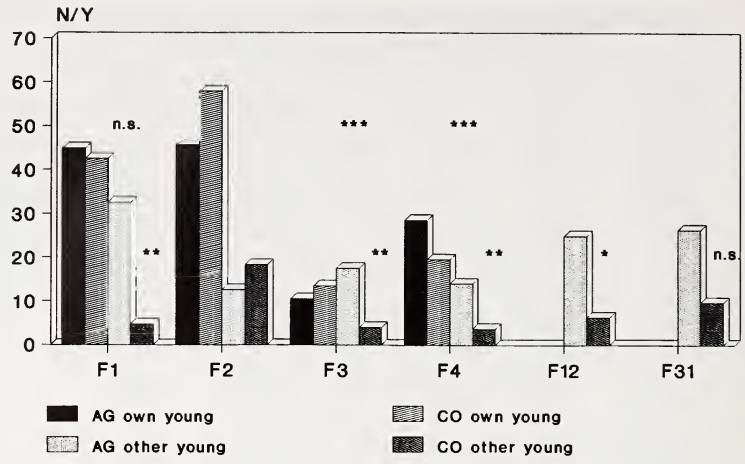

Fig. 4. Frequencies of agonistic and contact behaviour (including "Following in close distance" and "Retrieving") the females directed towards own and towards other young (frequency: average amount of behaviour per young). AG own young: agonistic behaviour towards own young, CO own young: contact behaviour towards own young, AG other young: agonistic behaviour towards other young, CO other young: contact behaviour towards other young. The statistical tests for the frequencies of contact behaviour of the specific females refer to the frequencies of F2. For own young: Chi^2-test (two-tailed, df = 1): * $p < 0.02$, ** $p < 0.01$, *** $p < 0.001$; for other young: Binomial test (two-tailed): * $p < 0.02$, ** $p < 0.01$

grooming of the ear region only in paired agoutis. This behaviour probably corresponds to "Nibble" described here. In addition to the preferences of F1 and F3 for each other (cf. Table 2) the existence of a mutual attachment is indicated by the nearly exclusive occurrence of "Nibble" with regard to the nearly complete absence of this behaviour between the other females (Table 2). It is assumed that, after the phase of expulsion of immature animals, females no longer recognise the young animals as their offspring. Smythe (1978) observed that both sexes harass any subadult they meet, even the progeny of adjacent territory-holders on their parents' territories. Nevertheless the attachment between F1 and F3 may be attributed to an enduring activation of components of mother-young-attachment.

The exaggerated display of maternal behaviour of F2 extended to young other than her own (cf. Fig. 4) points to a readily activated maternal state in this female, going along with higher frequencies of agonistic behaviour towards the other females. F2, F31, F12 and especially F4 enforced retreat of other females by agonistic efforts. F4 employed higher escalated agonistic behaviour ("Chase" and "Head-thrust") towards F2. Similar to F12 ("Chase") (cf. Table 4), F31 uses less escalated agonistic behaviour ("Bite-attempt") towards F12.

These different social relations and reactions can be seen as specific activations of motivational and behavioural programmes, which enable the females to cope with their specific social situation. In addition to the different relations and reactions, the females showed different levels and states of arousal. F2, F12 and F31 were aroused more and specifically in their efforts to gain and maintain superiority, showing higher frequencies of specific arousal indicating behaviour with increasing RIs (cf. Table 5). F4 was highly and specifically aroused when subordinated to F2 and F12 with less agonistic display, showing higher frequencies of "Bury" with decreasing RIs. There are two possible explanations for the absences of agonistic efforts in F1 and F3 to maintain superiority (cf. Table 4) and for changes in their superiority without corresponding changes in levels and states of arousal

(cf. Table 5): a) The attachment of F3 to F1 and the established pair-bond between F1 and M1 implied so much security in these females that changes in superiority were not of central importance to them; or b) No changes in dominance occurred; retreating in these females does not imply subordination, but their social attachments secure them in such a way that an agonistic effort is not always necessary to demonstrate their dominance.

The maternal state activated by F2 as soon as young were present also provides a source of security, but not to such an extent as the long-lasting attachments for F3 and especially for F1. Although maternal behaviour was of high intensity, including "defence" of the young, it still was adequate and functional. F2 showed more "Anal-licking", contact behaviour and especially "Nibble" towards her own than other young. The persistent orientation towards young and, when present, the perception of other young may "switch on" motivations (and possibly physiological processes) related to the maternal state leading to an incomplete form of a mother-young-attachment. Salzen (1978) discusses that "impoverished or stunted attachments will give exaggerated orientation behaviours". Such mechanisms are supposed to be relevant for F2 in relation to other young.

A specific activation of aggressive motivation occurred in females F4, F12 and F31. This activation showed less with respect to amounts of agonistic behaviour, but more in a persistent orientation towards keeping other females at distance. Especially in F4 this specific activation is assumed to correspond to her lack of social and spatial attachments. Henry and Stephens (1977) report that mice, not able to form territorial and social attachments, engage in a chronic struggle for dominance, accompanied by high arousal, which can lead to pathologic changes in organs and physiological reactions. For F4, which came into this group as a nearly adult female, it can be supposed that her spatial orientation as well as her familiarity with the other females, even after several years living in the enclosure, is still different from those of the other females born in this enclosure. It remains to be investigated whether and how the mechanisms described can be related to specific behavioural and motivational components of the species' natural equipment for a pair-bond. It seems possible, however, that specific components were overactivated to compensate short-comings of the non-pair-bonded females to such an extent that stress could be held low or moderate and regular reproduction remained possible.

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Zusammenfassung

Soziale Beziehungen und individuelle Bewältigungsreaktionen in einer Gehegegruppe mittelamerikanischer Agutis (Dasyprocta punctata)

Es wurde eine Gehegegruppe mittelamerikanischer Agutis, bestehend aus 20 Tieren, beobachtet. Die individuellen Situationen und Reaktionen der Weibchen in der Gruppe sollten erfaßt werden. Es bestand eine Paarbindung zwischen dem adulten Männchen und dem ältesten Weibchen F1 sowie eine gegenseitige Bindung zwischen F1 und ihrer adulten Tochter F3. Eine weitere adulte Tochter (F2) zeigte übertriebenes mütterliches Verhalten sowohl gegenüber den eigenen als auch gegenüber den Jungtieren der anderen Weibchen. F2 und deren subadulte Tochter sowie eine subadulte Tochter von F1 und ein nicht in der Gruppe geborenes adultes Weibchen zeigten keine dauerhafte soziale Bindung. Für diese vier Weibchen korrelierten die Häufigkeiten von einigen agonistischen Verhaltensweisen und von Erregungsindikatoren mit ihren Ausweichhäufigkeiten gegenüber bestimmten Weibchen. Dieses weist auf eine spezifische Aktivierung aggressiver Motivation, begleitet von spezifischen Erregungszuständen, hin. Es wird die Hypothese aufgestellt, daß sich in der Aktivierung und teilweisen Überaktivierung spezifischer Motivationen und Verhaltensbereiche diese individuellen Reaktionen entwickelten, über die die spezifischen sozialen Situationen der Weibchen zu bewältigen waren. Diese Mechanismen ermöglichten eine Gruppensituation, in der die Belastungen der Tiere mäßig blieben und eine regelmäßige Reproduktion möglich war.

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