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Social behaviour, mating system and testes size in Cuis (Galea musteloides)

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Abstract

Social behaviour, mating system and testes size were investigated in cuis (*Galea musteloides*) in order to elucidate the social mechanisms in an obviously promiscuous rodent. Therefore, quantitative behavioural measures were recorded with a total of more than 200 h observation time in 4 groups of animals (1–4 adult males; 3–5 adult females in 12–25 m² enclosures). Testes and body masses were determined in 21 males. The most conspicuous feature in all groups of cuis was the daily rhythm of huddling. Short-lasting phases of high activity alternated several times daily with phases of inactivity during which all or nearly all members huddled together with close bodily contact. The mating system was promiscuous. In none of the 8 mating chases did the alpha male succeed in preventing the lower ranking males from copulation. Promiscuous mating was achieved by the females' behaviour, which attracted the attention of all the males and made it impossible for a single male to monopolize her. The males' relative testes size was extremely high, which thus strongly supports the supposition that a promiscuous mating system is typical for cuis. Surprising for such a mating system were the high levels of intermale aggression which were even found when no female was receptive, and although clear dominance relationships existed between the males. The females were also organized in linear dominance hierarchies. In contrast to the males, however, they frequently directed socio-positive behaviour towards conspecifics of the same sex.

Introduction

As a general guideline, mating systems can be divided into four different categories: monogamy, polygyny, polyandry and promiscuity (KREBS and DAVIS 1993). In mammals polygynous systems predominate, whereas monogamy and above all polyandry are rare (WILSON 1975; EMLEN and ORING 1977; CLUTTON-BROCK 1989; ALCOCK 1993; KREBS and DAVIS 1993). These three forms, however, have been studied extensively (see for example KLEIMAN 1977; HENDRICHS 1978; GOLDIZEN 1987; CLUTTON-BROCK 1989; VAN SCHAIK and DUNBAR 1990) and there is good evidence that variations in mating systems can be attributed to variation in resource distribution and paternal care (EMLEN and ORING 1977; CLUTTON-BROCK 1989; ALCOCK 1993; KREBS and DAVIS 1993). Also the social mechanisms bringing forth these differences in mating behaviour – for example, territory formation, attaining and respecting dominance, building up social bondings, mate guarding – are well understood (cf. WILSON 1975; KUMMER 1984). Relatively little is known, however, about promiscuous systems, although they are widespread among mammalian species (KENAGY and TROMBULAK 1986). Especially in small mammals the social mechanisms inducing both male and female to mate several times with different individuals are largely unknown.

Variation in mating systems is frequently related to variation in relative testes size (HARCOURT et al. 1981; HARVEY and HARCOURT 1984; KENAGY and TROMBULAK 1986;

MøLLER 1988). In species in which only one male mates (polygynous and monogamous species, respectively) low testes weights in relation to body weights are found, whereas males of promiscuous species are characterized by high relative testes weights. Supposing that testes size is positively correlated with volume of ejaculate, sperm counts and sperm motility (MøLLER 1988; HARVEY and MAY 1989), it is reasonable to assume that in promiscuous species males do not compete for access to females via agonistic encounters, but that the competition is yielded to their semen, that is, sperm competition should arise. Indeed, in the promiscuous chimpanzee, for example, high relative testes weights and no aggressive competition for mating is found among males (VAN LAWICK-GOODALL 1968; SHORT 1979). But while the knowledge about the relationship between behaviour and testes size is advanced in primates, relatively few detailed data are available in small mammals of other groups.

The yellow-toothed cavy or cuis (*Galea musteloides*) is a small South-American rodent which occupies the open habitats of savannas and bushland. In man-made habitats, such as rock piles and brush fences, considerably high population densities are attained. Field observations on behaviour and the mating system are not available. The study of 5–8 males and 8–12 females in a 25 m² enclosure suggests, however, that a promiscuous mating system exists: Although the alpha male frequently guards the female during estrous, he obviously is not successful in preventing other males from mating (Roop 1972).

To extend our investigations in guinea pigs (e.g. SACHSER 1986, 1994; SACHSER et al. 1994) to a closely related non-domestic species we chose *Galea musteloides*, a member of the same subfamily Caviinae, which has already been studied under specific behavioural aspects (WEIR 1971, 1973; ROOD 1972; KÖNIG 1985; KÜNKELE and HOEK 1989). When we compared the abdomens of intact males of both species, testes size appeared to be much greater in cuis than in guinea pigs, although they had a significantly lower body weight. These differences in morphological traits are obviously related to variation in behaviour: In colonies of guinea pigs a polygynous mating system is found (SACHSER 1986), whereas Rood's (1972) observations point to a promiscuous mating system in cuis.

We therefore investigated the social behaviour and mating system in groups of cuis and determined testes size quantitatively in order to elucidate social mechanisms in a small promiscuous non-primate species.

Material and methods

Subjects

The cuis (*Galea musteloides*) used were either descendants of 4 pairs (4 males, 4 females) obtained from the Zürich Zoo (Switzerland) more than 10 years ago, or they were provided by Prof. Dr. H. HENDRICHS (Department of Behavioural Physiology, University of Bielefeld, Germany) in 1989 (1 male, 4 females) and 1990 (6 males, 11 females), respectively. All animals were marked individually using commercial fur dye ("Nyanzol D", Belmar Inc., North Andover, USA).

Animal care and procedures

Four groups of cuis (group 1, 2, 3, 4) were studied; these groups had been established 2–12 months before the investigations began. All individuals were sexually mature, i. e., the males had a minimum age of 3 months and the females had a minimum age of 4 weeks (Rood and WEIR 1970; HOLT 1977). Groups 2 and 3 were kept in outdoor enclosures of about 15 m²; group 4 was kept in an indoor enclosure (size: 12 m^2 ; 12:12 L:D cycle, photoperiod 07:00 to 19:00 h; temperature: $20\pm 2 \text{ °C}$). Group 1 was housed in an outdoor enclosure (size: 15 m^2) during the first 3 months of the study. The space available was subsequently enlarged by opening the door to an indoor enclosure (10 m^2). The indoor enclosures had stone flooring, which was covered with woodshavings and hay. The floor of the outside enclosures

was covered with earth and planted with small trees. Part of each outdoor enclosure was roofed, under which the floor was covered with straw and hay. All enclosures were structured with branches and rootstocks. Three to five nestboxes were placed to every group. During the cold season the outdoor enclosures were equipped with radiators. Commercial guinea pig diet, flaked oats, maize and water were available ad libitum. This diet was supplemented regularly with fruits. The enclosures were cleaned at intervall of 3 to 6 weeks.

In the 4 groups studied, 1–4 adult males and 3–5 adult females were present. Social behaviours were recorded quantitatively over periods of 1–20 consecutive weeks with a total of 232 h observation time (group 1: 177 h; group 2: 16 h; group 3: 29 h; group 4: 10 h; focal group sampling, continuous recording). The identity of each interaction partner was noted as well as who performed and who received the behaviour displayed. The period of observation was generally 2 h, either between 08:30 h and 12:00 h or between 15:00 h and 19:00 h. In addition, in group 1 the rhythm of "huddling" was determined during the 16 h-light-phase of a summer day: On 4 consecutive days we recorded for 4 h at minute intervals the number of animals who huddled together with bodily contact. Data recording was conducted by hand, using prepared checksheets. All cuis were weighed regularly at 14 day intervals and marked if necessary.

Behavioural measures

The categorization and nomenclature of behavioural patterns followed Rood (1972) and SCHWARZ (1991). The behavioural patterns considered were: huddling, sitting in bodily contact, approach; agonistic behaviours: retreat, head-thrust, bite, attack-lunge, chase, pursue, curved body posture, turn-around; courtship and sexual behaviours: naso-anal licking, chin-rump following, mounting, intromission, ejaculation, taking the lordosis position; vocalization: churr. A description of these behavioural measures is given below where required.

Testes and body masses

Testes and body masses were determined in 21 healthy, mature males aged from 5 to 27 months which had lived in groups of 1–4 males and 1–2 females. Body masses were taken immediately before the males were sacrificed. The testes were subsequently rapidly cleaned from fat and adherent tissue, and for each individual the mass of both testes (excluding epididymides) was determined to the nearest 0.01 g. Relative testes size was calculated according to KENAGY and TROMBULAK (1986), that is: relative testes size = observed mass of testes / predicted mass of testes; predicted mass of testes = 0.035* body mass^{0.72}.

Statistics

Testes and body masses are given as means ± SD. Behavioural data are presented as medians.

Results

Huddling and rhythms of activity

In all four groups the cuis showed distinct ultradian rhythms of activity: Short-lasting phases of high activity, which were often characterized by frequent agonistic interactions alternated several times daily with phases of inactivity during which all or nearly all members of a group huddled together with close bodily contact (Figs. 1, 2). Even two cuis which had just been engaged in an escalated fight could be seen in this contactual resting posture only a few minutes later. A quantitative analysis of 89 huddling events in group 1 revealed that it took on average 13 min until all members of the group came together to huddle. Huddling itself lasted for a mean period of 46 min and it was ended on average within 10 min. Surprisingly, huddling was displayed at a wide range of temperatures, from lower than 0 °C in winter to about 30 °C in summer.

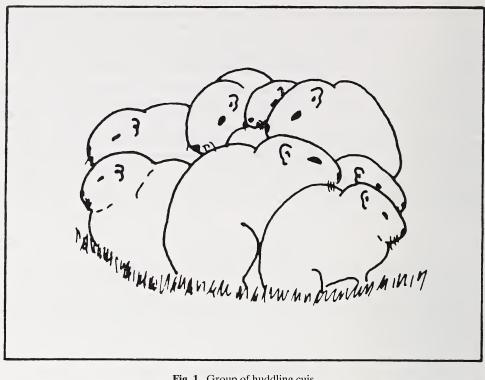


Fig. 1. Group of huddling cuis.

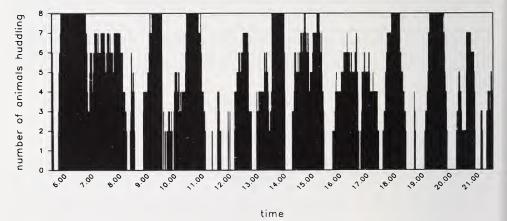


Fig. 2. Diurnal rhythm of huddling in a group of 8 adult cuis (group 1: 4 males, 4 females) living in an outdoor enclosure. The data were recorded in July during the whole phase of daylight.

Agonistic behaviours and dominance relationships

A complete range of agonistic behaviours of differing intensities was found. At the lowest intensity one individual approached another, which in turn immediately retreated. Threat displays and fights were hereby avoided. During more escalated forms of agonistic encounters overt aggressive behaviours were performed, that is head-thrusting, biting, attack-lunges, chasing and pursuing occurred. A still higher escalation was the display of

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curved body posture by one or two individuals simultaneously which might change into an escalated fight. At this highest agonistic intensity both individuals jumped at each other, bit and turned around. Dominance relationships between the individuals could be derived from the direction of the aggressive behaviours displayed as well as from the outcome of agonistic encounters. Although the lower ranking animals generally retreated immediately when a more dominant approached, the dominant frequently chased, pursued and bit them. As a consequence, most subordinate males and some subordinate females had scratches on their backs (cf. ROOD 1972).

Dominance relationships between males

In all four groups the males established clear dominance relationships. High ranking positions were maintained by frequently directing overt aggressive behaviours towards subordinates. Changes in dominance positions occurred, as is illustrated exemplarily for

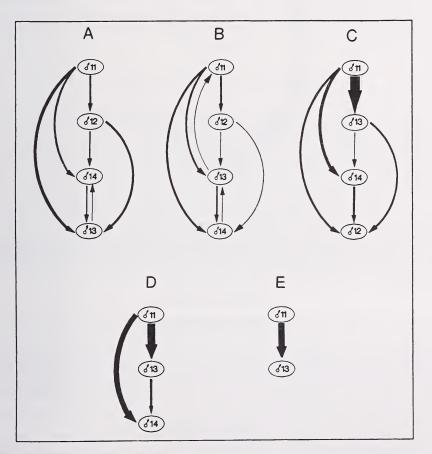


Fig. 3. Distribution of offensive aggressive behaviours (sum of head-thrusting, biting, attack-lunges, chasing, pursuing) among the adult males in group 1. The arrows point to recipients; the width of the arrows is proportional to frequencies. The 20-week observation time (177 h) is divided into 5 phases: A: 07.08.–11.08. (10 h); B: 13.08.–15.08. (6 h); C: 16.08.–17.08. (3 h); D: 20.08.–14.09. (38 h); E: 17.09.–21.12. (120 h).

group 1. At the beginning of the observation the males had organized themselves into a linear dominance hierarchy (Fig. 3A): M 11 was the highest, M 12 the 2nd, M 14 the 3rd and M 13 the lowest ranking male. (From previous observations it was known, that this rank order had been stable for at least 4 weeks before the start of the detailed observation.) M 11 held the highest ranking position throughout the whole 20 weeks of observation time. During the 2nd week changes in lower ranking dominance positions occurred. First – after an escalated fight – M 14 and M 13 reversed their positions (Fig. 3B). Thereafter M 13 and M 14 attained dominance over M 12 (Fig. 3C) and frequently chased and bit this male. Although no woundings were detected, M 12 died a few days later. However, it could not be decided whether death was the consequence of the changed dominance relationships, or whether M 12 was defeated because he fell ill and died from an undiagnosed disease. During the following 4 weeks the remaining 3 males organized themselves into a linear dominance hierarchy (Fig. 3D). After the death of the lowest ranking male (M 14) a clear and stable dominance relationship persisted between the alpha and beta males during the following 14 weeks (Fig. 3E).

In two groups a change in the alpha position occurred. Surprisingly, in both cases the subordinates had lower body masses than the dominants when they defeated their opponents (407 vs. 546 g; 317 vs. 364 g). In general the alpha positions, however, were filled by the heaviest males.

Dominance relationships between females

In three out of four groups (group 2, 3, 4) the females organized themselves in a similar way as the males: They formed linear dominance hierarchies including all adult females. This finding is shown exemplarily for group 3 (Fig. 4). F 31 took the alpha position and her daughters F 33, F 32 and F 34 the 2nd, 3rd and 4th respective hierarchal positions. In group 1, female F 15 and her three daughters were also organized in a linear hierarchy, with F 15 at the alpha position throughout the whole of the 20 week observation time. Three older unrelated females, however, which took the lowest ranking positions during 15 out of 20 weeks, hardly ever directed aggressive behaviours towards each other. So in this group it was not possible to arrange all females in a linear order.

The adult females' rank positions were largely independent of their body weights and ages. A juvenile female in group 1, for example, attained dominance over two fully grown females when she was not older than 6 weeks and had a distinct lower body weight than her opponents (170 g vs. 325 g and 264 g, respectively).

Aggression between the sexes

In all groups offensive aggressive behaviours were not only directed towards individuals of the same sex but also towards cuis of the opposite sex: Males and females could be involved both in agonistic interactions of low intensities as well as in threat displays and escalated fights. The frequencies of aggressive behaviours, however, were much lower between the sexes than within each sex. Furthermore, aggressive behaviours among males occurred on average more than twice as often as among females (Fig. 5).

In contrast to the intrasexual aggression, aggressive behaviours between the sexes were often bidirectional: Those males or females, respectively, which frequently displayed aggressive behaviours towards certain cuis of the opposite sex, were frequently attacked themselves by these same individuals. Moreover some males and females were never seen to direct aggressive behaviours towards each other. Thus it would not seem to be reasonable to calculate dominance relationships between the sexes.

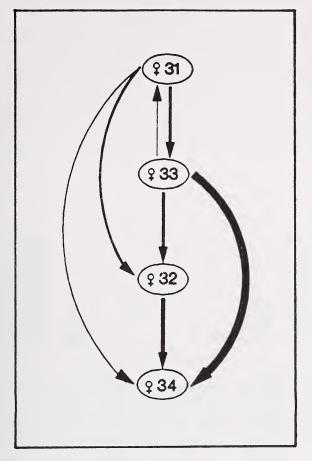


Fig. 4. Distribution of offensive aggressive behaviours (sum of head-thrusting, biting, attack-lunges, chasing, pursuing) among the adult females in group 3 during a 4 week observation time (29 h). The arrows point to recipients; the width of the arrows is proportional to frequencies.

Socio-positive behaviours

The cuis were not only involved in agonistic interactions, but socio-positive behaviours also occurred. Frequently one individual approached another and sat down in close bodily contact. Such neighbouring pairs often synchronized their feeding. In contrast to huddling, sitting in bodily contact occurred during phases of activity. It was frequently recorded as occurring between the females as well as between the sexes. However, it rarely occurred among the males (Fig. 5).

Mating system

During the present study an estrous could be observed 8 times (in 3 different groups, in 7 different females; cf. Tab. 1). In all cases mating behaviour was promiscuous. Not only the dominant male mounted, intromitted and ejaculated but also the second and third-ranking males. It was true that the dominant male tried to guard the receptive female, but he never succeeded. Promiscuous mating was achieved by the behaviour displayed by the fe-

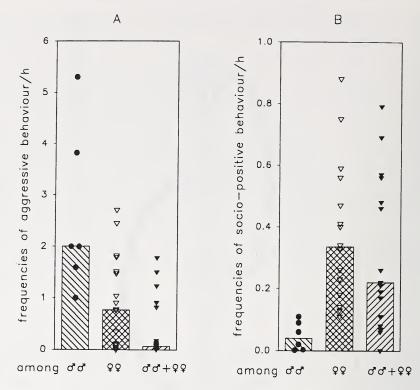


Fig. 5. Frequencies of aggressive behaviours (A) and socio-positive behaviours (B) (sitting in bodily contact during non-huddling times) among adult cuis (group 1) during a 19-week observation time (167 h). Circles and triangles give the frequencies of these behaviours for each male-male (N = 6), malefemale (N = 24) and female-female dyad (N = 18); columns represent medians. A statistical evaluation is not feasible because the samples consist of dependent and independent data.

male: She unexpectedly started to race around, stopped abruptly and started racing again. Thereby she often changed direction. By this rather conspicuous behaviour she attracted the attention of all the males, and these at once engaged in a mating chase, i.e., they fol-

group	female	number of males present	number of males copulating
1	F 15	3	3
1	F 17	2	2
1	F 17	2	2
1	F 18	3	3
3	F 31	2	2
2	F 21	2	2
1	F 13	4	2*
1	F 14	4	3*

Table 1. Mating chases

* Estrus was not observed from the beginning of the mating chase

lowed the running female. This procedure was accompanied by extremely high levels of aggression between the males. Especially the alpha male directed aggressive behaviour towards subordinate males. The males omitted a typical vocalization (the "churr", cf. Rood 1972) which only occurred around estrous. From time to time the female stopped abruptly, took the lordosis position, and copulated with that male which was just directly behind her. In none of the 6 cases which were recorded from the beginning was the mating period terminated before the female had copulated with all males present (Tab. 1), irrespective of whether it was a spontaneous or a post-partum estrus.

Testes mass

The mass of both testes of the males (excluding epididymides) amounted to 7.28 g \pm 1.51 g (n = 21). Their body weights were 402 g \pm 58 g (n = 21) on average. The relative testes size, calculated according to the formula of KENAGY and TROMBULAK (1986), amounted to 2.77 \pm 0.44. This value can be directly compared with the relative testes sizes of other mammals. Figure 6 shows that the relative testes size of *Galea musteloides* was much higher than that which is found in species in which only a single male copulates with each female. In contrast, these values were among the highest ever recorded in a terrestrial mammalian species with a known promiscuous mating system.

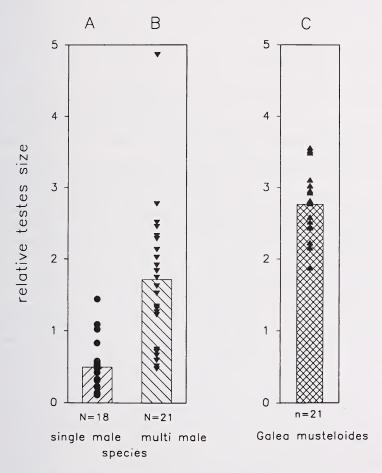


Fig. 6. Relative testes masses (according to KENAGY and TROMBULAK 1986; for details cf. methods) of mammals. A: species with single-male mating systems (monogamous and polygynous species);
B: species with multi-male mating systems (promiscuous species); C: cuis (*Galea musteloides*). Data in A and B refer to KENAGY and TROMBULAK (1986). Species listed in their publication were only considered here when their mating systems were known and sample size for testes mass was >1. In A and B each circle and triangle, respectively, represents the mean relative testes mass of a given species, columns give mean values for single- (N = 18) and multi-male species (N = 21), respectively. In C triangles represent relative testes masses of individual male cuis (n = 21); the column represents the mean value for this species.

Discussion

The most conspicuous feature in all groups of cuis was the daily rhythm of huddling (cf. also Rood 1972). Short-lasting phases of high activity, which were often characterized by frequent agonistic interactions, alternated several times daily with phases of inactivity during which all or nearly all members of a group huddled together with close bodily contact. Huddling was the behavioural pattern shown most of the time by the cuis (SCHWARZ 1991), its behavioural significance, however, is not yet clear. There are three likely functions: (1) It might have thermoregulatory benefits, as demonstrated in muskrats and degus (CANALS et al. 1989; BAZIN and MACARTHUR 1992). Surprisingly, cuis perform huddling not only at cold temperatures, but also at temperatures of up to 30 °C, which points against thermoregulation (CONTRERAS 1984). (2) A further function of huddling might be to synchronize the behavioural activities of the group members. The risk of predation might be hereby decreased. Indeed, the cuis were frequently seen feeding directly before and after huddling, and in the case of the closely related Cavia aperea it is well established that they synchronize their feeding in the wild (Rood 1972; CASSINI 1991). (3) A role in the development of an odour typical of the group might also be possible. Submandibular glands are present in both sexes (see photograph in WEIR 1971). The secretions are released on the surface of the skin. During huddling the odour can be spread throughout the animals of a group. Hereby group cohesion might be promoted. This mechanism would also explain the extremely aggressive response of group residents to unfamiliar intruders (Rood 1972).

The behavioural data presented here point to a promiscuous mating system in *Galea musteloides*. In none of the 8 mating chases observed did the alpha male succeed in preventing the lower ranking males from copulating. Thus, throughout the whole observation time of this investigation both males and females mated several times with different individuals. From this aspect our data confirm RooD's (1972) observations. However, we do not agree that during the mating chase the female is driven around by the males. According to our data the female, in contrast, played the active role: She always initiated the mating chase; it was her conspicuous behaviour that attracted all the males' attention and made it impossible for a single male to monopolize her. We therefore state that the promiscuous mating was primarily due to the females' behaviour.

What might be the adaptive significance of this phenomenon? A high benefit for the female should be expected, since her behaviour results in an optically and acoustically rather conspicuous mating chase, which might attract not only further male conspecifics but also predators. It is generally assumed that sexual selection favours mate choice in females. The more selective the female's behaviour is, the better her chance of finding the best partner (TRIVERS 1985; ALCOCK 1993; KREBS and DAVIS 1993). In our and Rood's (1972) study, however, the receptive females did not behave in a selective manner at all. In contrast, they attracted the attention of all males and showed no signs of refusing to mate with specific males. Apparently a selection pressure has acted on the females of this species to copulate with as many males as possible. Thus, the number and quality of sperm competing to fertilize the ovae might be increased. To our knowledge it has not yet been determined in mammals whether promiscuous mating will increase a female's reproductive success. Adders, however, which copulate with more than a single male, produce more live offspring than females with single matings (MADSEN et al. 1992). At present we are investigating whether these findings are also true in the case of *Galea musteloides*.

From laboratory studies it cannot be reliably derived which mating system a given species will display in the wild. Our data on testes size, however, strongly support that a promiscuous mating system is typical for cuis. The relative testes size was not only much higher than in species with a polygynous mating system, but it was one of the highest values ever recorded for a terrestrial mammal with a promiscuous mating system (cf.

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KENAGY and TROMBULAK 1986). The comparison with the closely related guinea pig (which is a member of the same sub-family of the Caviinae) further supports that a functional relationship exists between testes size and mating system in cuis. Guinea pigs living in colonies do not establish a promiscuous mating system but a polygynous one (JACOBS 1976; SACHSER 1986): The highest ranking males are able to monopolize "their" receptive females because female guinea pigs behave more passively during estrous than female cuis. Furthermore, the highest ranking males respect each other's ownership. Body weights are much higher in guinea pigs than in cuis (about 1 000 g vs. 400 g). The mass of both testes in the males is, however, significantly higher in cuis (7.28 g vs. 4.50 g; cf. SACHSER 1984). In addition HOLT (1977) reported in two individual male cuis 737×10^6 and 970×10^6 sperm/ ml ejaculate, respectively, whereas in guinea pigs a distinctly lower concentration was found (42×10^6 sperm/ml ejaculate; FREUND 1969). Thus, the Caviinae obviously provide a low-level taxon with diverging mating systems and corresponding functional variations in testes size.

In those mammalian species studied so far with promiscuous mating systems a high compatibility between the males was described even during estrous, i. e., levels of aggression were low. Indeed, males should not waste time and energy in agonistic encounters or even risk the danger of being injured when reproductive success is decided by "sperm competition" (SHORT 1979).

Surprisingly, in cuis we recorded extremely high levels of aggression between the males around estrous. Especially the alpha male directed aggressive behaviour towards subordinate males. These observations agree with Rood's (1972) findings. One might argue that these high levels of aggression resulted from artificial housing. An alternative explanation, however, would seem to be more likely.

In the literature there is not much information about which male will be the father of the offspring in a promiscuous mating system. There is, however, good evidence that gonadal activity might be rank-dependent in dominance structured social systems, especially when high ranking positions are established and maintained by overt aggression (e.g. CHRISTIAN 1980; KEVERNE 1983; SACHSER and PRÖVE 1986; IZARD 1990). Thus, chronic social subordination is frequently associated with low testosterone titers and hereby the amount and quality of sperm might be impaired (see, for example, von HOLST 1969). In this case a male would benefit by suppressing male conspecifics through aggressive behaviour, even if he is not able to prevent them from mating. This would explain the high frequencies of overt aggressive behaviour even when no female was receptive. Furthermore, this makes it comprehensible why dominants frequently chased, pursued and bit lowerranking males, although clear dominance relationships were already established.

In accordance with Rood (1972) we found linear dominance hierarchies among the females of *Galea musteloides*, a trait that seems to be common in the Caviinae (*Galea spixii, Kerodon ruprestris* (LACHER 1981), *Cavia aperea* (Rood 1972), *Cavia aperea* f. *porcellus* (THYEN and HENDRICHS 1990). Compared to the females of *Kerodon rupestris* (LACHER 1981), female cuis were generally competitive. It is, however, not clear what the benefit of a high hierarchical position might be. LACHER (1981) supposed that in *Kerodon* reproductive success is correlated with dominance rank. Quantitative data concerning this aspect are, however, missing in all wild species of the Caviinae. In colonies of the domestic guinea pig, high ranking females do indeed have higher reproductive success than the lower-ranking ones (SACHSER 1984). Surprisingly, there were not only aggressive encounters found among the females of *Galea*, but they also directed socio-positive behaviour towards each other. Furthermore, communal nursing usually occurs in this species (KÜNKELE and HOEK 1989). It remains to be studied which factors trigger the permanent change between conflict and cooperation in female cuis.

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Zusammenfassung

Sozialverhalten, Paarungssystem und Hodengewichte bei Wieselmeerschweinchen (Galea musteloides)

In mehr als 200 Beobachtungsstunden wurde das Verhalten von Wieselmeerschweinchen, die in vier Gruppen lebten, quantitativ erfaßt (Gruppenzusammensetzungen: 1-4 Männchen, 3-5 Weibchen; Gehegegrößen: 12-25 m²). Zusätzlich wurden von 21 Männchen die Körper- und Hodengewichte bestimmt. In allen Gruppen zeigten die Tiere einen auffälligen ultradianen Aktivitätsrhythmus. Phasen hoher Aktivität wechselten sich täglich mehrfach mit ausgeprägten Ruhezeiten ab, in denen alle Individuen einer Gruppe in engem Körperkontakt bei- und übereinander lagen. Das Paarungssystem war promiskuitiv.Während keiner der acht beobachteten Paarungsjagden gelang es dem dominanten Männchen, ihm unterlegene Artgenossen an der Kopulation zu hindern. Hervorgerufen wurde die Promiskuität durch ein auffälliges Verhalten der Weibchen: Während des Östrus lenkten sie die Aufmerksamkeit aller Männchen auf sich und machten es unmöglich, von einem einzigen Männchen monopolisiert zu werden. Das relative Hodengewicht der Wieselmeerschweinchen war im Vergleich zu anderen Säugetierarten extrem hoch. Auch dieser Befund unterstützt die Annahme eines promiskuitiven Paarungssystems bei dieser Spezies. Überraschend für ein solches Paarungssystem war jedoch das hohe Maß an aggressivem Verhalten zwischen den Männchen, das auch auftrat, wenn kein Weibchen östrisch war, und obwohl klare Dominanzbeziehungen zwischen den Männchen existierten. Die Weibchen organisierten sich ebenfalls in einer linearen Dominanzhierarchie. Im Gegensatz zu den Männchen richteten sie jedoch häufig sozio-positives Verhalten gegen gleichgeschlechtliche Artgenossen.

References

ALCOCK, J. (1993): Animal Behavior. 5th Ed. Sunderland, Massachusetts: Sinaur Associates.

- BAZIN, R. C.; MACARTHUR, R. A. (1992): Thermal benefits of huddling in the muskrat (Ondatra zibethicus). J. Mammalogy 73, 559–564.
- CANALS, M.; ROSENMANN, M.; BOZINOVIC, F. (1989): Energetics and geometry of huddling in small mammals. J. Theor. Biol. **141**, 181–189.
- CASSINI, M. H. (1991): Foraging under predation risk in the wild guinea pig *Cavia aperea*. Oikos **62**, 20–24.
- CHRISTIAN, J. J. (1980): Endocrine factors in population regulation. In: Biosocial mechanisms of population regulation. Ed. by M. N. COHEN, R. S. MALPASS, and M. G. KLEIN. New Haven, London: Yale Univ. Press. Pp. 55–115.
- CLUTTON-BROCK, T. H. (1989): Mammalian mating systems. Proc. Roy. Soc. Lond. (B) 236, 339-372.
- CONTRERAS, L. C. (1984): Bioenergetics of huddling: Test of a psycho-physiological hypothesis. J. Mammalogy 65, 256–262.
- EMLEN, S. T.; ORING, L. W. (1977): Ecology, sexual selection, and the evolution of mating systems. Science 197, 215–223.
- FREUND, M. (1969): Interrelationship among the characteristics of guinea pig semen collected by electro-ejaculation. J. Reprod. Fert. 19, 393–403.
- GOLDIZEN, A. W. (1987): Facultative polyandry and the role of infant-carrying in wild saddle-back tamarins (*Sanguinus fuscicollis*). Behav. Ecol. Sociobiol. **20**, 99–109.
- HARCOURT, A. H.; HARVEY, P. H.; LARSON, S. G.; SHORT, R. V. (1981): Testis weight, body weight and breeding systems in primates. Nature 293, 55–57.
- HARVEY, P. H.; HARCOURT, A. H. (1984): Sperm competition, testes size, and breeding systems in primates. In: Sperm competition and the evolution of animal mating systems. Ed. by R. L. SMITH. Orlando: Academic Press. Pp. 589–600.

HARVEY, P. H.; MAY, R. M. (1989): Out for the sperm count. Nature 337, 508-509.

- HENDRICHS, H. (1978): Die soziale Organisation von Säugetierpopulationen. Säugetierkdl. Mitt. 26, 81– 116.
- HOLT, W. V. (1977): The postnatal development of the testis in the cuis (*Galea musteloides*). Lab. Anim. **11**, 87–91.
- IZARD, M. K. (1990): Social influences on the reproductive success and reproductive endocrinology of prosimian primates. In: Socioendocrinology of primate reproduction. Ed. by T. E. ZIEGLER and F. B. BERCOVITCH. New York: Wiley-Liss. Pp. 159–186.
- JACOBS, W. W. (1976): Male-female associations in the domestic guinea pig. Anim. Learn. Behav. 4, 77–83
- KENAGY, G. J.; TROMBULAK, S. C. (1986): Size and function of mammalian testes in relation to body size. J. Mammalogy **67**, 1–22.
- KEVERNE, E. B. (1983): Endocrine determinants and constraints on sexual behaviour in monkeys. In: Mate choice. Ed. by P. BATESON. Cambridge: Cambridge Univ. Press. Pp. 407–420.

KLEIMAN, D. G. (1977): Monogamy in mammals. Quart. Rev. Biol. 52, 39-69.

König, B. (1985): Maternal activity budget during lactation in two species of Caviidae (*Cavia porcellus* and *Galea musteloides*). Z. Tierpsychol. **68**, 215–230.

KREBS, J. R.; DAVIS, N. B. (1993): An introduction to behavioural ecology. Oxford: Blackwell.

- KÜNKELE, J.; HOECK, H. N. (1989): Age-dependent discrimination of unfamiliar pups in *Galea muste-loides* (Mammalia, Caviidae). Ethology 83, 316–319.
- KUMMER, H. (1984): From laboratory to desert and back: a social system of hamadryas baboons. Anim. Behav. **32**, 965–971.
- LACHER, T. E. (1981): The comparative social behaviour of *Kerodon rupestris* and *Galea spixii* and the evolution of behaviour in the Caviidae. Bull. Carnegie Mus. Nat. Hist. **17**, 1–71.
- MADSEN, T.; SHINE, R.; LOMAN, J.; HAKANSSON, T. (1992): Why do female adders copulate so frequently? Nature **355**, 440–441.
- Møller, A. P. (1988): Ejaculate quality, testis size and sperm competition in primates. J. Hum. Evolut. 17, 479–488.
- Rood, J. P. (1972): Ecological and behavioural comparison of three genera of Argentine cavies. Anim. Behav. Monogr. 5, 1–83.
- Rood, J. P.; WEIR, B. J. (1970): Reproduction in female wild guinea pigs. J. Reprod. Fert. 23, 393-409.
- SACHSER, N. (1984): Auswirkungen unterschiedlicher sozialer Situationen auf Verhalten und Physiologie von Hausmeerschweinchen. Diss. Unversität Bielefeld.
- SACHSER, N. (1986): Different forms of social organization at high and low population densities in guinea pigs. Behaviour 97, 253–272.
- SACHSER, N. (1994): Sozialphysiologische Untersuchungen an Hausmeerschweinchen. Hamburg und Berlin: Parey.
- SACHSER, N.; LICK, C.; STANZEL, K. (1994): The environment, hormones, and aggressive behaviour: A 5year-study in guinea pigs. Psychoneuroendocrinol. **19**, 697–707.
- SACHSER, N.; PRÖVE, E. (1986): Social status and plasma testosterone-titers in male guinea pigs (*Cavia aperea* f. procellus). Ethology **71**, 103–114.
- SCHWARZ, E. (1991): Verhalten und soziale Organisation der Wieselmeerschweinchen (Galea musteloides Meyen, 1833). Diplomarbeit, Universität Bayreuth.
- SHORT, R. V. (1979): Sexual selection and its component parts, somatic and genital selection, as illustrated by man and the great apes. Adv. Stud. Behav. 9, 131–158.
- THYEN, Y.; HENDRICHS, H. (1990): Differences in behaviour and social organization of female guinea pigs as a function of the presence of a male. Ethology **85**, 25–34.
- TRIVERS, R. (1985): Social evolution. Menlo Park, California: Benjamin Cummings Publ.
- VAN LAWICK-GOODALL, J. (1968): The behaviour of freeliving chimpanzees in the Gombe Stream Reserve. Anim. Behav. Monogr. 1, 161–311.
- VAN SCHAIK, C. P.; DUNBAR, R. I. M. (1990): The evolution of monogamy in large primates: A new hypothesis and some crucial tests. Behaviour **115**, 30–62.
- VON HOLST, D. (1969): Sozialer Stress bei Tupajas (*Tupaia belangeri*). Die Auswirkungen des sympathischen Nervensystems und ihre Beziehung zu hormonell ausgelösten ethologischen und physiologischen Veränderungen. Z. Vergl. Physiol. 63, 1–58.
- WEIR, B. J. (1971): The evocation of oestrus in the cuis, Galea musteloides. J. Reprod. Fert. 26, 405-408.

- WEIR, B. J. (1973): The role of the male in the evocation of oestrus in the cuis, *Galea musteloides*. J. Reprod. Fert. Suppl. **19**, 421–432.
- WILSON, E. O. (1975): Sociobiology. The new synthesis. Cambridge (Mass.): Belknap Press of Harvard Univ. Press.
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