Ethology **103,** 1051—1059 (1997)

ISSN 0179-1613

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Temporal Pattern of Agonistic Interaction in Two Gerbil Species (*Rhombomys opimus* and *Gerbillus perpallidus*) Differing in Resistance to Social Pressure

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GOLTSMAN, M. E. & VOLODIN, I. A. 1997: Temporal pattern of agonistic interaction in two gerbil species (*Rhombomys opimus* and *Gerbillus perpallidus*) differing in resistance to social pressure. Ethology **103,** 1051—1059.

Abstract

This study compares temporal patterns of intraspecific agonistic interactions in two gerbil species in order to indicate interspecific differences in levels of social resistance. Both cross-sex and same-sex pairs of great gerbils (*Rhombomys opimus* Licht., 1823), and only same-sex male pairs of pallid gerbils (*Gerbillus perpallidus* Setzer 1958) were observed during staged encounters on a neutral arena. Analysis of three latency measures — latency to first agonistic interaction; latency to overt aggression (attack and/or 'arrested' fight); and latency to establishment of a stable winner—loser asymmetry among opponents — revealed both similarities and differences among the species. Latencies to first agonistic interaction were similar (did not differ significantly) among species and sexes. However, great gerbil males showed significantly more long latencies to establishment of a stable asymmetry among opponents, than great gerbil females or pallid gerbil males. So, the periods of symmetrical struggle in agonistic conflict last longer in great gerbil males, than in great gerbil females or pallid gerbil males. These differences in temporal pattern of agonistic interaction may reflect sex and species differences in resistance to social stress.

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Introduction

A common method of studying aggressive behaviour in rodents is to arrange an intraspecific encounter of two conspecifics in a neutral arena (AGREN & MEYERSON 1977; BEGG & NELSON 1977; DEMPSTER & PERRIN 1989; DEMPSTER et al. 1992). The typical course of an agonistic encounter is fairly stereotypic in many rodent species (GRANT & MACKINTOSH 1963). Upon being placed in the apparatus, the animals spend the first few minutes exploring the arena and one another (social investigation). After a short period of habituation, the animals begin to display postures that may for several reasons be regarded as threat actions. Firstly, appearance of such items is connected with high probability of escalation of overt aggression (attacks, arrested fights, etc.). Secondly, attacks are often undertaken directly from these postures. Finally, these actions are sometimes enough to motivate the opponent to take flight, adopt defeat postures and cry. After the

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mutual threatening actions, one of the opponents attacks, and that leads to a fight. After a time, a stable asymmetry is established: only one of the opponents attacks and threatens further, whereas the second one only defends itself with submissive postures and escapes. So, in the course of establishment of a dyadic relationship we can distinguish three subsequent stages: (1) physical environment and social exploration; (2) symmetrical struggle; and (3) asymmetrical agonistic interaction.

Based on our model of behavioural interaction (GOLTSMAN 1984; GOLTSMAN & BORISOVA 1993; GOLTSMAN et al. 1994), we suppose that during the period of symmetrical struggle, animals influence each other, attempting to suppress the onset of offensive activity of the opponent. The next stage, the stable winner—loser relationship, is consequendy the result of the successful suppression of aggressive activity by one of the opponents. It can be expected, therefore, that the more resistance to an opponent's suppressing activity is expressed by both fighters, the longer the period of symmetrical struggle ought to be.

We suggest that the resistance to the opponent's suppressing activity is not only a personal characteristic of individual animals, but also an integral characteristic of social groups differing in life histories. Animals subjected to enhanced social tensions should exhibit greater resistance to social inhibition of any important behavioural activity (GOLTSMAN 1984; GOLTSMAN et al. 1994). As a consequence, more-social animals are predicted to display greater resistance to inhibition of offensive activities. If this is the case, a clear distinction in resistance would thus be expected in species endowed with various degrees of sociality ('sociality modes') and between sexes owing to differences in male vs. female behavioural ecology.

In this paper, we examine the temporal pattern of agonistic encounters in two gerbil species to assess the intersexual and interspecific differences in behavioural patterns and timing. In test session 1, the sexual differences in the temporal pattern were investigated in great gerbils. In test session 2, we examined the interspecific differences of the temporal pattern between male great gerbils and male pallid gerbils.

Test Session 1: Homo- and Heterosexual Encounters in Great Gerbils

Materials and Methods

Subjects and Housing Conditions

Forty males and 28 females of great gerbils (*Rhombomys opimus* Licht., 1823) of first and second captive generations were used, progenitors of which were trapped in Ariskumy, Kazakhstan. Gerbils were housed in heterosexual pairs in terraria (60 X 29 X 35 cm) or plastic cages (45 X 30 X 15 cm). The light regime in the animal room was 16L:8D. Food (grain mix, vegetables, apples) was provided ad libitum. Wood shavings were used as bedding. All the animals were sexually mature and older than 7 months.

Testing Procedure

Pair encounters occurred in a neutral arena in the plastic box (78 X 78 X 75 cm) with a transparent glass front wall. Bedding was absent. The box was washed out with warm water and rubbed with ethanol between encounters to reduce possible pheromonal effects. Tests were conducted between 1100h and 1600h, in the light phase of the daily cycle.

Only unfamiliar, unrelated animals were used in staged encounters. Each animal was tested only once during the study. Animals were transported individually in clean glass vessels and released simultaneously into the arena. During the next 10 min, two observers recorded the behaviour of different members of the pair employing a focal animal observation procedure (ALTMANN 1974) using a 30-channel event recorder. All social interactions between animals: sniffing, allogrooming, threatening actions (sideways posture, boxing, patrolling, etc.) and overt aggression (attack, fight, flight, etc.) were registered (detailed descriptions of behaviour: GOLTSMAN et al. 1977). In all, 56 encounters between animals (20 male—male, 19 female—female, 17 male—female) were analysed.

Behavioural Analysis

Two measures were taken from this data set: latency to first agonistic interaction and latency to establishment of a stable winner—loser asymmetry among opponents. The appearance of the establishment of the stable asymmetry was defined as the end of the agonistic action, after which one of the opponents ceased entirely to initiate aggressive actions and behaved as a loser. After that, a 'loser' displays only defensive behaviour with submissive postures and escapes, in contrast to a 'winner', which displays offensive behaviour in parallel with exploring and marking activities.

The time period from onset of first agonistic interaction to establishment of a stable asymmetry was defined as the duration of symmetrical struggle.

The Mann—Whitney U-test was used for statistical comparisons (ZAR 1984).

Results

Table 1 shows frequencies of threats and attacks and/or arrested fight appearance in three groups of tests differing in sexual composition of opponents. Aggressive patterns were rarer in female—female than in male—male tests (52.6% vs. 75.0%). However, in the tests in which aggression occurred, the escalation of aggression to attack and/or fight was observed more frequently in female—female than in male—male encounters (80% vs. 47%). In heterosexual encounters, males were always winners; arrested fights often did not occur in these tests.

Fig. 1 compares latencies to first agonistic interaction and latencies to establishment of a stable asymmetry in cross-sex and same-sex encounters of great gerbils. Latencies to first agonistic interaction did not differ significantly among male—male, female—male and female—female encounters. Latencies to establishment of a stable asymmetry were significantly longer in male same-sex encounters than in female same-sex ($U = 1$, $n_1 = 15$, $n_2 = 10$, $p < 0.0001$) or in female-male encounters ($U = 10$, $n_1 = 15$, $n_2 = 9$, $p < 0.001$).

Table 1: Levels of aggression in intraspecies same-sex and cross-sex encounters of great gerbil

Test group	n	Percentage of encounters in which aggression escalates to level[1]: I	II	III
Male—male	20	35.0 (n = 7)	40.0 (n = 8)	25.0 (n = 5)
Female-female	19	42.1 (n = 8)	10.5 (n = 2)	47.4 (n = 9)
Male—female	17	—	53.0 (n = 9)	47.0 (n = 8)

[1] Level I, encounters including threatening actions and attacks and/or arrested fights; level II, encounters including threatening actions only; level III, encounters without aggression.

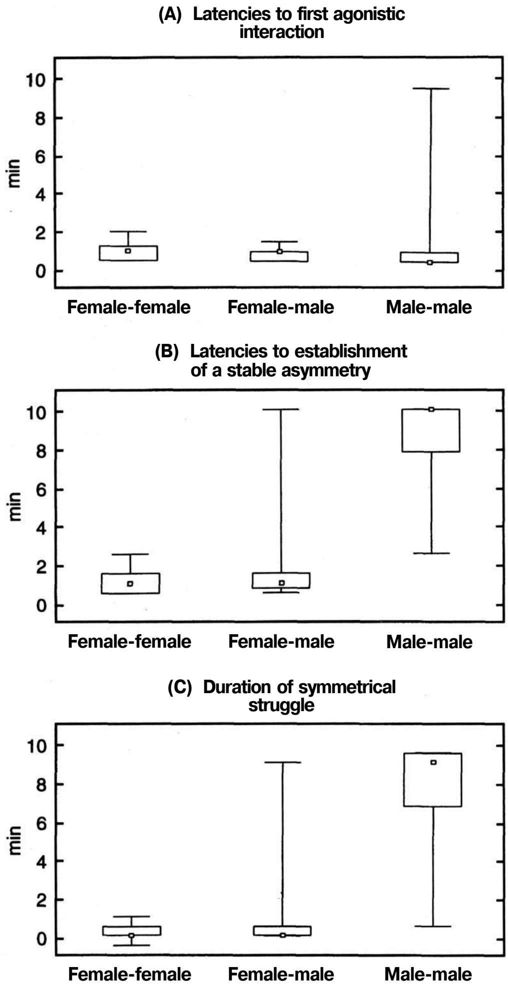

Fig. 1: Time periods (min) during cross-sex and same-sex pair encounters of great gerbils. Points represent medians, boxes quartiles, vertical lines minimum and maximum values. (C): a single case of appearance of the establishment of a stable asymmetry before the first agonistic interaction gives the negative value for female—female interaction

Accordingly, durations of symmetrical struggle were significantly longer in male-male than in female—female ($U = 3$, $n_1 = 15$, $n_2 = 10$, $p < 0.0001$) or in female—male encounters ($U = 10$, $n_1 = 15$, $n_2 = 9$, $p < 0.001$).

Differences between males and females were most evident in encounters where arrested fights did not occur (Fig. 2). No male behaved as a loser if only threats were performed. In contrast, females' latencies to establishment of a stable asymmetry did not differ significantly between tests with and without arrested fighting.

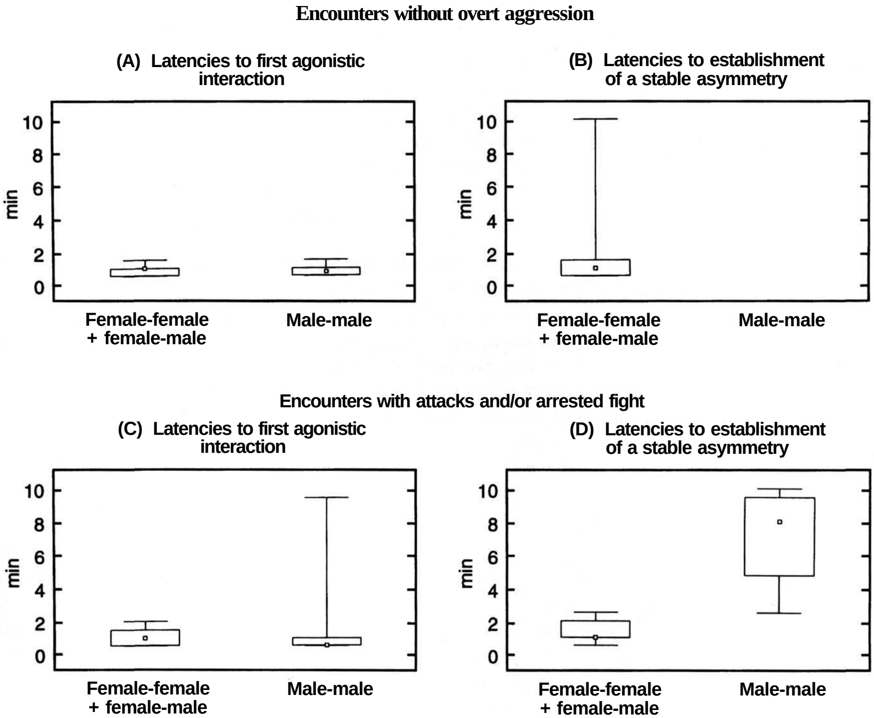

Fig. 2: Time periods (min) during cross-sex and same-sex pair encounters of great gerbils in relation to aggression level. Conventions as in Fig. 1. (B): a stable asymmetry does not establish in male-male encounters without overt aggression

In cross-sex tests, latencies and periods of symmetrical struggle did not differ significantly from corresponding values obtained in female—female encounters.

Test Session 2: Intraspecific Male Encounters in Great Gerbils and Pallid Gerbils

Materials and Methods

Subjects and Housing Conditions

Fourteen male great gerbils and 20 male pallid gerbils (*Gerbillus perpallidus* Setzer 1958) were used. Twelve great gerbils were wild-trapped in the Buchara region of Uzbekistan 5 mo before the experiment; the other two were second-generation laboratory-raised animals. All pallid gerbils were obtained from a captive population sustained for a few years in Moscow Zoo, Moscow, Russia.

The gerbils were housed in male-female pairs (9 great males and 14 pallid males) or individually (5 great males and 6 pallid males) in plastic cages (45 X 30 X 20 cm) with the natural light/dark cycle. The length of the isolation period for the individually housed males was 1-2 mo. Tests among individually housed and pair-housed males were conducted separately. Food (grain mix, carrots, bread) was provided ad libitum. Wood shavings were used as bedding. All males and females were sexually mature and older than 8 mo (great gerbils) or 3 mo (pallid gerbils).

Testing Procedure

Pair encounters occurred in a neutral arena in an opaque box (60 x 75 x 65 cm) made from hard plastic with a glass front wall. Bedding was absent. The box was washed out with warm water between encounters and was rubbed with ethanol. Tests were conducted during the second half of a day.

Only unfamiliar, unrelated animals were used in staged encounters. Each male was tested only once a day and no more than four times in all. Seven great gerbil and 13 pallid gerbil males were tested singly, whereas seven great gerbil and seven pallid gerbil males were tested more than once. Males were not tested again after their defeat. Intertest intervals in the case of repeated testing on the same subject were from 1 to 38 d ($\bar{X} = 8.7 \pm 3.2$) for great gerbils and from 1 to 35 d ($\bar{X} = 9.2 \pm 2.5$) for pallid gerbils.

Animals were transported individually in clean glass vessels and released simultaneously into the arena. The test period was 30 min long for great gerbils and 15 min long for pallid gerbils. This difference in testing period was related to more rapid encounters developing in pallid gerbils in comparison with great gerbils. In both species, testing periods considerably exceeded latencies to establishment of a stable asymmetry among opponents. Longer testing encounters between pallid gerbils may provide a higher risk of trauma.

Tests were videotaped with two videocameras situated above and in front of the arena. Videotapes were analysed according to an instantaneous observation procedure (ALTMANN 1974) with 1 s time interval. Twelve encounters between great gerbil males (5 among individually housed and 7 among pair-housed) and 17 encounters between pallid gerbil males (6 among individually housed and 11 among pair-housed) were analysed.

Behavioural Analysis

Onsets of threats (sideways posture, frontal posture, patrolling), overt aggression (attack and arrested fight) and submissive defensive postures, as well as durations of these actions, were extracted from video records (detailed descriptions of behaviour: GOLTSMAN et al. 1977). Three latency measures were taken from this data set: latency to first agonistic interaction; latency to overt aggression; and latency to establishment of a stable asymmetry among opponents. The occurrence of the establishment of stable asymmetry and duration of symmetrical struggle were defined as in test session 1.

The Mann—Whitney U-test was used for statistical comparisons (ZAR 1984).

Results

Fig. 3 compares latencies to first agonistic interaction, latencies to first attack or arrested fight and latencies to establishment of a stable asymmetry in male-male encounters of great and pallid gerbils. Latencies to first agonistic interaction did not differ significantly between species ($U = 101$, $n_1 = 12$, $n_2 = 17$, $p = 0.965$). However, great gerbils showed significantly longer values of duration than pallid gerbils in latencies to overt aggression ($U = 43.5$, $p < 0.01$), in latencies to establishment of a stable asymmetry ($U = 20.5$, $p < 0.001$) and in periods of symmetrical struggle ($U = 9.0$, $p < 0.001$). Similarly, both intervals from first agonistic interaction to onset of overt aggression and intervals from onset of overt aggression to establishment of a stable asymmetry were significantly longer in great gerbils than in pallid gerbils ($U = 11.0$, $p < 0.001$ and $U = 57.5$, $p < 0.05$ correspondingly; $n_1 = 12$ and $n_2 = 17$ in all cases).

It is particularly remarkable that pallid gerbil males acknowledged their defeat after the first threat, also representing the first agonistic action in 17.6% of all cases, while in other cases they did this after the first and single arrested fight. Great gerbil males never acknowledged their defeat after threatening actions only, but did this after the first arrested fight in 50% of cases or otherwise after a series of arrested fights.

General Discussion

The present study indicates that: 1. The length of time from the first agonistic interaction to establishment of a stable winner—loser asymmetry is significantly longer in

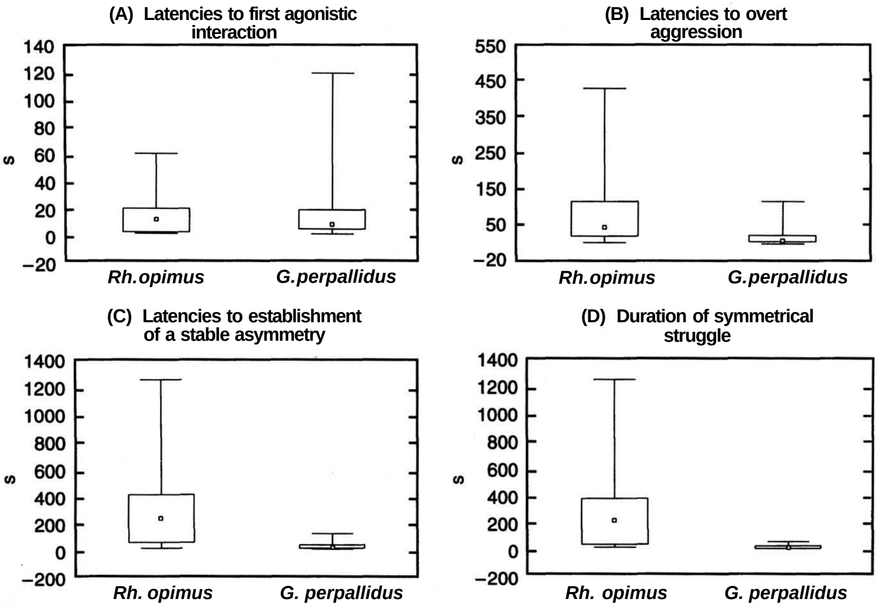

Fig. 3: Time periods (s; note differing vertical scales) during intraspecific pair encounters of great and pallid gerbil males. Conventions as in Fig. 1

great gerbil males than in great gerbil females; and 2. The period from the first agonistic interaction to establishment of a stable winner-loser asymmetry is significantly longer in great gerbil males than in pallid gerbil males.

We did not specifically account for intensity of agonistic interaction in the present analysis. Nevertheless, we suggest that the more prolonged aggression in great gerbil males cannot be ascribed to its lower intensity compared with aggression in great gerbil females or in pallid gerbil males. Indeed, the winner-loser relationships became established just after the first fight or before any agonistic action in pallid gerbil males and great gerbil females. In great gerbil males, in about half the cases the asymmetry was manifested after a series of fights and never before the first agonistic interaction.

So, we can conclude that the period of symmetrical struggle, i.e. the period spent ascertaining mutual relationships during agonistic conflict, lasts longer in great gerbil males than in great gerbil females or in pallid gerbil males. This time pattern of symmetrical struggle appears to be a characteristic of the resistance to social stress.

The period of symmetrical struggle considered in our analysis includes threatening, overt aggression and resting of both partners. Among these behaviours, only overt aggression is performed in physical body contact, and it occupies a relatively small proportion of this period. Furthermore, in some cases, animals adopt defeat postures or escape during or after threatening by the opponent only, neither being attacked at all, nor taking part in contact fighting. This reveals the psychological characteristics underlying the symmetrical struggle induced by a given experimental situation. It means that gaining victory or losing in this context are determined by the possibilities of animals to withstand the opponent psychologically rather than physically. It has been shown that the mere presence of the opponent could evoke severe stress in an animal (e.g. VON HOLST 1986).

It is interesting to compare the interspecific and intersexual differences shown in the present work with reported differences in the resistance to pain stress. This resistance has not been evaluated in great and pallid gerbils, whereas in Mongolian gerbil *(Meriones unguiculatus)*, a closely related species, no sexual differences in pain tolerance were found (BEATTY & HOLZER 1978), in contrast to many other mammals, in which males tolerate stronger pain than females (ELLIS 1986). If resistance to pain reflects resistance to social stress, it suggests that the sexual behavioural dimorphism found in the great gerbil is absent in the Mongolian gerbil. But more probably, resistance to social stress and resistance to physical and pain stress are determined by different factors.

If we assume that the duration of the symmetrical struggle periods reflects resistance to social stress, then we may conclude that great gerbil males are more resistant to social stress than great gerbil females or pallid gerbil males.

Great gerbil ecology (KUCHERUK et al. 1972; NAUMOV et al. 1972) and social behaviour (GOLTSMAN et al. 1977) have been studied, making it possible to connect the differences in stress resistance with sex differences in ecology and life history of these species. Great gerbils live in family groups composed of one adult male, one or a few adult females and their offspring from one or a few litters. All family members share the same territory. However, males are more mobile than females, because compared with females they use much larger home ranges, they more often and for longer times leave the family's territory, visiting neighbours' ranges. Males defend and scent-mark the family's territory much more actively than females. Furthermore, great gerbil males take part in agonistic interactions much more frequently than females. These sex-specific differences in lifestyles suggest that males require more resistance to social stress than females. Therefore, one would expect longer duration of agonistic interactions as well as a greater duration of the symmetrical struggle in males than in females of this species. The results presented here are consistent with this hypothesis.

Unfortunately, almost nothing is known of pallid gerbil socioecology. However, some observations carried out in enclosures (MEDER 1989; VOLODIN et al. 1996) suggest that the basic social organization of the pallid gerbil is individual territoriality, and thus the pallid gerbil appears to be a less social species than the great gerbil. On this ground, resistance to social pressure could be expected to be higher in the great gerbil than in the pallid gerbil, and our results fit well with such an assumption.

There is another possible explanation of our results. A classical explanation for longer duration of threat periods is the expectedly more complex 'ritualization' of behaviour in more social species. Indeed, threatening postures of great gerbil look more expressive and remain unchanged for a longer time period than the corresponding ones displayed by pallid gerbil. However, the period of symmetrical struggle comprises not only threats but biting fights, and there occurs a higher number of arrested fights before the asymmetry is established in great gerbil than in pallid gerbil. Furthermore, there is no sound reason suggesting that the behaviour of great gerbil males is more ritualized than the corresponding female behaviour.

Acknowledgements

We are grateful to Dr N. G. BORISOVA for valuable criticism of the manuscript. We thank E. V. VOLODINA for translating the text into English. We wish to thank Dr I. J. PAVLINOV for judgement of pallid gerbil species identity on the basis of morphological characters. We also thank Prof. Dr W. PFLUMM and an anonymous referee for very valuable comments and correcting the English of the manuscript. This work was supported by the Moscow State University and the Foundation for Russian Universities.

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Received: March 13, 1996

Accepted: September 16, 1996 (W. Pflumm)