



Social dominance and bodily conditions in small groups of male and female laboratory rats of known familiarity

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Abstract

Studied was the significance of relationships between characteristics of behaviour, competition and bodily conditions for the social dominance rank in rats. Adult virgin male and female rats of the inbred strain DA of known familiarity membership were studied. In groups of three rats 6 behavioural categories per animal were registered on 6 test days and the competition success in water, food and runway tests was determined. The body and 6 organ masses were measured and the levels of 3 β -hydroxysteroid dehydrogenase (HSDH) and 5 α -reductase (REDU) activity in the liver and corticosterone were determined in blood. In females, significant correlations existed between the parameters appeasement behaviour, successful food competition and low corticosterone and HSDH levels. Aggressive activity occurred between females to almost the same extent as between males, but was not correlated to the other characteristics. By contrast, in males high aggressive behaviour, successful water and food competition were closely related. In addition, high body and organ masses influenced the experimental outcome to a greater extent than behavioural gestures. Only males showed significant familiarity differences in body mass and organ masses of heart, kidneys and adrenals. In females, appeasement behaviour and successful coping against stress proved to be prerequisites for achieving high dominance ranks whereas a good bodily condition and aggressiveness was the case for males.

Introduction

Functionally, social dominance is preferentially defined as the acceptance of priority distribution between animals in a number of goals (HAND 1986; ADAMS and BOICE 1989). Conceptually, dominance is increasingly understood as a property of a relationship and not as an individual character of a certain animal (BARRETTE 1993; BERNSTEIN 1981; MOORE 1993). DREWS (1993) defined social dominance operationally as a complex relationship between individuals, which cannot be adequately described by individual terms such as aggressiveness, bodily strength or stress resistance. According to DREWS (1993), agonistic interactions however represent a particularly major dominance factor.

Because male rats are considered to be more highly motivated towards aggressiveness and sexuality than females (MATUSZCZYK and LARSSON 1993; POOLE and FISH 1976; TIMMERMAN 1978), dominance tests were preferentially carried out on these. The frequencies of aggressiveness and submissive behaviour and copulation were often recorded as the decisive and quantifiable dominance measures. Such behavioural contrasts do not only determine the social structures between the animals, but also their physiological condition (HOLST 1990).

As yet, however, only few comprehensive studies for intact female rats exist, which, apart from social parameters (BLANCHARD et al. 1984; ZOOK and ADAMS 1975) have also in-

cluded somatic and biochemical characteristics at the same observation time. Such intercorrelations, however, are necessary in order to differentiate between the effects of bodily conditions, stress and agonistic activity on dominance ranks. The aim of the present study is to investigate under laboratory conditions whether aggressive behaviour as well as other social or competitive gestures are significantly correlated with somatic characteristics. In addition, it was of interest whether the decisive dominance factors are equal in male and female rats. The extent to which the definition of dominance according to DREWS (1993) is generally applicable, can only be assessed after obtaining such information.

Studies on genetically defined animals are also expected to produce results as to whether the complex correlations between behavioural arousal and activation of the sympathetic-adrenal axis (e.g. HENRY and STEPHENS 1977; HOLST 1990; KORZ 1991, 1993; SACHSER 1994) can be demonstrated in a similar manner in male and female rats.

Also, the family membership of animals in this study was known, allowing first orientating results on individual genetic effects to be presented, as previously demanded by BARRETTE (1993) and DEWSBURY (1990).

Material and methods

Animals

Nine virgin male and female agouti-coloured DA-ZTM-rats (Breeder: Laboratory Animal Science Unit, Medical University of Hannover, Germany), 78 days old on arrival, were used. The animals originated from 7 different families (A, B, C, Af, Bf, Cf, Df) with identical birth dates and were ear-marked individually for identification.

From the time of arrival to the end of training (Fig. 1), the animals were kept singly in polycarbonate (Makrolon) cages type III (39×23×15 cm). During the entire period of the experiment, rats were maintained in groups in Makrolon type IV cages (55×33×20 cm) and kept under standardized conditions (room temperature: $21 \pm 2^\circ\text{C}$; relative humidity: $50 \pm 5\%$; feed: pellets type 1324, Altromin Lage/Lippe, Germany) and water ad lib. under an inversed light cycle (artificial light 19.00–8.00 h; 40 W dimmed red-light during the dark).

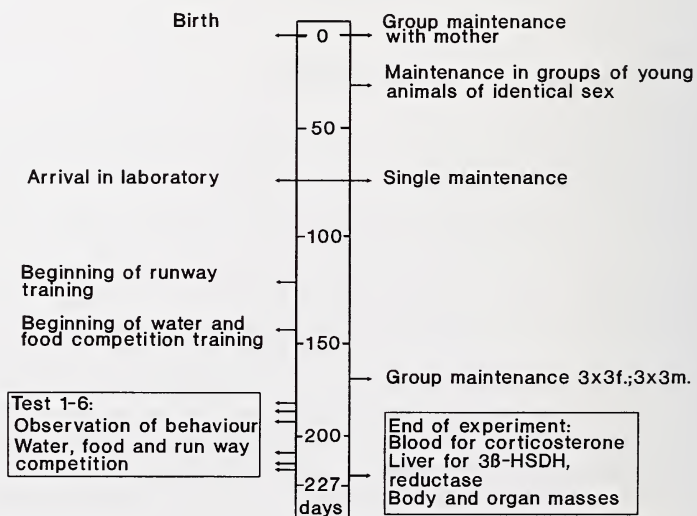


Fig. 1. Experimental design – In relation to age of rats in days, conditions of maintenance, training period, dominance tests and post-mortem evaluations (m. = male, f. = female).

All studies were carried out between July 1985 and February 1986 in accordance with the regulations of the German Animal Protection Law, 1972. Some findings for male rats, especially on sexuality, have already been published (MILITZER et al. 1984).

Training procedure

During this time the animals were kept individually in order to learn the competition tests without external influence. Training for the competitive experiments was carried out during the dark phase 8.00–13.00 h. Runway training was initiated 55 days after arrival of the rats (Fig. 1). Each of the rats, starved for 22 h, was allowed to acquaint itself with the runway, whose gates were open, in the first 3 days for 4 min per day. The rats were then trained by allowing them to hurry into the alley after opening the start box gate and to wait for 3 sec at the central gate. Upon opening, animals ran into the goal box opposite, where they were rewarded with a food pellet.

Seventy days after arrival, the conditioning of the rats to the food and water competition test box (Makralon type IV, 55×33×20 cm) was initiated. Ten times within 35 days, the animals were placed separately into the testbox. Through a 3.2 cm diameter hole in the small side of the box they were able to drink for a maximum of 2 min from an externally positioned water bottle.

Subsequently, food in the form of powder diet (type 1321, Altromin Lage/Lippe) was offered contained in a 7 cm high metal case (diameter 2.7 cm) fastened vertically to the floor in the middle of the cage. For each training time, the animals individually had 3 min time to take up food (for types of the test cages, see: MILITZER et al. 1984).

At the end of the training, at 183 days of age, the rats were individually marked by colouring the hair and divided into groups of three of the same sex, i. e. 3 female and 3 male groups. These groups remained unchanged throughout the experiment. The first rank test was carried out on the following day.

Test design

With the exception of the runway test, the behaviour observations and the competition tests were always carried out in the home cage. For each group of rats on the same day the following 4 test methods were carried out 6 times at intervals of 5 days to two weeks (Fig. 1). The sequence of tests remains constant, although the test was always started with another group.

a) Observation of social behaviour

During the first 10 min under dark phase conditions, the behaviour of the 3 rats in each cage was tape-recorded, always by the same observer (8.00–9.30 h). The frequency of 34 distinct behavioural elements per animal were registered and combined in major categories (LEHMAN and ADAMS 1977; SILVERMAN 1978).

Aggressive behaviour: bite and kick, full aggressive, offensive upright and sideways postures,

Submissive behaviour: defensive upright and sideways posture, submission,

Social exploration: nose, back, anal and tail sniffing,

Autogrooming: face, side, anal grooming, scratching,

Allogrooming: kick or comb body fur of another rat,

Threat behaviour: teeth exposed, turn of head towards to another rat,

Escape behaviour: retreat, fleeing and crouching.

b) Water and food competition test

The thirsty animals (28.5 h water deprivation) were offered water for 3 min. Only one rat could reach the water bottle through the wall hole at any time. Before the beginning of the food test, the container with powder diet was fixed in the centre of the home cage and the entrance to food was opened for 5 min by means of a pole operated from the outside. The drinking and feeding time per rat and test was recorded by 2 observers using a stop clock. These times were converted to their natural logarithms and evaluated. The tests were repeated after 1.5 h (from 10.00–13.00 h).

c) Runway test

Two animals from each group were tested for 2 min in an alternative and randomized order. Simultaneously from both start boxes, the rats were released into the runway. The animals met at the central gate and attempted to push each other off the alley. The rat that pushed the defeated animal back into

its start box was the winner. With a single repetition 1.5 h after the first test, 6 runs per group and day were conducted. The mean time required to oust the rat starting from the opposite side was determined (from 14.00–17.00 h).

d) Morphology and biochemistry

One day after the last rank test the rats were sacrificed by decapitation (8.00–9.30 h). The animals were bled no later than 100 sec after the first cage contact. Blood serum (0.5 ml) was collected and stored at -20°C . Corticosterone was determined fluorimetrically (STAHL et al. 1963). The corpses were autopsied and the following organs were dissected and weighed: thymus, heart, liver, spleen, kidneys, and adrenals. The activity of 3β -hydroxysteroid dehydrogenase (HSDH) and 5α -reductase (REDU) was determined in cold perfused liver tissue (LAX et al. 1976; SCHRIEFERS et al. 1971).

e) Biostatistical analysis of data

The main interest focussed on the presentation of the relations between the characteristics for the overall experiment and not on the description of individual rank relations. Since no normal distribution was to be expected above all in the behavioural data, only the coefficients of variation were calculated for all characteristics. Thus, no SD's are shown in figures 2 and 3. In the first step, means and coefficients of variation for each characteristic and sex were calculated from the absolute frequencies. Correlations (Spearman's r) between the observed characteristics irrespective of group from the overall experiment were evaluated. In accordance with others (ASPEY and BLANKENSHIP 1977) a principal-component factor analysis with rotation of factors by the Varimax procedure was included.

Finally, the morphological data of individually known animals were grouped according to their family membership. They were checked by Student's t -test because they are distributed normally in contrast to the ethologic data.

Results

The major characteristics during the course of the tests are exemplified in figures 2 and 3. An increase in behavioural activities was observed for up to 2 weeks after group combination, after which no differences are seen at the various test days. The means for drinking time and food uptake show a similar pattern (Fig. 3). For trained rats, the passage times in the runway are roughly similar over the experimental period. Apart from the expected sex difference, body mass shows regular increases except during the initial test week. From the course of the curves in figures 2 and 3, the summary of data for the overall experimental period appears justified (Tab. 1).

An examination of the group means shows only slight differences between the average behavioural activities of males and females. They differ merely in the longer duration of food uptake in the case of females in the competition tests although the differences are not statistically different. For behavioural and competition parameters, aggressive behaviour in both sexes shows the largest variance with variation coefficients of 95 and 100%. In females submissive behaviour and allogrooming with threat are also characterized by large coefficients. In addition, the larger spread in competition test results in males is indicative of considerable individual differences.

The known sex and body mass dependent differences are apparent from the morphometrical data in table 1. Thus, body mass and the organ masses of heart, liver, kidneys and spleen are considerably larger in males than in females. By contrast, the heavier adrenals and thymi are found in females. The coefficients of variation for body and organ masses are less than 12%. In males, the larger coefficient of variation for body mass at the start of the experiment differs from that of the females by 10%. Sex differences are also seen in the higher corticosterone and reductase levels in females and higher liver HSDH activities in males. The coefficients range between 3.4 and 129.5%. The latter extreme value is explained by the fact that the reductase activity was below the level of detection in 7 male rats.

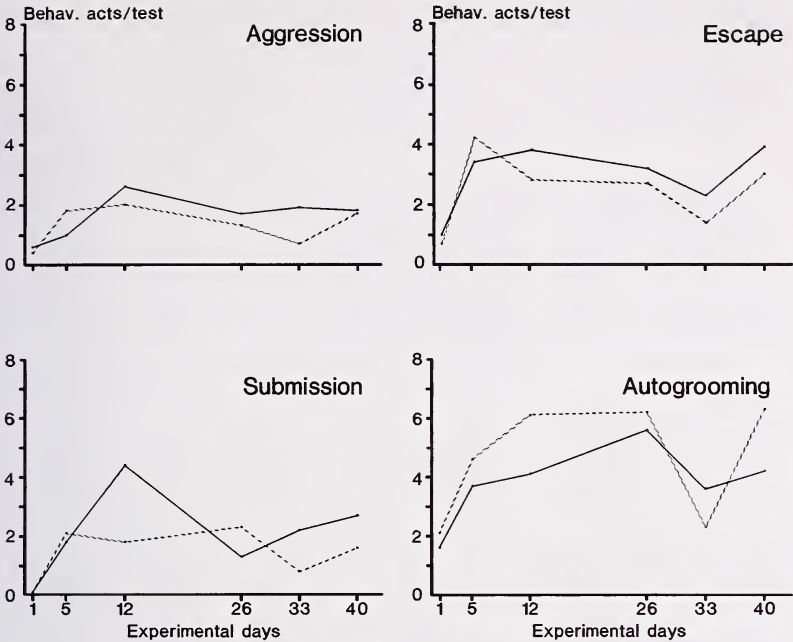


Fig. 2. Means of behavioural acts per experimental day and sex group for male (—) and female (---) DA rats on the 6 test periods

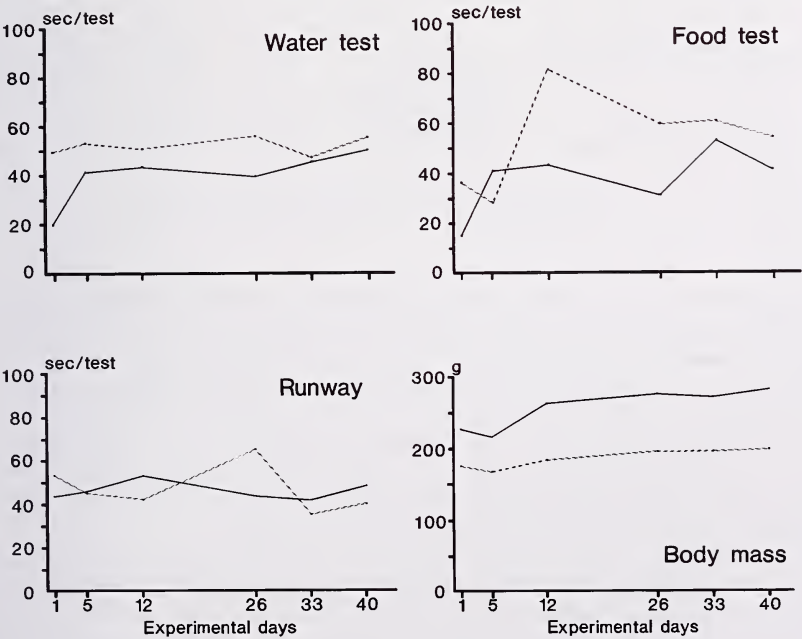


Fig. 3. Means of the competition test results per experimental day and sex group and development of body mass (details see figure 2)

Table 1. Group means and coefficients of variance of all behavioural, competitive and somatic characteristics

No.	Terms/Abbreviation	Dimension	Group means ($\bar{x}$)		Variation coefficients in %	
			Female	Male	Female	Male
Behaviour						
1	Aggression = AGGR	Behav. frequency/test	1.3	1.6	100.0	95.0
2	Submission = SUBM	Behav. frequency/test	1.4	2.1	71.4	52.4
3	Social exploration = SOEX	Behav. frequency/test	6.4	5.6	25.0	34.4
4	Autogrooming = AUTO	Behav. frequency/test	4.6	3.8	43.5	52.4
5	Allogrooming/threat = AGOO	Behav. frequency/test	1.4	2.1	71.4	52.5
6	Escape = ESCA	Behav. frequency/test	2.4	2.9	46.2	45.7
Competition test results						
7	Water test = WATE	Success in s/test	51.6	45.1	66.9	71.4
8	Food test = FOOD	Success in s/test	63.6	36.4	51.4	61.5
9	Runwaytest = RUNW	Runtime in s/test	46.8	46.0	47.4	65.0
Morphometry						
10	Body mass at start = BMAS	g	66.5	72.7	8.7	18.7
11	Body mass at end = BMEN	g	198.9	282.4	2.8	8.2
12	Heart mass = HERT	mg	633	857	5.3	8.2
13	Liver mass = LIVE	mg	6 097	10 144	7.2	8.3
14	Kidney mass = KIDN	mg	1 310	1 788	5.2	7.9
15	Adrenal mass = ADRE	mg	48	34	11.6	8.8
16	Thymus mass = THYM	mg	151	111	12.3	9.9
17	Spleen mass = SPLE	mg	327	398	5.9	9.3
Biochemistry						
18	Plasma corticosterone = CORT	$\mu\text{g/ml}$	0.49	0.28	42.3	39.1
19	5 α -reductase = REDU	nmol/min/mg microsomal protein	29.7	7.29*	3.4	129.5*
20	3 β -hydroxysteroid-dehydrogenase = HSDH	nmol/min/mg microsomal protein	2.79	9.33	15.0	9.7
Note: Number of animals n = 9, * n = 2						

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From the total of 9 behavioural and competition characteristics studied, 10 significant correlations are found for females, but only 2 for males. In females, social exploration is negatively correlated with allogrooming, escape and drinking time in the water competition test ($F = 16$, $r = 0.73$ – 0.90 , $p < 0.05$). Success in water competition is correlated with long runway times i. e. failure in runway test ($F = 16$, $r = 0.78$, $p < 0.05$). Female rats successful in food competition often show defensive behaviour such as submission, allogrooming and escape behaviour ($F = 16$, $r = 0.72$ – 0.74 , $p < 0.05$). Males only show significant positive correlations between aggression and water competition as well as the latter and food competition ($F = 16$, $r = 0.73$ and 0.77 , $p < 0.05$).

Vice versa, there are only 5 significant correlations between the morphological and biochemical data and the results of the competition tests in the case of females, but 8 for males (Tab. 2). The organ masses of heart, kidneys and spleen are correlated with the initial body mass of males and those of heart, kidneys, liver and spleen among themselves (Tab. 2: No. 1 to HERT, KIDN, SPLE; No. 3, 4 to KIDN and SPLE; No. 5 to SPLE). Females only show a positive correlation between body mass at the beginning and end of

Table 2. Correlation coefficients of the absolute data for body and organ masses, biochemical and competition test results in female and male rats

No.	Abbr.*	Sex	Morphometry					Biochem.				Competition				No.
			BMEN	HERT	LIVE	KIDN	ADRE	THYM	SPLE	CORT	REDU	HSDH	WATE	FOOD	RUNW	
Morphometry																
1	BMAS	f.	.68	-.19	-.29	-.36	-.28	.54	-.02	.90	-.04	-.03	-.60	.35	-.51	1 f.
		m.	.17	.70	.53	.83	.25	.42	.74	-.11	-	-.14	-.15	-.08	.27	m.
2	BMEN	f.	-	.36	-.20	.09	-.26	.39	.35	.79	.03	.59	-.26	.19	-.19	2 f.
		m.	-	.59	-.08	.36	.57	.17	.32	-.09	-	.50	-.07	.19	-.25	m.
3	HERT	f.	-	-	-.13	.24	-.39	-.32	.28	-.01	.53	.66	.41	-.06	.21	3 f.
		m.	-	-	.49	.88	.64	.38	.72	-.13	-	-.12	-.16	.15	-.02	m.
4	LIVE	f.			-	.54	.11	-.47	.11	-.21	-.22	-.16	.42	.16	.42	4 f.
		m.			-	.77	.38	.38	.85	-.31	-	.21	.61	.61	.59	m.
5	KIDN	f.				-	.53	-.66	.62	-.05	-.24	-.04	.63	-.26	.64	5 f.
		m.				-	.63	.49	.89	-.28	-	-.06	.16	.27	.35	m.
6	ADRE	f.					-	-.29	.32	-.08	-.24	-.53	.41	-.01	.59	6 f.
		m.					-	.22	.49	-.53	-	-.02	.26	.27	-.08	m.
7	THYM	f.						-	-.08	.29	-.29	.27	-.69	.12	-.73	7 f.
		m.						-	.33	.41	-	-.55	-.01	.15	.64	m.
8	SPLE	f.							-	.17	-.36	.26	.39	-.17	-.06	8 f.
		m.							-	-.41	-	-.07	.42	.49	.35	m.
Biochemistry																
9	CORT	f.								-	.12	.14	-.37	.39	-.18	9 f.
		m.								-	-	-.18	-.52	-.06	.08	m.
10	REDU	f.									-	.19	.23	.49	.37	10 f.
		m.									-	-	-	-	-	m.
11	HSDH	f.										-	-.17	-.16	-.24	11 f.
		m.										-	.13	.20	-.29	m.

Note: Significant coefficients with $p \geq 0.05$ (*italic*); * abbreviations see table 1

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the experiment; both characteristics are positively correlated with the corticosterone level. A low thymus mass is seen in females successful in the water test and those defeated in the runway test (Tab. 2: No. 1 to BMEN, CORT; No. 7 to WATE, RUNW).

The results of factor analysis shown in table 3 are not biased by triangular correlations, e.g. between the body mass and the other somatic characteristics as are the linear correlations in table 2.

Factor I exclusively describes the behavioural characteristics in females and is positively loaded through submission, allogrooming and escape as well as the outcome of food competition. As in males, social exploration is negatively loaded and thus opposite to the defensive behavioural activities in females. In males, characteristics of bodily condition such as body mass at start, masses of kidneys and spleen are positive in Factor I while the frequency of social exploration is negative (Tab. 3: No. 3, 10, 14, 17). The total variance in the experiment for both sexes can be mainly explained by factor I.

Factor II contains the result of water competition and autogrooming for males and females. In addition, the kidney mass and runway time are positively loaded for females, while body mass at start, thymus mass and corticosterone level are negative in this factor (Tab. 3: No. 4, 7, 9, 10, 14, 16, 18). For males, factor II becomes positively loaded by the parameters aggressive behaviour and autogrooming, the result of water and food competition and liver mass.

In factor III for females, aggression is negatively loaded while heart mass and the HSDH activity are positive. Defensive categories of behaviour such as submission, allogrooming/threat and escape are found in the case of males. Of the three factors, III possesses the least significance for the total variance in the experiment and is in no way correlated with the competition results in both sexes.

Table 3. Results of the orthogonal factor analysis (Varimax) for all test characteristics, separately evaluated for female and male rats

No.	Characteristics	Factor I		Factor II		Factor III		No.
		Female	Male	Female	Male	Female	Male	
1	Aggression	-.13	-.24	.25	.63	-.71	-.07	1
2	Submission	.93	.41	.11	-.20	-.06	.69	2
3	Social exploration	-.81	-.83	-.51	.23	.08	-.03	3
4	Autogrooming	.21	.11	.62	.70	.04	-.19	4
5	Allogrooming/threat	.93	.41	.11	-.20	-.06	.69	5
6	Escape	.83	-.14	.04	-.58	-.25	.68	6
7	Water competition	.47	-.05	.84	.95	.20	-.08	7
8	Food competition	.89	-.04	-.24	.77	-.06	.09	8
9	Run way competition	.43	.46	.74	.42	-.02	-.26	9
10	Body mass at start	.19	.92	-.84	-.05	-.02	.13	10
11	Body mass at end	.14	.20	-.55	-.17	.56	.55	11
12	Heart mass	.11	.35	.23	.01	.95	.29	12
13	Liver mass	.23	.58	.36	.72	-.27	.13	13
14	Kidney mass	.04	.85	.66	.28	.10	.42	14
15	Adrenal mass	.16	.30	.53	.29	-.48	.56	15
16	Thymus mass	-.20	.60	-.77	-.05	-.02	.03	16
17	Spleen mass	.13	.72	.22	.46	.27	.31	17
18	Corticosterone	.37	-.08	-.67	-.53	.12	-.26	18
19	5 α -reductase	.55	—*	.01	—*	.42	—*	19
20	3 β -HSDH	-.16	-.41	-.29	.60	.79	-.08	20

Note: High factor loadings $\geq .60$ (*italique*); n = 9, * n = 2

Table 4. Means of the absolute body and organ masses in families of female and male rats

No.	Characteristics	FEMALES			MALES				
		Family Bf (n = 4)	Sign. a)	Family Cf (n = 3)	Family A (n = 3)	Sign. a)	Family B (n = 3)	Sign. a)	Family C (n = 3)
1	Body mass at end	g							
		197	n. s.	201	271	n. s.	305	*	271
2	Heart mass	mg							
		629	n. s.	625	805	*	936	*	830
3	Liver mass	mg							
		6 376	n. s.	5 935	10 201	n. s.	10 340	n. s.	9 891
4	Kidney mass	mg							
		1 310	n. s.	1 301	1 740	n. s.	1 925	*	1 698
5	Adrenal mass	mg							
		47	n. s.	48	33	*	36	n. s.	34
6	Thymus mass	mg							
		143	n. s.	167	103	n. s.	119	n. s.	112
7	Spleen mass	mg							
		325	n. s.	336	397	n. s.	424	n. s.	374

Note: n = number of rats; a) t-test: n. s. = no significance, * = $p \geq 0.05$

Since in the case of females there was only one representative from family Af and Df, only the 2 families Bf and Cf with at least 3 rats will be compared. Furthermore, since only 3 family groups could be studied in the case of males, these findings are only of an orientating nature. Table 4 shows the body and organ masses at the end of the experiment for the different families. It thus becomes clear that there are no familial differences in body and organ masses in these females. By contrast, males from families B and C show significant differences in body mass as well as heart and kidney masses. Significant differences are only seen for heart and adrenal masses between family A and B.

Discussion

Instead of the usual large collectives, where comparatively few characteristics were registered (GÄRTNER et al. 1991), as many of these as possible were studied in only small groups of rats of both sexes. Priority was given to the study on the significance of correlations in behaviour compared with other competitive and somatic characteristics. These data could only then be strictly compared and temporally evaluated in parallel in one experiment, if the number of animals was restricted to 9 per sex. Here, the significance and orientation of different characteristic relationships were tested and not the assignment of individually known social dominance ranks to somatic data. It was also important for later assessments of comparable rat groups that all studies were carried out under typical laboratory conditions. Thus, adult but sexually inexperienced rats were included in unisexual groups. All major burdens arising from prolonged deprivation, hormone injections or organectomy, usual in investigations on aggressive behaviour (ALBERT et al. 1989, 1991), were excluded. The present studies thus represent a first step towards assessing highly interwoven relations between behaviour, sex and genetics even in small laboratory animal collectives.

Sex-specific behaviour and competition in relation to social dominance

Most importantly these results show that aggressive behaviour in these female rats does not correlate with characteristics that also should reflect high dominance ranks. For example, priority of access to restricted resources is achieved by the females without correlation to agonistic activities. This is in contrast to males, where a positive correlation be-

tween aggressive behaviour and other competitive test results exists. Aggressive behaviour in females is only seen in factor III, which is the least involved in total variance of dominance in this study. This confirms the finding that aggressiveness has less decisive effects in female rats (SEWARD 1945), although no differences in the absolute frequencies of agonistic and competitive behaviour between male and female groups were seen here (ZOOK and ADAMS 1975). In addition, the only other investigation on social dominance in non-burdened female rats, where other rivalry fields apart from aggressive behaviour were studied, showed no correlation between aggression, food and water competition in high ranking females (BLANCHARD et al. 1984).

The female response in the different test situations consists of frequent defense (submission, escape) and intensive appeasement behaviour through social body contacts (allogrooming). More frequent defensive behaviour in females compared to males has already been described (SWANSON et al. 1982). These findings are also in agreement with other reports, describing the more pronounced exploration and escape behaviour (ARCHER 1975) and lower aggressive behaviour with increasing social exploration (THOR and HOLLOWAY 1982) as being typical of female rats. Females reacted with a stronger inquisitive behaviour than males. After receiving a shock treatment, they were thus more willing to reinspect the site (PRIMUS and KELLOG 1990; VAN HEST et al. 1987). Even in the present study, the females could not be prevented from endeavouring to achieve access to food despite competition. They were apparently more successful in accomplishing this through frequent appeasement behaviour than the more aggressive male rats.

By contrast, strong aggression in male rats has always been suspected to be a prerequisite for a high ranking position and successful competition for limited resources (FRANCIS 1988). In the present study, this relationship was substantiated experimentally based on the significant positive correlation between aggression and competition success (factor II). A positive but only weak significant relation between food competition and aggression has also been described for male colony rats (BLANCHARD et al. 1984). The pronounced aggressive male behaviour thus corresponded closely to the original concept of social dominance, the "peck order" (SCHJELDERUP-EBBE 1922). Even today this is considered particularly suitable because of its high descriptive value (DREWS 1993).

Apart from care of body surface in rats and primates, allogrooming, of the types of behaviour additionally determined, is thought to carry out appeasing functions following successful contact behaviour (BOLLES 1960; BEAGLEY 1976). This correlation is underlined by the similarly orientated factor loadings for allogrooming, submission and escape in factor I and III for both sexes. Allogrooming and threat behaviour can thus be considered as signs that the access to the restricted resources in a group is not determined primarily by aggressive acts. Thus, in the case of females, the mutual food uptake occurs under socially relaxed conditions although actually rivalry ought to rule. Even among non-kin animals allogrooming is considered to be tension-reducing and bond-establishing (SPRUIJT et al. 1992).

In addition, non-social behaviour such as autogrooming, scratching and digging are considered to be signs of arousal as a result of social demands (DE BOER et al. 1990; KORZ 1991). Such activation of the hypophysis-adrenal-system through the competition tasks could also be seen in some of rats studied here. In any case, the significant correlations between autogrooming and the results from water and food competition would appear to justify this interpretation. Allo- and autogrooming are never found as common loadings in factor analysis from this experiment and should thus be carefully differentiated in the evaluation of dominance tests.

Somatic, biochemical and familial dominance factors

The greatly diverging results on dominance testing in rats frequently seen by many authors can be explained by changing contextual factors (FRANCIS 1988). Such effects arise not only through methodologically different external test conditions but also through the non-uniform internal situation of the animals.

In the present study, an attempt was made to ascertain different somatic and physiological influences on social behaviour involving quantifiable characteristics. Thus, a positive correlation between metabolically active organs in terms of kidney mass in females or liver in males and the duration of water and food uptake during competition becomes apparent even in groups of three rats. However, the opposite effect, i.e. a negative correlation between liver mass and food competition has also been described in stress-burdened groups of 10 males (SNEL 1982). Nevertheless, both observations indicate that not only typical patterns of behaviour but also the metabolic situation affect the success of competition.

In contrast to ALBERT et al. (1992), the present study did not concern itself with the easily affected gonadal hormones, but instead for the first time with the hepatic microsomal enzymes, 3β -hydroxysteroid dehydrogenase (HSDH) and 5α -reductase (REDU) involved in their metabolism. Both show a sex-specific pattern. Thus, HSDH is higher in the males and shows a reversible reaction to loss of androgens. Oestradiol acts in an anti-androgenic manner, thus lowering the activity of HSDH. REDU is not dependent on the continuous presence of androgens, so that REDU-activities are many times higher in females than in males (LAX 1987; LAX et al. 1983). REDU shows no recognisable effect in either sex with respect to aggressive, submissive or competitive characteristics studied. However, above all, the low HSDH activity in females is an expression of an anti-androgenic predominance, so that aggressiveness is reduced, but the bodily activity as measured by heart mass is not affected.

In this study, the corticosterone level shows significant relations to body mass and success in water competition only in the females. Also the correlation of runway results to thymus mass shows that female rats achieve access to limited resources without becoming seriously stressed. Apparently they preferred those behaviours that avoided a stress induced activation of the hypothalamic-adrenal axis ("behavioural release mechanism" according to CONNER et al. 1971).

Effects of stress on the adrenal and thymus masses as well as the level of corticosterone related to the social situation of rats have been frequently studied (SELYE 1973; HENRY 1993). Up to now, a negative relation between "thymico-lymphatic tissue" and the adrenal mass was considered to be typical of stress (SNEL 1982; STERN and HARTMANN 1972). Further findings on male rats confirmed the relationship between heavy thymus, low corticosterone level and dominance (RAAB et al. 1986). Higher corticosterone levels occur in stressed females than in males; in this case the activity of the hypothalamus-pituitary-adrenal axis is enhanced (ALOISI et al. 1994).

In the case of males, a good bodily condition due to large body and organ masses is the first and aggressiveness is the second prerequisite for the taking up of a dominant relationship. Social behavioural gestures apparently do not decisively influence the dominance position of male rats.

The possibility of "inheritance of dominance" has recently been intensely discussed based on investigations on cockroaches, deer mice and macaques (BARRETTE 1993; DEWSBURY 1993). It was agreed that social dominance as a relationship between individuals cannot itself be inherited. Genetic differences, i.e. in aggressiveness (DREWS 1993), between individual animals, however, can influence behaviour characteristics in such a way that higher social ranks are frequently achieved above average. One then speaks of a "quasi-inheritance of dominance".

These evaluations of suitable somatic data for a few, individually known genetically uniform rats thus represent only a first attempt to register the effect of family membership and somatic characteristics on dominance. Indeed, it could be shown in the inbred males that there are significant familial differences in the body mass and organ masses of heart, kidneys and adrenals. The animals are thus organically fit to different extents and reach differing dominance ranks and finally variously high Darwinian fitness, e.g. via copulatory efficiency (GÄRTNER et al. 1981, 1989; MILITZER and REINHARD 1982). By contrast, the isogenic females from only 2 families showed no significant differences in organ masses. Since several males always commonly compete for a female in heat, such familial differences should be significant only in males with respect to reproductive success. These differences cannot be explained by chromosomal inheritance in the stringently bred isogenic DA animals. Rather, they must be an expression of very early ontogenetic variations in the embryonic plasmatype genome (GÄRTNER et al. 1991; BAUNACK et al. 1986).

The present study indicates that there is a number of combinable factors of varying context affecting social dominance behaviour in different ways between male and female rats. It is thus understandable that there is no generally accepted biological concept up to now despite an overwhelming number of studies on dominance in laboratory rats. At least two sex-specific behaviours to achieve more dominant position, however, emerge to explain these findings: Coping in stress-burdened social situations can be alleviated by behaviour minimising increased arousal (KORZ 1991, 1993; SACHSER 1994). This is the preferred method of choice in our female rats and explains the low significance of aggressiveness as dominance component. Despite stress burden, social dominance is reached through bodily superiority and aggressiveness (HENRY 1993). This applies mainly to male rats in this study. However, aggressive behaviour is only one of many factors determining dominance in males.

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Zusammenfassung

Soziale Dominanz und körperliche Kondition in kleinen Gruppen weiblicher und männlicher Laborratten bekannter Familienzugehörigkeit

In jeweils 3 individuell bekannten Dreiergruppen von weiblichen und männlichen Laborratten wurden Merkmalskombinationen ermittelt, die soziale Dominanzbeziehungen charakterisieren können. Die Ratten waren adulte, nicht verpaarte Tiere des Inzuchtstammes DA aus bekannten Familien. An 6 Testtagen wurden 6 Verhaltenskategorien je Tier und der Konkurrenzserfolg im Wasser-, Futter- und Laufgang-Test erfaßt. Am Versuchsende wurden Körpermasse, die Masse von 6 Organen, 3 β -Hydroxysteroid-dehydrogenase (HSDH) sowie 5 α -Reduktase (REDU) in der Leber und Kortikosteron im Blutplasma bestimmt. Verglichen wurden nicht individuelle Dominanzränge, sondern der Zusammenhang zwischen allen Merkmalen mittels Korrelations- und Faktorenanalyse. Bei den Weibchen fanden sich gesicherte Korrelationen zwischen häufigem Beschwichtigungsverhalten, erfolgreicher Futterkonkurrenz und niedrigen Kortikosteron- und HSDH-Spiegeln.

Aggressionen wurden zwischen Weibchen zwar im gleichen Umfang wie zwischen Männchen beobachtet, zeigten jedoch keinen gesicherten Zusammenhang zu anderen Merkmalen. Dagegen ließ sich bei den männlichen Ratten häufiges aggressives Verhalten und erfolgreiche Futter- und Wasserkonkurrenz als gemeinsamer Faktor beschreiben. Nur bei den Männchen bestanden signifikante Familien-

unterschiede in der Körpermasse und der Organmasse von Herz, Nieren und Nebennieren, die auch unterschiedliche Dominanzränge erklären können.

Beschwichtigungsverhalten und Stressvermeidung erwiesen sich bei den Weibchen, körperliche Überlegenheit und Aggressivität bei den Männchen als Voraussetzung für das Erreichen höherer Dominanzpositionen.

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