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Strategies of aggressive fighting reflect degree of sociality in three species of gerbils

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Abstract. Animals living in communities should develop non-injurious ways of conflict resolution. A comparative study of aggressive fighting strategies in closely related species provides a good approach to investigating this statement. In the present study, we observed intraspecies male-male conflicts in a neutral arena for three species of gerbils, graded on their levels of sociality, from the least social, the pallid gerbil, *Gerbillus perpallidus*, to the much more social Mongol gerbil, *Meriones unguiculatus*, and great gerbil, *Rhombomys opimus*. From videotapes, we estimated winner-loser distances, and the duration of interactions and non-aggressive intervals between them, using 1 s scan sampling method. We found that patterns of aggression showed prominent interspecies differences. Great gerbils used a strategy of conflict delay—using, for the most part, very weak distant threats and standing immobile in static postures for a long time, with rare short blocks of contact threats or overt aggression. Mongol gerbils used a strategy of quick, short interactions, often in tactile contact. Rivals utilised threat postures or moved simultaneously, keeping the inter-individual distance unchanged. Pallid gerbils showed a very hard strategy of fighting, characterised by high levels of overt aggression, with fast changing of both distances between individuals and behavioural actions. We concluded, that male-male fighting strategies are in good agreement with species-specific social organisations in these gerbils.

Introduction

Gerbils (Gerbillinae) are a compact group of rodents, living in desert and semi-desert areas of Asia and Africa. This group has important agricultural and epidemiological significance, because they live on grazing areas, forage on grass and seeds, and are hosts of epidemical diseases that affect both humans and livestock. Gerbils represent a uniform group, possessing similar morpho-physiological adaptations for living in arid environments (Pavlinov et al. 1990). However, different gerbil species show high variability in their use of habitats, construction and use of hides, food, day/night activity and spatial-ethological structure. The discrepancy between similar external appearance and similar physiological adaptations to living in arid conditions, on the one hand, and high variability in social structures, on the other hand, makes this group very promising for comparative behavioural research, such as the evolution of sociality (Goltsman et al. 1994).

Extraction of stereotyped postures from behavioural observations is not the best approach to revealing interspecies differences, because most of important behaviours may be described only by using parameters of the entire behavioural continuum (Golani 1976, 1992; Moran et al. 1981). In our study, gerbils' ethograms are very similar, and behavioural differences are found mostly in kinematic characteristics, such as duration of behavioural actions, speed, and acceleration of speed during movements (Goltsman and Borisova 1993; Volodin and Goltsman 1998). In the present study, we tested aggressive conflicts in three species of gerbils differing in sociality—two social species, the great gerbil, *Rhombomys opimus*, and Mongol gerbil, *Meriones unguiculatus*, and a solitary species, the pallid gerbil, *Gerbillus perpallidus*, in order to compare differences in aggressive behaviour in these species in relation to their sociality.

Materials and methods

We videotaped intraspecies male-male conflicts in a neutral arena. We conducted 21 tests for the great gerbil, 26 tests for the Mongol gerbil, and 20 tests for the pallid gerbil. All of the 15 great, 26 Mongol and 20 pallid male gerbils were adult, captive-born animals, housed with 1-2 females or with females and their offspring (Volodin et al. 1996). Tests were made among unrelated and unfamiliar conspecifics in a plastic enclosure 76.5 cm x 58 cm x 65 cm.

A short time after the beginning of the test, one of the males becomes the winner and the second one becomes the loser, and this asymmetry is retained until the end of the test (Goltsman and Volodin 1997). From videotapes,

we measured winner-loser distances, and the duration of aggressive interactions and non-aggressive intervals between them using a 1 s scan sampling method (Altmann 1974). In total, 34,022 s for great gerbils, 29,856 s for Mongol gerbils and 15,308 s for pallid gerbils were sampled. Thus, we analysed 355, 781 and 331 aggressive interactions and 340, 760 and 301 non-aggressive intervals for the great, Mongol and pallid gerbils, respectively.

Results

In all three species, male-male conflicts occurred as aggressive interactions interspersed by non-aggressive intervals (Figure 1). In turn, aggressive interactions could be broken down into distant threats, contact threats, and fighting and chasing.

The percentage of time spent in aggressive interactions decreases progressively in the order great > Mongol > pallid gerbils (Figure 2). However, the severity of the aggressive interactions showed a reversed pattern: fighting and chasing and contact threats took more time in the pallid gerbil in comparison to the Mongol gerbil, and more time in the Mongol gerbil in comparison to the great gerbil, which had the maximum percentage of distant threats. All the differences were significant ($p < 0.001$, White t-test).

Aggressive interactions were significantly longer in the great gerbil than both in the Mongol and in the pallid gerbils ($p < 0.001$, Mann-Whitney U-test), whose duration of aggressive interactions did not differ (Figure 3). Non-aggressive intervals were the shortest in the Mongol gerbil (Figure 3).

Distant threats were longest in the great gerbil, intermediate in the Mongol gerbil, and shortest in the pallid gerbil and all differences were significant ($p < 0.001$, Mann-Whitney U-test; Figure 2). The duration of contact threats and fighting and chasing were more similar between species, but the difference was still significant between the Mongol and pallid gerbils ($p < 0:01$, Mann-Whitney U-test) (data not shown).

During aggressive interactions, the great gerbil usually keeps a distance from 0.1 to 0.75 body lengths from his opponent, whereas the Mongol and pallid gerbils maintain a shorter distance of tactile contact. All the differences were significant ($p < 0.001$, White t-test) (Figure 4).

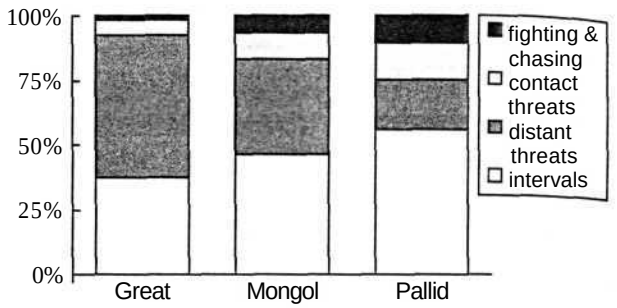

Figure 2. Total percentage of time the gerbil species spent displaying different behaviours during aggressive interactions—fighting and chasing, contact threats and distant threats—and non-aggressive intervals between aggressive interactions.

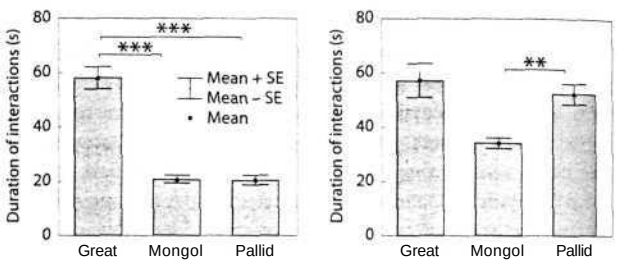

Figure 3. Duration of aggressive interactions and non-aggressive intervals (mean ± se) in the three gerbil species, where *** = $p < 0.001$; ** = $p < 0.01$.

Distance changing rates during non-aggressive intervals were similar in all the three species. In contrast, the distance changing rates during aggressive interactions did differ significantly between the species and graded from the most in the pallid gerbil, through intermediate in the Mongol gerbil, to the least in the great gerbil ($p < 0.001$, Mann-Whitney U-test) (Figure 5). It is interesting that in the great gerbil, the distance changing rate was much lower during aggressive interactions than during non-aggressive intervals ($p < 0.001$, Wilcoxon t-test); in the

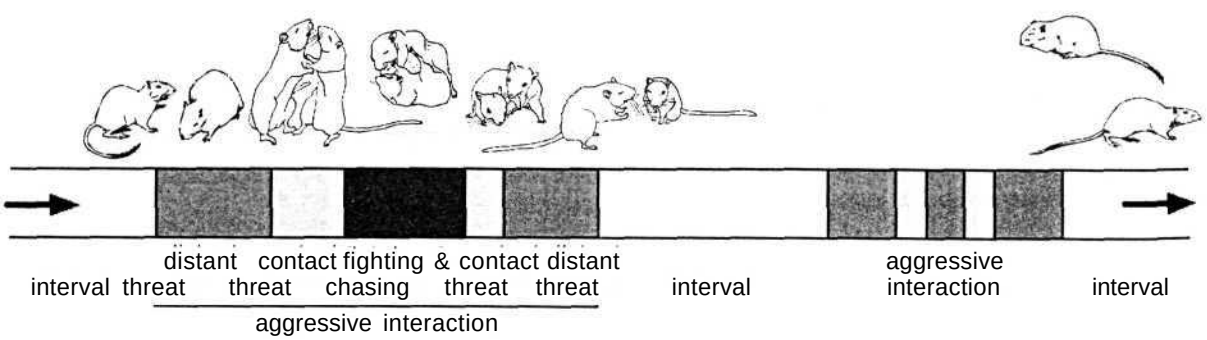

Figure 1. Schematic illustration of a sequence of actions among combatants during male-male conflicts in the three gerbil species observed in the study. Gerbil postures (from left to right): lateral threat posture (distant threat); boxing (contact threat); fighting; displacement (contact threat); frontal threat posture (distant threat); out of aggressive interaction (non-aggressive interval).

pallid gerbil, the relations were reversed ($p < 0.05$, Wilcoxon t-test); and in the Mongol gerbil, the rates were similar in both the cases.

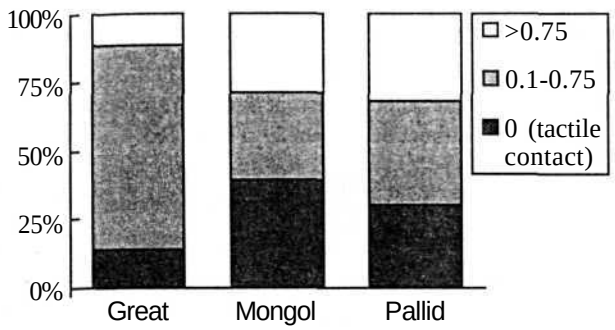

Figure 4. Total percentage of time keeping different winner-loser distances during aggressive interactions in the three gerbil species. Units of body length are the measure of distances.

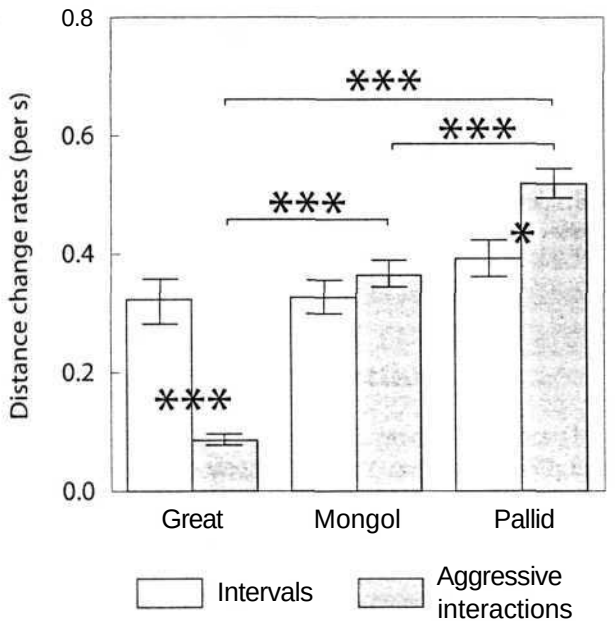

Figure 5. Rate of distance change during non-aggressive intervals and aggressive interactions (mean ± se) in the three gerbil species, where *** = $p < 0.001$; * = $p < 0.05$.

For the great gerbil, aggressive interactions were characterised by long immobility of both combatants, keeping a constant distance apart without body movement (static keeping of a constant distance apart) (Figure 6). In total, the great gerbils remained immobile more than 80% of the time during interactions. The aggressive strategy of Mongol gerbils was intermediate between the great and pallid gerbils: 39% of the time they were immobile, 22% keeping a constant distance by using synchronised movements (mobile but keeping a constant distance apart), and 39% of the time in changing the distance apart. In contrast, pallid gerbils mainly 'danced' around each other, changing the distance apart every 2 s of an interaction. Even when the distance apart was constant, pallid gerbils were immobile only 26% of the time, and spent nearly equal time in synchronised movements that maintained a constant distance apart. All the differences were significant ($p < 0.001$, White t-test, excluding mobile keeping of distances in the Mongol and pallid gerbils).

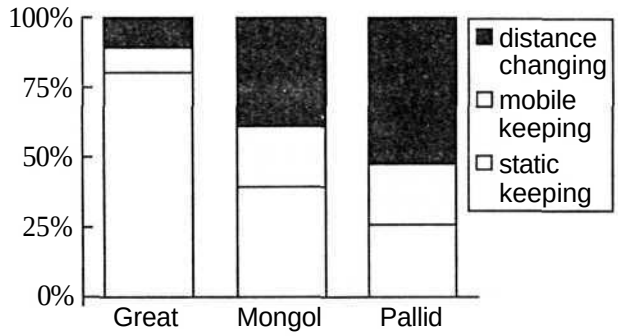

Figure 6. Total percentage of time gerbils spent with the winner-loser distance changing, mobile but keeping a constant distance apart, and static keeping of a constant distance apart during aggressive interactions in the three gerbil species.

Discussion

The differences we found in observing male-male conflicts represent distinctive species-specific strategies of aggressive fighting, graded in severity in accordance with degree of sociality in the species studied. The most social species, the great gerbil, used a strategy of a conflict delay, utilising for the most part prolonged distant threats, with rare, short periods of contact threats or fighting and chasing. Mongol gerbils used a strategy of quick and short aggressive interactions. Rivals showed threat postures or moved simultaneously, keeping a constant distance apart. The solitary pallid gerbils showed a severe strategy of aggressive fighting, with much fighting and chasing, and rapid changing of both distances and orientation.

Psychological intimidation is a very important aspect of aggressive fighting, and these interspecies differences may be discussed from the viewpoint of resistance to social suppression from a conspecific male (Goltsman et al. 1994; Goltsman and Volodin 1997). We hypothesised that more prolonged aggressive interactions demand more resistance from the participants. The time spent in aggressive interactions was the most in the great gerbil, intermediate in Mongol gerbil, and least in the pallid gerbil. Therefore, accordingly to our hypothesis, species-specific strategies of aggressive fighting show that the great gerbil possesses the highest resistance to social suppression, Mongol gerbil an intermediate resistance, and pallid gerbil the lowest one.

The enhancing of resistance may be among the mechanisms that promote the adaptation of animals to exist in social environments of high density. The differences we discovered in resistance to social suppression are in good agreement with the species-specific degree of social density in natural populations (Pavlinov et al. 1990; Goltsman et al. 1994). The observed data on differences in strategies of aggressive fighting in these three species suggest the existence of behavioural mechanisms corre-

lated with social organisation in gerbils. In an ecological framework, these mechanisms may be among the factors that determine population density in gerbils in nature.

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