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GENERAL BIOLOGY

Dynamics of Agonistic Interaction between Paired Animals in Three Gerbil Species

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Pairing in neutral territory is a common method for studying aggressive behavior in rodents [7, 9, 10]. Agonistic interactions in most rodent species follow the same pattern [13]. During the first several minutes after pairing, the animals inspect the place and each other and then begin to demonstrate postures that can be interpreted as threats, since this demonstration usually precedes acts of direct aggression. An animal often attacks the other immediately after demonstrating the threatening posture; sometimes, the opponent capitulates before being attacked and demonstrates this by assuming submissive postures. After the phase of mutual threats, one of the partners attacks, and the attack is followed by fighting. Later, stable asymmetry in the relationships is achieved: one of the partners continues to threat and attack, while the other only defends, assumes submissive postures, and flees. Thus, four phases can be identified: investigation and evaluation of the situation, mutual threats, direct aggressive actions, and, at last, contest asymmetry.

The goal of this study was to compare three gerbil species in duration of the first three phases preceding the formation of the winner-loser asymmetry, and in the strain of agonistic interaction between the animals during the last phase. Based on a general model of behavioral interaction [2, 11], we considered the fighting phase in agonistic encounters of two animals as a period of mutual attempts to inhibit agonistic activity of the partner. Obviously, fighting leads to psychological and physical exhaustion, and the longer the fighting phase, the greater resistance to pressure from the opponent is required. This paradigm makes it possible to consider interspecific differences in the dynamics of agonistic behavior as a manifestation of varying resistance of species to inhibition of behavioral activity.

Three gerbil species with different social and ecological characteristics were chosen for comparison: the Great (*Rhombomys opimus)* and Mongolian gerbils (*Meriones unguiculatus)* that live in family groups in the wild, and the pallid gerbil (*Gerbillus perpallidus)* that presumably lives singly [1, 3, 4]. The Great (n = 14), Mongolian (n = 26), and pallid (n = 20) gerbils used in experiments were sexually mature males at ages of 8, 5, and 3 months, respectively. They were kept in the vivarium of the Biological Faculty (Moscow State University). All Mongolian and pallid gerbils and two Great gerbils were born and raised in captivity; 12 Great gerbils were trapped in Bukhara oblast (Uzbekistan) 5 months prior to experimentation.

Males of Great and pallid gerbils were kept in pairs with females or singly. Each male Mongolian gerbil was kept either with a female, and their offspring younger than 2 months, or with one or several females. Their plastic cages measuring 45 x 30 x 20 cm had mesh tops and contained saw dust for bedding. The gerbils were fed *ad libitum* with oat and sunflower seeds, dry bread, and carrot and apple slices, but no water was given. They were kept at a photoperiod natural for Moscow at 18-23°C.

A Textolite chamber (76.5 x 58 x 65 cm) with a glass front wall, and a floor divided into squares measuring 10 x 10 cm was used as a neutral environment for pairing the animals. The chamber contained no bedding. Before the experiments, it was washed with water and wiped with alcohol to kill odors.

The pairing experiments with Mongolian gerbils were carried out from 11 a.m. to 9 p.m. at the end of the reproductive season (August and September). The Great and pallid gerbils were paired during the afternoon at the beginning of the reproductive season (March-June).

Only unfamiliar and unrelated animals were used in the experiments. Each Mongolian gerbil was tested no more than four times; the interval between the experiments was no less than 3 days. Each Great or pallid gerbil was tested in a maximum of six experiments, but no more than once a day. The gerbils participated in the experiments until the first defeat.

The animals were taken from their home cages with clean glass and then simultaneously let out on the floor of the chamber. The experiments lasted for 30 min with

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Table 1. Median time intervals (s) characterizing the development of agonistic interaction and significance levels for paired interspecific comparisons by the Mann-Whitney U-test

Period	Parameter	Great/Pallid		Great/Mongolian		Mongolian/Pallid	
		Number of experiments					
		12	17	12	19	19	17
T1	Median	11.5	8	11.5	15	15	8
	Mann-Whitney test	U=101 p = 0.965		U = 98.5 p = 0.529		U = 143 p = 0.557	
T2	Median	48	10	48	28	28	10
	Mann-Whitney test	U = 43.5 p = 0.009		U = 71 p = 0.081		U = 117 p = 0.158	
T3	Median	240	23	240	29	29	23
	Mann-Whitney test	U = 20.5 p = 0.003		U = 43.5 p = 0.042		U = 116 p = 0.149	
T2-T1	Median	42	0	42	2	2	0
	Mann-Whitney test	U = 11 p = 0		U = 43.5 p = 0.004		£/=108.5 p = 0.083	
T3-T2	Median	25	4	25	5	5	4
	Mann-Whitney test	U = 57.5 p = 0.049		U = 76 p = 0.120		U = 141.5 p = 0.530	
T3-T1	Median	214.5	6	214.5	12	12	6
	Mann-Whitney test	U = 9 p = 0		U = 31.5 p = 0.001		U = 118 p = 0.167	

Note: T1 is the time until the first agonistic interaction; T2 is the time until the first attack or fight; and T3 is the time until the appearance of stable asymmetry.

Mongolian and Great gerbils, and 15 min with pallid gerbils (because agonistic interactions between pallid gerbils proceeded at a greater rate, and the risk of traumatic outcome increased at longer times). A total of 12, 19, and 17 experiments with Great, Mongolian, and pallid gerbils, respectively, were performed.

All encounters were videotaped synchronously with two cameras showing the top and side views. The behavior of each partner was analyzed on a 1-s time base [7] by determining the times to the first agonistic interaction (T1), to the first attack or fight (T2), and to the moment from which asymmetry became stable (T3), i.e., the moment after which the winner and the loser became evident, with the former continuing to attack and the latter only defending.

The moment of the asymmetry appearance was defined as the turning point from which one of the partners stopped initiating aggressive acts until the end of the experiment; therefore, from this moment on, its agonistic behavior included only defense against attacks, attempts to escape, and demonstration of submissive postures. For example, if after a series of mutual sideways threats followed by attacking, fighting, and chasing, one of the opponents began submissive behavior until the end of the experiment, the point of cessation of fighting (or the start of chasing) was taken as the point of the asymmetry appearance. If direct aggression was not preceded by threatening postures, T2 could be equal to T1; T3 could be less than T2 if asymmetry was observed immediately after demonstration of threatening postures, in the absence of attacks or fighting.

The results were processed statistically by nonparametric tests with the use of the STATISTICA v. 4.5 program package.

The three gerbil species did not differ in T1 values (Table 1). Other phases (with one exception) were significantly longer in Great gerbils than in Mongolian or pallid gerbils. The last two species insignificantly differed, despite the fact that the values observed for Mongolian gerbils were always intermediate relative to those for great and pallid gerbils (Table 1).

Compared to both Mongolian and pallid gerbils, Great gerbils spent significantly more time in mutual fighting (the T3-T1 interval from the first threats to the appearance of asymmetry; Table 1). Both the period of demonstration for threatening postures before the first attack (T2-T1) and the period of direct aggression

(T3-T2) were longer in Great gerbils; however, the differences from pallid gerbils were statistically significant (Table 1).

Mongolian and pallid gerbils did not differ significantly in durations of either demonstration of threatening postures before first attacks (T2-T1), acts of direct aggression (T3-T2), or the entire period of mutual fighting (T3-T1; Table 1). However, a closer inspection showed that Mongolian gerbils were more consistent in their progression from threat to direct aggression and asymmetry and that the extent of strain they experienced during fighting was intermediate between the extremes observed in Great and pallid gerbils.

In fact, threatening postures before the first fight were observed in all experiments with Great gerbils, 74% of the experiments with Mongolian gerbils, and only 47% of the experiments with pallid gerbils. The difference between Great and pallid gerbils was significant at $p = 0.005$ (t-test for fraction comparison). In Great gerbils, 50% of the experiments showed that the winner and loser were settled after a single fight. In the other 50%, a series of attacks and fights had occurred before the winner-loser asymmetry became stable (Table 2). In Mongolian gerbils, the winner and the loser were settled after a single fight in 84% and several fights in 16% of the experiments. Conversely, in 17.6% of the experiments with pallid gerbils, one of the partners capitulated before the start of direct aggression, only after threats; in other cases, the first agonistic interaction rapidly expanded into a fight whose outcome determined the winner (Table 2).

The gerbils of all three species were involved in agonistic interaction at an equal rate, The fighting period was longest in Great gerbils; their extent of strain during fighting was also greater than in Mongolian or pallid gerbils. The last two species did not differ in durations of mutual fighting, but fighting was more intense in Mongolian gerbils.

It is conceivable that the course of agonistic interaction of two specimens depends on their morphological and physiological characteristics (such as metabolic rates, which increase with decreasing body size and weight in animals [5, 6]). According to this hypothesis, low rates of agonistic interaction might be expected in large Great gerbils, high rates—in small pallid gerbils, and intermediate rates—in Mongolian gerbils. Our data are consistent with this hypothesis. However, no difference was found in the course of agonistic interaction between female Great gerbils and male pallid gerbils in pairing experiments [12]. In addition, the durations of aggressive interactions did not correlate with the body size in three of the *Meriones* genus species [11]. Although, the body size has a modulating effect on the struggle strategy, this effect cannot explain all interspecific differences observed.

On the other hand, the duration and strain of mutual fighting may reflect different resistance to social stress [2, 12]. Mutual fighting involves threats, direct aggression, and rest of both partners. Only direct aggression implies physical contacts of the animals, but its duration is small compared to the entire period of fighting. In some cases, gerbils took defensive postures and retreated without going into contact fighting, even before being attacked. This means that for a particular animal, the chance to be a winner in the experimental situation used depended on its physiological rather than physical capacities for resisting the opponent.

Table 2, Percentage of experiments with the winner settled after (I) first threats (without fighting), (II) a single fight, and (III) several fights

Gerbil species	Number of experiments	Percentage of experiments of a particular type		
		I	II	III
Great gerbil	12	0	50	50
Mongolian gerbil	19	0	84	16
Pallid gerbil	17	18	82	0

If we assume that the duration and strain of mutual fighting reflect the resistance to social stress, then Great and pallid gerbils should be the most and the least resistant species, respectively, whereas Mongolian gerbils should have intermediate characteristics.

The absence of significant differences between "social" Mongolian gerbils and "solitary" pallid gerbils may result from the insufficient sensitivity of the experimental procedure used. We analyzed the videotapes on a 1-s scale, where aggressive interactions of Mongolian gerbils are short, with the medians of various threats, fights, and chases below 4 s [11]. We believe that the tendency to longer periods of mutual fighting in Mongolian vs. pallid gerbils will be confirmed on larger samples and with the use of more accurate techniques to calculate the time lengths.

A possible mechanism of adaptation for animals to increasing social density is an increased resistance to inhibition of their behavioral activity by their partners [2]. In general, the differences in resistance to social inhibition of the three species studied agree well with the species-specific levels of social density in their natural colonies.

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