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GENERAL BIOLOGY

Characteristics of Movement Velocity of Animals Placed together in Pairs in Two Allied Species of Jirds

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Southern jirds *(Meriones meridianus* Pall.) and clawed jirds *(M. unguiculatus* Milne-Edw.) are two allied species of the family Gerbillidae, which comprises about 100 species [2]. According to both morphological and ecological characteristics, the representatives of the family are similar to each other. Therefore, they are appropriate objects for comparative taxonomic, ecological, and behavioral studies [1, 3-5].

Southern and clawed jirds are similar in size and general appearance. Although the groups formed by southern jirds differ significantly from the groups of clawed jirds in composition and structure of relationships, the behavioral repertoires (e.g., behavioral interactions) of the two species are very similar to each other [3]. Nevertheless, the difference in behavioral acts between the species is recognizable even at a glance. It seems that the behavioral difference between the species is manifested in the dynamics of behavioral acts rather than in the pattern of the acts. Although these species are virtually indistinguishable in terms of general configuration of complete locomotions and postures, which constitute the basis of ethograms, the interspecies difference in the temporal characteristics of the behavioral acts is obvious. The visual impression of the interspecies difference in the mobility kinematics seems very interesting at least in two aspects. First, there is an intriguing connection between the difference in the mobility kinematics and interspecies difference in the social ecology of jirds [1]: the rate of movement is higher in socially less active species. In the jird pairs observed in this work, the movements of southern jirds looked more rapid and reactive than the movements of clawed jirds. Second, although kinematic characteristics of locomotion have not yet been used in studies of specific team behavior, they seem very promising in this regard. It was shown in the previous study that clawed, Libyan, and southern jirds differ from one another in the duration of agonistic acts [6]. The goal of this work was to study the interspecies difference in the kinematic characteristics of stereotype acts during aggressive interactions between jirds, taking into consideration the situation specificity of the acts.

Adult mature males of southern and clawed jirds (six specimens each) were used. All animals were born and grown in captivity. Males were kept together with females but without progeny. The animals were kept in plastic cages (45 x 30 x 20 cm) with a wire-gauze top. Wood sawdust was used as litter. The animals were fed on oat and sunflower grains, dry bread, pieces of carrot and apple, and freshly cut grass. The food was always unlimited, but the animals received no water. The natural photoperiod and a constant ambient temperature of 20-23°C were maintained in the room.

Individually labelled males were arranged in pairs at a neutral territory in a textolite chamber (76.5 x 58 x 65 cm). The frontal wall of the chamber was made of glass. The floor of the chamber was delineated into squares (10 x 10 cm) and not covered with litter. Before use, the chamber was washed with water and wiped with ethanol to eliminate the odor.

Animals were taken from cages using clean glass beakers and put to the bottom of the chamber simultaneously in pairs. The duration of each experiment was 10 min. Once the animals were placed into the chamber, their behavior always resulted in similar interaction patterns: after a short period of adaptation to the chamber, the animals started to examine one another. The contacts between the animals were either nonaggressive (various types of sniffing) or weakly aggressive (threat and defensive postures). Strong aggression with pursuit was not observed.

A total of nine experiments with southern jirds and eight experiments with clawed jirds were performed from July 21 to August 13. Only animals that were unfamiliar with each-other were used for the experiments. Each male jird was used for observation no more than once per day and no more than five times throughout the entire series of experiments.

The animal behavior and locomotory acts were automatically recorded with a video camera mounted above the experimental chamber.

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The video records were processed in a frame-by-frame viewing mode using arbitrary metric and time scales. The time scale was measured by the number of frames (one frame per 0.04 s). The metric scale was measured according to the video monitor size (1 mm of animal movement on the TV screen equalled a distance of 2.51 cm in the chamber).

The locomotion activity of the two species of jirds in the test situation consisted of a series of brief movements interrupted by stops. For further analysis, we selected the starting events of all movements (jumps) of each animal, which met the following requirements: (1) the motion started when the animal had remained immobile for at least six frames in succession without changing orientation or position; (2) the mean acceleration, as measured before attaining maximum velocity, was no less than 1 mm/frame^2.

Thus, we recorded all jumps of animals both during quiet movement of partners in the chamber and during their movement at maximum acceleration.

A total of 2172 jumps were counted (1108 jumps of southern jirds and 1064 jumps of clawed jirds). The positions of the animal's nose and crest were drawn frame-by-frame from the TV screen. Eight to 15 frames from the beginning of the jump were drawn (Fig. 1). The concomitant behavioral activity and directions of movement during the jump were also detected.

The behavioral events detected in this work fell into four types: (1) jumps associated with nonaggressive contacts between the partners; (2) jumps associated with aggressive behavior; (3) jumps associated with defensive behavior; and (4) jumps that were neither followed by the contacts between the partners nor resulting from the contacts between them. The direction of motion (to the partner or from the partner) was specially recorded for the jump types 1 to 3 (i.e., for the jumps associated with contacts between the partners).

The following parameters were determined for each jump:

V_{max}, the maximum momentary velocity (the maximum distance, in millimeters, at which the animal crest moved during one frame), mm/frame;

t_1, the time interval from the beginning of movement of the animal's nose to the moment at which V_{max} was attained (in frames);

t_2, the time interval from the beginning of movement of the animal's crest to the moment at which V_{max} was attained (in frames);

a_1, the mean acceleration during the time interval from the beginning of movement of the animal's nose to the moment at which V_{max} was attained (V_{max}/t_1) (in mm/frame^2);

a_2, the mean acceleration during the time interval from the beginning of movement of the animal's crest to the moment at which V_{max} was attained (V_{max}/t_2) (in mm/frame^2); and

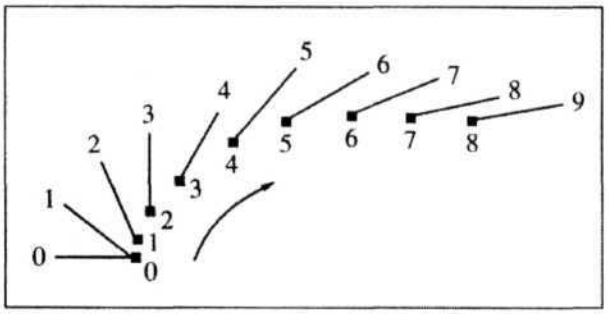

Fig. 1. Frame-by-frame drawing of one jump. An arrow shows the direction of movement of animal. Each dash shows position of animal's head and neck in one frame. Thick and thin ends of the dash show positions of animal's crest and nose, respectively. Figures at the dashes indicate the number of frames from the beginning of movement of the crest or the nose. 0, the last frame.

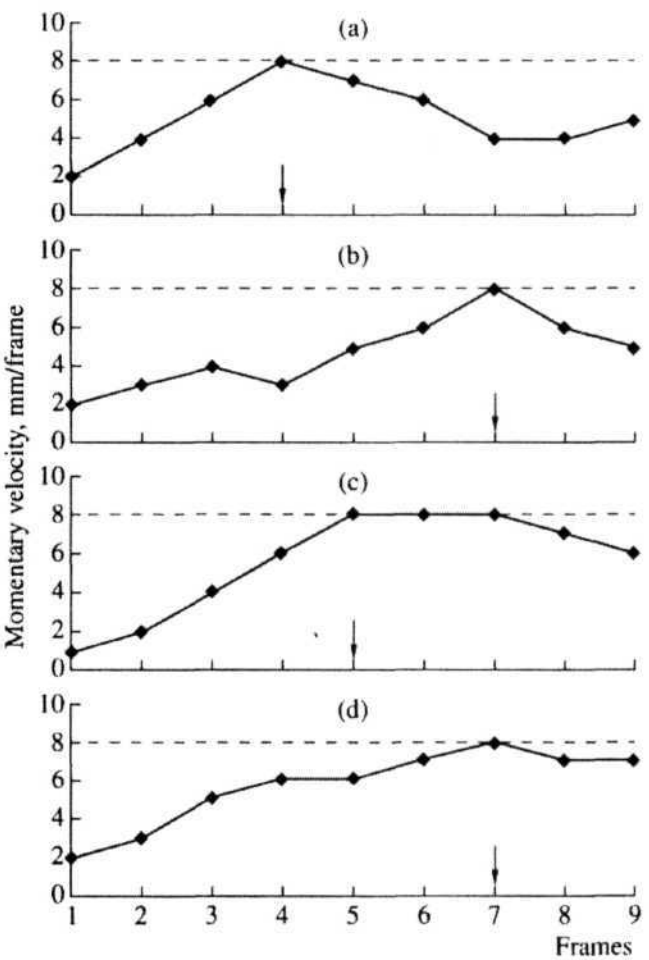

Fig. 2. Four methods of measurement of the maximum momentary velocity (V_{max}): (a) by the first maximum of velocity; (b) by the second maximum of velocity; (c) by the first plateau of velocity; (d) by the second plateau or the maximum of velocity. The horizontal dashed line shows the value of V_{max}. Arrows show the time t at which the V_{max} value is attained. For explanations, see the text.

Table 1. Intraspecies and interspecies variation (mean SD/SD of the means) of jump parameters in two species of jirds

Species	$\dot{V}_{max}$	t_1	t_2	a_1	a_2
Southern jird	1.47	3.88	3.58	2.57	4.74
Clawed jird	4.21	7.42	8.17	5.56	7.24

dt, the time interval from the beginning of movement of the animal's nose to the beginning of movement of the animal's crest (in frames); t_1 coincided with t_2 and a_1, coincided with a_2 if the movement started without a turn.

According to the type of acceleration of animal, the maximum momentary velocity of the jump from an immobile state was measured by one of four alternative methods (Fig. 2): (1) by the .first maximum of velocity, which was followed by its decrease; (2) by the second maximum of velocity, provided that between the first and the second maximums there was only one frame with the velocity lower than the first maximum; (3) by the first frame of the velocity plateau, which was followed by its decrease (a velocity plateau was assumed to be an unchanged velocity during two or more frames); and (4) by the first value of the second plateau of velocity or by the velocity maximum observed after the first plateau, provided that the first plateau comprised no more than two frames and no velocity decrease was observed between them.

Data were processed by the method of data summation, an analytical procedure in which multiple measurements of behavior of the same animal are processed as independent events. This procedure is correct if the intraindividual variation is wider than the interindividual variation [7]. This was actually observed in our experiments. As is seen from Table 1, the ratio of the mean standard deviation to the standard deviation of the mean is significantly more than 1 for the five parameters of the beginning of movement. The significance of the difference was estimated using Mann-Whitney (U-test from the nonparametric statistics package STATISTICA 4.5.

The starting events in five pairs of situations were compared in the two species of jirds. Specifically, the jump parameters were compared in the following situations:

(1) aggressive (offensive) behavior and defensive jumps;

(2) contacts and contactless jumps;

(3) nonaggressive contacts and jumps during agonistic contacts;

(4) moving toward the partner by jumps and moving away from the partner;

(5) aggressive approaching by jumps and defensive movement away from the partner (Tables 2, 3).

As is seen from Tables 2 and 3, virtually the same behavioral differences between these situations was observed in the two species of jirds.

The locomotion activity of southern and clawed jirds was compared in terms of eight different types of behavior, using the total array of experimental data (Table 4). In almost all types of behavioral activity, southern jirds exhibited a statistically and significantly higher acceleration to the maximum velocity than clawed jirds. In cases of aggressive behavior, the defensive movement toward or away from the partner, the difference between southern and clawed jirds was statistically insignificant, but the *p* value was less than 0.09.

Major situational trends in the change of velocity parameters of movement were similar in both species of jirds (compare Tables 2, 3). Probably, the main factors underlying the dynamics of velocity parameters of the two species of jirds were also similar. We think that the difference between the velocity parameters of movement in all compared situations was determined by the same factor: defensive situations were more ner-

Table 2. Comparison of pairs (context I vs. context II) of the mean values of jump parameters of southern jirds in different situations

The context in which the jump was observed	Result of comparison						The context in which the jump was observed
I	$\dot{V}_{max}$	t_1	t_2	dt	a_1	a_2	II
Aggressive behavior	<***	<*	-	-	-	-	Defensive behavior
Nonaggressive contacts	-	-	-	>**	<*	-	Agonistic contacts
Without contacts	<**	<**	<***	>*	-	>*	During contacts
Moving toward the partner	<***	<**	<*	-	<**	<*	Moving away from the partner;
Moving toward the partner during offence	<***	<*	-	-	—	–	Moving away from the partner during defense

Note: Difference is statistically significant according to Mann-Whitney (U-test: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; a dash means that the difference is statistically insignificant.

Table 3. Comparison of pairs (context I vs. context II) of the mean values of jump parameters of clawed jirds in different situations

The context in which the jump was observed	Result of comparison						The context in which the jump was observed
I	V_{max}	t_1	t_2	dt	a_1	a_2	II
Aggressive behavior	<***	<*	<*	-	-	-	Defensive behavior
Nonaggressive contacts	<**	-	<*	>**	-	-	Agonistic contacts
Without contacts	<***	<*	<***	>*	-	-	During contacts
Moving toward the partner	<***	<**	-	-	-	-	Moving away from the partner;
Moving toward the partner during offence	<***	<*	<*	—	—	—	Moving away from the partner during defense

Note: Denotations are the same as in Table 2.

Table 4. Difference between mean values of jump parameters of southern and clawed jirds for different forms of behavior

The context in which the jump was observed	Parameters					
	V_{max}	t_1	t_2	dt	a_1	a_2
	s-c	s-c	s-c	s-c	s-c	s-c
Nonaggressive contacts	-	-	_	-	>**	>*
During aggressive behavior	-	-	-	-	-	>*
During defensive behavior	-	-	-	-	>*	>*
Without contacts	-	-	<**	>*	>***	>***
Moving toward the partner	-	-	-	-	-	-
Moving away from the partner	-	-	-	-	>***	>***
Moving toward the partner in an aggressive context	-	-	-	-	>*	>*
Moving away from the partner in a defensive context	-	-	-	-	-	>**
Total	>*	-	<**	>*	>***	>***

Note: s, southern jirds; c. clawed jirds; > or < means that the mean value of the given parameter in southern jirds is higher or lower than the mean value of this parameter in clawed jirds, respectively. The other denotations are the same as in Table 2.

vous and stress-inducing than offensive situations; contact situations were more nervous and stress-inducing than contactless situations; agonistic contacts were more nervous and stress-inducing than nonaggressive contacts; and removal of the partner was more nervous and stress-inducing than approaching. More nervous situations were characterized by higher maximum velocities of jumps and duration of periods within which these maximum velocities were attained.

A different pattern was observed when analyzing the acceleration values. There was no acceleration increase as situation tension increased. The same types of acceleration were exhibited by animals in both nonaggressive and agonistic interactions. In other words, in the two species of jirds, acceleration was less dependent on the situation than other temporal parameters.

The interspecies comparison revealed that there was no statistically significant difference between the situation-dependent characteristics in the two species of jirds. However, in almost all situations, the acceleration values in southern jirds were significantly higher than in clawed jirds. It was acceleration rather than the maximum velocity that gave the impression that southern jirds are characterized by higher reactivity than clawed jirds.

There was a statistically significant interspecies difference in the duration of the period *At* during which the maximum velocity of the crest and the nose was attained in contactless situations. This was probably due to the fact that only in this situation, which is the least stressful, southern jirds usually turned the head before jumping and changed the direction of the movement. As the situation tension increased, this turn of head became less pronounced in both southern and clawed jirds, and the difference between t_1 and t_2 became less significant.

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