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Authors: Blank, David, and Yang, Weikang

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Play behaviour in goitered gazelle, *Gazella subgutturosa* (Artiodactyla: Bovidae) in Kazakhstan

David BLANK^{1,2} and Weikang YANG¹

¹ Key Laboratory of Biogeography and Bioresource in Arid Land, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi, China; e-mail: yangwk@ms.xjb.ac.cn

² Institute of Zoology, Kazakh Academy of Sciences, Alma-Ata, Kazakhstan; e-mail: blankdavidalex@yahoo.com

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Abstract. In this paper, play behaviour of goitered gazelles is considered for the first time. Young gazelles demonstrated play activity most often, followed by adult males and sub-adults, then adult females. Locomotor play (running, jumping) was the most frequently observed play behaviour, while social play (fighting, sexual play) was noted considerably less often and mostly with males. Adult gazelles played mainly in May and gazelle young in June, and primarily in the evenings (19:00-20:00). Most acts of play lasted from several seconds to a half-minute. Young gazelles played often during their suckling period or, at least in the presence of their mothers. Adult females frequently became involved in their young's play, while males played during grazing or butting. In describing goitered gazelle play patterns, we tested five hypotheses: practice-exercise, surplus energy, locomotor play ontogeny, different play types for specific stages of aging, and the social function of play. Our data for playful behaviour of goitered gazelles supported four of the five hypotheses, but contradicted the fourth listed above, which states, at least for Cuvier's gazelles, that locomotor play appears and disappears earlier than social play. The cause of this difference in results may lie in the different conditions under which groups were observed or the different extent of the studies.

Key words: gazelles, locomotor play, motor playing, social play, ungulate

Introduction

Play is a typical phenomenon for most mammalian species, in addition to a number of birds, single species of reptiles and fishes and even cephalopods (octopus), and it is an important element in human social behaviour and cultural traditions as well (Beach 1945, Chick 2008). Many researchers of both animal and human behaviour have investigated play and tried to answer the main question: what is play for. Fagen (1981) listed a total 39 definitions which were proposed over the years.

There are four main hypotheses for explanation of this phenomenon: the traditional hypotheses of surplus energy and preparation of young for adult life, and the more modern ones of optimal arousal and competence-effectiveness models (Chick 2008). According to the first hypothesis, play is motivated by a need to expend surplus energy. The second model

asserts that despite its high costs, mammals continue to play because it teaches their offspring to skills and improves their general abilities (motor and cognitive skills), resulting in possible payoff for these animals through their entire lifespan (hunting, foraging, social abilities – Allen & Bekoff 1997). When individuals play they typically use action patterns that are also used in other contexts, such as anti-predatory behaviour, mating, or fighting (Bekoff 2001). According to the arousal hypothesis, animal play for optimization of their arousal level, while the competence hypothesis states that animals satisfy their physical needs through play (Chick 2008). No single hypothesis can explain all cases of play behaviour, therefore new models to explain play continue to appear. For example, Fagen (1974) hypothesized that novel behaviour originating in play, spreads within a cohort and then becomes adaptive and typical for the whole species. And

a game-theoretical model of play posited by Dugatkin & Bekoff (2003) maintained that during social play animals learn the ground rules that are acceptable to others (how hard they can bite, how roughly they can interact) and how to resolve conflicts, play fairly and trust others. Or Bekoff (2004) theorized that play is a “foundation of fairness” and Spinka et al. (2001) that it is “a training for the unexpected”.

Play patterns are quite popular subjects for the investigation of human behaviour (Bekoff 2004, Chick 2008), however there are considerably fewer published materials for playful behaviour in animals (Bekoff 1995). Moreover, mammal researchers concentrated their efforts mostly on primates under laboratory conditions (Fagen 1981, Bekoff 2004, Tacconi & Palagi 2009), and domestic animals or rodents in captivity (Chepko 1971, Byers & Walker 1995, Jensen & Kyhn 2000, McDonnell & Poulin 2002). Information on play patterns of wild animals in their natural environments is quite limited or completely absent for many species (Bekoff 2004). Play patterns in goitered gazelles (*Gazella subgutturosa* Guldenstaedt, 1780) have not been reported before now, therefore we have tried to describe this behaviour in detail in this paper and test the major traditional hypotheses of play.

Practice-exercise hypothesis

It is well-known that young ungulates have a considerably higher mortality compared to adults, because young are smaller, less experienced and weaker targets, making them easy prey for carnivores (Gazzola et al. 2005). Therefore, fast muscle and bone development and improvement in skills necessary to flee carnivores are the keys for the survival of young in small sized ungulate species such as the goitered gazelle. In this regard we considered the motor playing hypothesis, or preparation of young for adult life hypothesis, which states that the function of play is an adaptive modification for developing the neuromuscular system (Byers & Walker 1995), particularly the brain (Byers 1999). Therefore play is a primarily juvenile phenomenon, although adult play occurs in some species, but always at a much lower rate than that of juvenile play (Bekoff & Byers 1981). Moreover, juvenile play has a distinct ontogeny, when it appears at low rates at the beginning of life, increases to a peak and then declines with maturation (Espmark 1971, Pratt & Anderson 1979, Carl & Robins 1988, Miller & Byers 1991). According to this hypothesis, we supposed that young goitered gazelles would play much more often than adult individuals, and that

this phenomenon would be observed mostly during a discrete, short period of postnatal development.

Surplus energy releasing hypothesis

This is the most traditional hypothesis, appearing as far back as the time of poet Schiller. It is proposed that when an organism stays in optimally favorable conditions, with an abundance of high quality food and a low threat from carnivores or pressure from human activity, and when other needs are not strongly engaged, there is a condition of unspent energy, which is necessary to release for the achievement of physiological equilibrium in the body. This excess energy is released through play, and play appears in the condition of surplus time and energy (Beach 1945). In this regard we suspected that goitered gazelles would play more frequently during the most favorable season of year.

Locomotor play ontogeny hypothesis

As a consequence of the surplus energy hypothesis, the assumption could be made that young would play the most while at the age of intensive suckling. Indeed, it was found that locomotor play decreased in young deer (*Odocoileus virginianus* – Muller-Schwarze et al. 1982), piglets (Newberry et al. 1988) and cattle (Jensen & Kyhn 2000) concurrent with the decrease in the mother’s milk supply during gradual weaning. In this connection, we wanted to test our third hypothesis: if there was a correlation between a notable decline in locomotor play in young goitered gazelles to the decrease in their milk supply.

Different play types for specific stages of aging hypothesis

Gomendio (1988) reported on play behaviour of young Cuvier’s gazelles (*Gazella cuvieri* Ogilby, 1841) stating that locomotor play started at high frequencies for neonates and accounted for the major proportion of total play, but then declined in their early months of development. In contrast, sexual play and play-fighting were observed infrequently shortly after birth, increased to peak between four and six months, and then decreased in later months (Gomendio 1988). In this context, we wanted to test the fourth of our hypotheses: if these differences in the times of locomotor play and sexual-fighting play appeared for goitered gazelles, as well.

Social functions of play hypothesis

Gomendio (1988) also proposed that both young and adult males were involved in social play

(fighting) more often than females, and that no such sexual differences existed for locomotor play. In this connection, we wanted to test the fifth of our hypotheses: if adult and sub-adult goitered gazelle males engaged in more fighting play than females in our study area. We were unable to do this comparative analysis for goitered gazelle young, because the focal observation method of our study in the field made it impossible to distinguish the sex of calves younger than 4-months across large distances.

Study Area

Our study area was located in the Ili Hollow which is situated in the desert zone of Central Asia, which typically has very long solar radiation (up to 3000 h per year), aridity and a continental climate. It is possible to divide the climate of these deserts into two periods: a warm and dry season from mid-May till mid-October, and a wet and cold season during end-autumn, winter and spring. The lowest temperatures are registered in January (average -8.7°C , absolute minimum -42°C) and the highest in July (average $+24^{\circ}\text{C}$, absolute maximum $+41^{\circ}\text{C}$). Precipitation does not rise above 100 mm per year, with 70 % of the total falling during spring (May, 27 mm), less in autumn-winter (November, 21 mm), with summer is usually rainless (August and September are the driest, 12 mm). Snow falls from November to March. However, due to strong winds from various directions, the Ili Hollow is devoid of snow. The average wind velocity in this area is 2.5-3.6 m/sec (maximum in January – 4.5 m/sec, minimum in August – 2.4 m/sec), with an absolute maximum of 40 m/sec. Humidity is less than 10 % during summer days, and 40-65 % in winter days. The growth period of plants is rather long at 210-240 days (Unatov 1960).

The Ili Hollow is a vast tectonic depression located between ridges of the Junggar Alatau (Tien Shan) mountains in southeastern Kazakhstan. Mountains (550-1817 m above sea level) are situated within the Hollow, with slightly inclined planes from foothills to the River Ili at a 3–7 degree slope. This region is a gravel desert, which is scarred with a thick network of dry river beds, karst craters and depressions, and intermingled with clusters of small hills and plateaus. A major zone in the central part of the Hollow is occupied by the valley of the River Ili. Three types of vegetation are found here: 1. Brush deserts, where species from family Chenopodiaceae are predominant; 2. Extremely arid areas, where there are many bare plots without any vegetation or where only *Nanophyton erinaceum* grows; and 3. Waterside

vegetation, where low riparian forests are common. The goitered gazelle is the most common wild ungulate species to be found in the Ili Hollow. Another large mammalian species is khulan (*Equus hemionus* Pallas, 1775), introduced in the Ili Hollow in 1982. From time to time, gazelles graze on the lower slopes and mountain hills not far from Siberian ibex (*Capra sibirica* Pallas, 1776) and argali (*Ovis ammon* Linn., 1766). The wolf (*Canis lupus* Linn., 1758) is the only serious predator for gazelles, although sometimes foxes (*Vulpes vulpes* Linn., 1758) attack neonates.

Material and Methods

Observations were carried out in the Ili Hollow (southeastern Kazakhstan) during 1981-1987. The main method of our study was continued focal observations for long periods of time (up to nine hours) using binoculars (magnification 8 \times) and a telescope (magnification 30-60 \times). Observation posts were usually established on elevated points.

We used definitions from both the Gomendio (1988) and Jensen & Kyhn (2000) studies for describing play behaviour of goitered gazelles. Play behaviour was categorized as locomotor play, social play, and object or ground play. Locomotor and object play were defined as locomotor experimentation with objects or the environment or with one's own body and motor patterns, experimentation which tended to develop and perfect adaptive responses to the physical environment (Fagen 1974). Locomotor play included vigorous jumping, kicking and/or running along a straight, circle, zigzag or loop-like trajectory, interrupted by short stops then turning back or veering in a new direction (Table 1). Such play was typically performed by several young at the same time, running in parallel trajectories, but in contrast to social play, it did not involve physical contact. Object and ground play or play by butting different objects was observed very rarely (only three times during our entire study), so consequently it was not inserted in Table 1. Social play or "behavior testing" functioned as active social experimentation among individuals to determine relative strengths and abilities of individuals and to allow for the prediction of future behaviour (Fagen 1974). Social play involved fighting, when two or more individuals faced each other, pushing or butting (Table 1), but unlike serious fights, play fighting was terminated without submission, flight or chase (Reinhardt & Reinhardt 1982, Vitale et al. 1986). Social play also included playful mounting, horn-forehead threats, muzzle pushing and invitations for play ("bow" according to Bekoff 2004).

Table 1. Description of the recorded playing patterns (ethogram) in goitered gazelle.

Play type	Description
Locomotor play:	All acts connected with movements of any body part or the whole animal body in the presence or absence of partner and no involve physical contact.
Running:	
Run chasing or lone-rushing	Running with partners (chasing) or alone (lone-rushing) in straight trajectory to some direction and back or by circle around the mother or group of adult gazelles or among other gazelles in zigzag or loop manner. Tail is erected and ears pressed to the head. Movement forward.
Run + signal jumps	Running with high jumps: all four legs are lifted from the ground and the whole body is elevated 0.5-0.7 m above ground surface. Tail is erected and ears pressed to the head. Movement forward-upward.
Run + tossing hind legs	Gazelle runs and tosses the hindquarter in the same time: two hind legs are lifted from the ground and hindquarter of the body is elevated (tossed) and waved from side to side. Both hind legs are kicked in a posterior direction. Tail and ears are in different position. Movement forward, spinning and reverse direction.
Gaits:	
Trot	It is a two-beat gait between a walk and a run, in which the legs move in diagonal pairs, but not quite simultaneously.
Gallop	It is a four-beat gait, which is faster than trot.
Career	It is very fast gallop, when front legs are stretching forward and hind legs are stretching backward for maximum possible extent.
Jumping:	
Jump + spinning	All four legs are lifted and the body is elevated above ground surface. Spinning (until 360°) movements in the air.
Jump + moving forward-backward	The same like former, only movement forward and backward.
Jump + kick up	The same like former, only kicking up by hind or all 4 legs in the air.
Head shaking-waving	Head is shaken or waved up-down or from side to side in playful irregular manner or sometimes rotates widely.
Social play:	All acts connected with movements directed to the partner.
Horn-forehead threat	One gazelle walks toward other one with lowered head and horns or forehead directed forward.
Butting	Two gazelles are standing front to front, butting head (horns, forehead) against head (horns, forehead) of partner in a playful manner, no chasing.
Muzzle pushing	The same like butting, only gazelles fight with the muzzle side.
Mount	One gazelle is mounting another staying on the place or following him by walk in vertical two-pedal position like male doing posture and movements during mating with female.
Invitation for play	The body is ascended from front to back, the head is lowered, legs are stretched forward, tail is twitched from side to side. The posture is similar to that of dog making invitation for play ("bow" for dogs).

To distinguish age, detailed descriptions were made of the horns (for males only), and muzzle and neck colouration. An exact determination of a gazelle's age was impossible under field conditions, so based on focal observations the gazelles were divided into three age groups: 1. Young (up to seven months) with body size noticeably smaller than an adult's, a bright dark spot on the muzzle, and males with crooked horns up to half the length of their ears; 2. Sub-adults or yearlings (up to 20 months) with body size slightly less than an adult's, a grey spot on the muzzle, and males with crooked horns equal to ear length; and 3. Adult gazelles (more than 20 months) with no spots on the muzzle above the nose, and

males with lyrate horns 1.5-3 times longer than their ears (Zhevnerov 1984).

The total time for all observations was approximately 1750 h, which included 38.3 h in March, 191.7 h in April, 469.8 h in May, 374.0 h in June, 173.3 in July, 51.0 h in August, 29.9 h in September, 50.2 h in October, 224.1 h in November and 147.7 in December. For statistical analyses, we used the General Log-linear model test (Hierarchical Log-linear Analysis, Saturated Model) and Z coefficient for testing the proportions and duration of different play types, which were performed by adult males, females, sub-adults and young within groups of various sizes across months and daytime hours. We used two indices for

Table 2. Proportion of various playing patterns, events and number of playing individuals.

Playing patterns	Cases number	Portion, %	Number of individuals	Portion, %
Run, chasing or lone-rushing	178	53.3	330	52.6
Run + signal jumps	42	12.5	83	13.2
Run + tossing hind legs	23	6.9	36	5.7
Run totally	243	72.7	449	71.5
Jumps + spinning	9	2.7	16	2.6
Jumps + moving forward-back	4	1.2	6	1.0
Jumps + kick up	8	2.4	15	2.4
Jumps totally	21	6.3	37	6.0
Butting	22	6.6	59	9.4
Head shaking-waving	26	7.8	44	7.0
Mounting each other	8	2.4	15	2.4
Horn-forehead threat	6	1.8	13	2.1
Muzzle pushing	1	0.3	3	0.5
Invitation for play	4	1.2	4	0.6
Horning plants and ground	3	0.9	3	0.5
Total	334	100	627	100

testing of play behaviour intensity: number of cases (number of observed play behavior cases per month irrespective of participants' number) and number of individuals (the total number of gazelles per month which participated in play). For the comparison, data from different years of the monthly changes in the proportion of different play types were merged. All statistical analyses were carried out using the SPSS 16.0 software package.

Results

Goitered gazelle young played most often compared to adult and sub-adult gazelles (61 %, $n = 558$; Log-linear model test, $Z = 3.830$, $P < 0.000$), followed by adult males (20 %) and sub-adults (7 % males and 4 % females), while adult females played least often (8 %, $n = 558$). Young played mainly in the presence of their mothers (98.6 %, $n = 143$; $Z = 10.157$, $P = 0.000$), rarely in the company of several peers (1.4 %) without the presence of adult females, and never alone.

Chasing each other by running was the most often observed form of play for gazelles, irrespective of age and sex (72.7 %, $n = 334$; Log-linear model test, $Z = 17.606$, $P = 0.000$), followed by less frequently noted forms of running with signal jumps or tossed hind legs (Table 2, $Z = 7.605$, $P = 0.000$). Other play patterns, such as shaking or waving their heads in an irregular manner, butting (play fighting) each other, or spinning were seen more rarely (Table 2). Compared to adult and sub-adult gazelles, young also demonstrated the highest variability of play patterns among other age groups ($Z = 6.506$, $P = 0.000$), while adult females had the least variability ($Z = -3.616$,

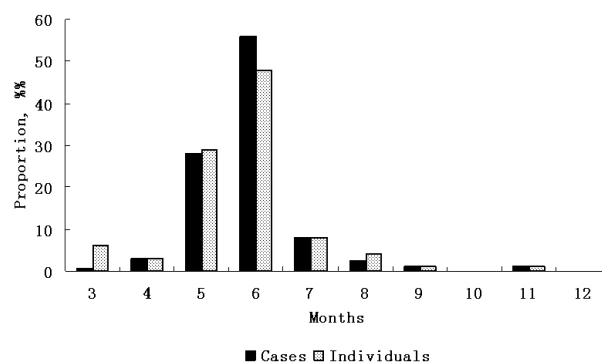


Fig. 1. Proportion of playing pattern over months (cases: number of observed cases, $n = 200$ and individuals: number of playing individuals, $n = 396$).

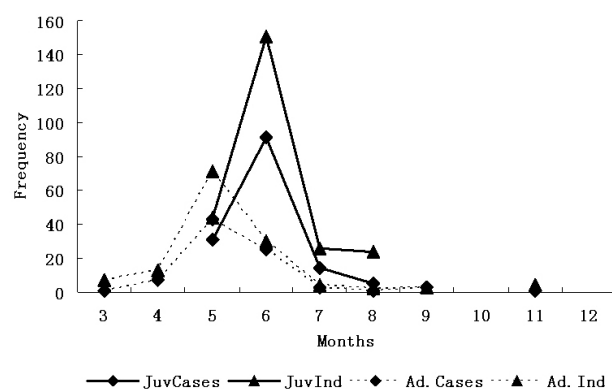


Fig. 2. Frequency of playing patterns of young and adult gazelles over months (frequency of play cases for young – JuvCases, $n = 141$ and for adults – Ad. Cases, $n = 84$; and frequency of playing individuals number – JuvInd, $n = 245$ and Ad. Ind, $n = 134$).

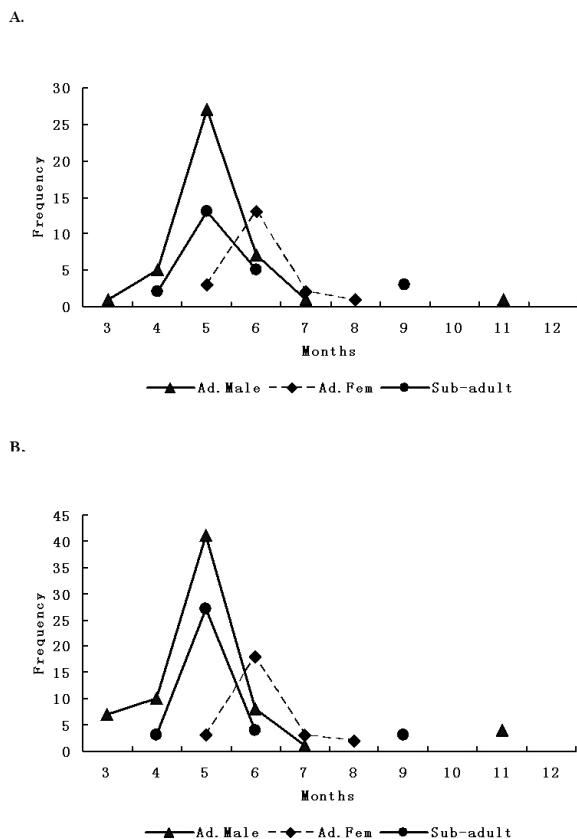


Fig. 3. Frequency of playing patterns in adult and sub-adult gazelles over months (A – frequency of cases: Ad. Male, $n = 42$; Ad. Fem, $n = 19$; Sub-adult, $n = 23$, and B – frequency of playing individuals number: Ad. Male, $n = 71$; Ad. Fem, $n = 26$; Sub-adult, $n = 37$).

$P = 0.000$), mostly chasing by running, sometimes accompanied by signal jumps. Adult male and sub-adult play pattern variability fell in between young and adult females.

Playing gazelles preferred to gallop (49 % cases, $n = 33$), followed by trotting (33 %) and careering (18 %). Their tails usually were erected vertically (76 %, $n = 26$), significantly less often seen in an intermediate (20.2 %) or lower position (3.8 %). Typically, the higher speed gaits were accompanied by a vertically erected tail and with the ears pressed to the head, while lower speed gaits were observed with a more lowered tail position and erected ears.

Usually, gazelles were engaged in play from several seconds to a half minute (54 % cases; Log-linear model test, $Z = 10.748$, $P = 0.000$), and more rarely periods of 0.5 to 1 min were also noted (14 % cases), although they did not differ from other longer periods ($Z = 1.739$, $P = 0.082$). We observed gazelles playing for longer amount of time, cases ranging 1.5 to 7 min, but these were very rare (1-7 % cases) and fluctuated

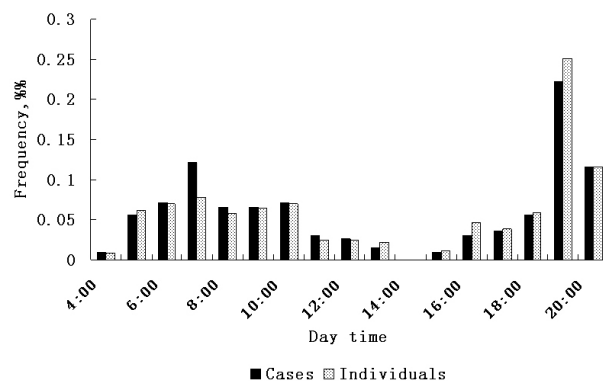


Fig. 4. Frequency of playing pattern during a day time (for observed cases, $n = 198$ and number of playing individuals, $n = 371$).

insignificantly ($P > 0.05$). All age and sex groups of gazelles (females, males, sub-adults and young) played usually within 0.5 min and the frequency of longer play bouts decreased in duration similarly for all gazelles; therefore there was not a significant difference in preference for play duration ($Z = -0.713$, -1.059 ; $P = 0.476$, 0.290), except for sub-adults with only short bouts of play ($Z = -2.726$, $P = 0.006$).

Playing goitered gazelles were observed mostly during May and June and very rare in other months (Fig. 1). Young goitered gazelles started to play regularly shortly after birth in May, increased their playing pattern frequency by three-fold during June, then abruptly decreased their play in July; and in August play was rarely observed and in September there were only a few separate cases noted (Fig. 2). In contrast, adult gazelles played significantly more often during May and less in June (Fig. 2). In other months, adult play behaviour was noted very rarely and not at all in October and December (Fig. 2). And young and adult gazelles demonstrate a significant difference in play intensity in May and June, less for July (Log-linear model test, $Z = 5.443$, 6.250 , 2.770 , $P = 0.000$, 0.000 , 0.006 , respectively), while other months did not show this difference ($P > 0.05$). Furthermore, the play behaviour frequency (cases of play) for males, females and sub-adults over the months demonstrated that the peak of play activity for males and sub-adults was observed in May, while females peaked in June (Fig. 3A). The graph showing the number of playing individuals gave almost the same results (Fig. 3B). And the Log-linear model test demonstrated this difference for May and June, and less for July ($Z = 2.907$, 3.674 , 2.341 , $P = 0.004$, 0.000 , 0.019).

Play of all gazelles, irrespective of age and sex, was divided mostly into two peaks of activity, a morning

Table 3. Proportion of locomotor and social play over months (young birth period was noted at mid-May in our study area).

	April	May	June	July	August	Total
Locomotor play (number/portion, %)						
Cases	1/0.6	39/21.9	112/62.9	20/11.2	6/3.4	178/100
Individuals	1/0.4	57/19.5	176/60.3	41/14.0	17/5.8	292/100
Social play (number/portion, %)						
Cases	-	-	20/76.9	5/19.2	1/3.9	26/100
Individuals	-	-	40/74.1	12/22.2	2/3.7	54/100
Object play (number/portion, %)						
Cases	-	-	2/	-	-	2/
Individuals	-	-	2/	-	-	2/

Explanation: Cases, number of registered cases of play; Individuals, number of playing individuals.

Table 4. Proportion of locomotor and social play for different age-sex classes during the whole period of study.

	Adult males	Adult females	Yearling males	Yearling females
Locomotor play (number/portion, %)				
Cases	37/67.3	31/	20/90.9	13/
Individuals	89/69.5	35/	29/90.6	23/
Social play (number/portion, %)				
Cases	15/27.3	-	2/9.1	-
Individuals	36/28.1	-	3/9.4	-
Object play (number/portion, %)				
Cases	3/5.4	-	-	-
Individuals	3/2.4	-	-	-
Totally:				
Cases	55/100	31/100	22/100	13/100
Individuals	100/100	35/100	32/100	23/100

Explanation: Cases, number of registered cases of play; Individuals, number of playing individuals.

peak (7:00-8:00) and an evening peak (19:00-21:00), with the highest number of playing gazelles observed in the evening after 19:00. Play behaviour was rarely observed during midday (Fig. 4). However, young and adult gazelles had slightly different playing activity over daytime hours, when young had peaks of play activity every 2-3 hours during morning hours (at 5:00, 7:00-8:00 and 10:00 a.m.), with a decrease during midday and a rise again to its daytime maximum after 19:00 (Fig. 4). Males played most often in the afternoon (after 16:00) with a peak at 19:00. Females were observed playing mostly in the evening, after 20:00 (Fig. 4). The Log-linear model test demonstrated a significant difference between young and adult females and males ($Z = -3.484$, -2.370 , $P = 0.000$, 0.018 , respectively). No gazelles had a significant differences in changing of playing activity over the period of a day ($P > 0.05$), except for late evening, after 20:00, when the young decreased

their play, females increased theirs, and males played very rarely ($Z = 10.118$, $P = 0.000$).

Locomotor play was observed from the second day of young life in May (22 %), reached a maximum in June (63 %), then decreased considerably during July and August (Table 3). Social play of young was observed starting in June, when it was at its highest frequency, then decreasing in July and in August to almost nothing (Table 3). And object play was observed only twice for goitered gazelle young. Comparison of proportions between locomotor play (80-85 %) and social play (20-15 %) of young demonstrated a high significant difference in frequency (Log-linear analysis, $Z = 5.001$, $P = 0.000$), while months had a lower effect ($Z = -1.318$, 6.985 , 0.525 , $P = 0.187$, 0.000 , 0.600 for June, July, August). Among adult and sub-adult gazelles, locomotor play was noted slightly more often for adult males (36 %, $n = 101$) than for adult females (31 %) and yearlings (33 %); and male yearlings were

observed in locomotor play more frequently (20 %, $n = 101$), than female yearlings (13 %). Social play was observed in adult males and male yearlings 2-3 and nine times, respectively, less often than locomotor play, and never for adult and yearling females (Table 4). All males, including adults and sub-adults, participated in locomotor play slightly more often than all females (Log-linear analysis, $Z = 2.615$, $P = 0.009$), although the interaction of age (adult, yearling) and sex (male, female) factors had a low significance ($Z = -2.065$, $P = 0.039$), while social play was observed significantly more rarely and only for adult and sub-adult males (Table 4; $Z = 4.837$, $P = 0.000$).

Most often, the young played with other young together, but in the presence of their mothers (39 % cases, $n = 459$). More rarely (24 %), they played alone, but also in the presence of mother, as well. Furthermore, almost 20 % of the play cases for both with or without playmates was observed during suckling. Young rarely played with adult males (3.1 %) or sub-adults (2.1 %, $n = 459$). Adult gazelles usually played during feeding (8.2 %) and butting with each other (5.2 %). We observed rare cases of gazelles playing while running against strong winds (2.1 %), while chasing of fox or other kinds of aggressive behaviour, and after rest (1 %).

The Log-linear model analysis demonstrated that young played in the company of other young usually in the female groups of three individuals (mother and her twin, $Z = 14.452$, $P = 0.000$), less often they played within larger groups of two sizes, 5 and > 10 individuals ($Z = 2.648$, -2.549 , $P = 0.008$, 0.011 , respectively). And this play was accompanied usually by suckling most often for the same groups of three individuals (mother and twin, $Z = 2.237$, $P = 0.025$). Playing single young were observed commonly in groups of two individuals (mother and young, 45 %, $n = 112$; $Z = 5.745$, $P = 0.000$), not so as often in groups of three (29 %), and more rarely in larger groups. Playing sub-adults were noted most often in groups of 2-3 individuals (57 %, $n = 30$) and rarely in larger groups. Adult males played usually in large groups of > 3 individuals (86 %, $n = 73$; $Z = -2.549$, $P = 0.011$). Only sub-adults (two cases or 7 %, $n = 30$) and an adult female (one case or 20 %, $n = 5$) played within being alone, while young and males played always within groups ($Z = -2.173$, $P = 0.030$).

Discussion

Let us consider each of our five hypotheses in more detail and define how each relates specifically to goitered gazelles.

Practice-exercise (or neuromuscular training) hypothesis

According to our data, goitered gazelle young played much more often and had the highest pattern variability of this behaviour compared to adults and sub-adults which supports the practice-exercise hypothesis. Brownlee (1954) was the first to propose that the function of play is a modification of muscle development and called these the “play muscles”. Later, Bekoff & Byers (1981) defined the broader term of “motor training”, implying that play contributed to the improvement of any subsequent motor functions, including muscle, bone and connective tissue development, brain, and peripheral nervous and cardiovascular systems progress, or any other development. This hypothesis, however, cannot explain the good physical condition found in animals deprived of play (Muller-Schwarze 1968, Chepko 1971), although Jensen (2001) found that calves of cattle played more after deprivation. This hypothesis does predict correctly that play is more typical for juveniles than adults and that juvenile play has a distinct ontogeny, beginning at a low rate in early postnatal life, rising to a peak and then declining (Byers & Walker 1995). Our data support these points for goitered gazelles (Fig. 3), and also coincide with the play behaviour of many other ungulate species (Espmark 1971 for reindeer – *Rangifer tarandus* Linn., 1758; Hass & Jenni 1993 for bighorn sheep – *Ovis canadensis* Shaw, 1804; Miller & Byers 1991 for pronghorn – *Antilocapra americana* Ord., 1815; Pratt & Anderson 1979 for giraffe – *Giraffa camelopardalis* Linn., 1758) etc. During the most intensive development period for juveniles, play usually occurs daily, and often at specific times of day (Byers 1984, Miller & Byers 1991). We observed the most frequent play behaviour of goitered gazelle young was during June (Fig. 2), when they were at their peak intensity in growth and development (Zhevnerov et al. 1983). So, our data on goitered gazelle coincide completely with the predictions of this hypothesis.

Surplus energy releasing hypothesis

This is the longest held hypothesis on play behaviour, and most of the efforts to test it have failed (Bekoff & Byers 1981). Muller-Schwarze (1968) and Chepko (1971), however, found that for both black-tailed deer (*Odocoileus hemionus* Rafinesque, 1817) and goats, there were no developmental differences between young that played and young that were deprived of play. And Jensen (2001) observed that after the deprivation of play, cattle calves increased their play activity in relation to the length of their

confinement. In our study, goitered gazelle young had their highest play activity in June. The most favorable time of development for gazelle young was their most intensive period of suckling at the end of May through June; suckling then decreased considerably in July (Blank 1986). Correspondingly, the play rate of young started to increase in May, reached its peak in June and dropped abruptly in July (Fig. 2). In this connection, our data supports the surplus energy hypothesis for gazelle young.

In most mammalian species adult play is nonexistent, or highly unpredictable, occurring at a negligible rate (Byers & Walker 1995). For goitered gazelles, adult individuals also play mostly in May and June, but rarely in other months and with a high degree of unpredictability (Fig. 2 and 3A, B). All adult and sub-adult gazelles, except adult females, played most often in May (Fig. 3A, B), which is the most favorable time of year in this region of Kazakhstan with moderate temperatures and maximum precipitation resulting in abundant, high-quality food (Zhevnerov et al. 1983, Zhevnerov 1984). Play by adult females occurred mainly during June, because they frequently participated in play bouts initiated by juveniles as it was noted for aoudad (*Ammotragus lervia* Pallas, 1777), as well (Habibi 1987). Therefore the play activity of adult females coincided with the maximum peak of play for their young in June (Fig. 2 and 3A, B). Over the hours in a day, young played every 2-3 hours during the morning while in their suckling period of growth (Blank 1986). The peak of young play was observed in the evening (after 19:00), during the most favorable windless warm weather and when most young had received their evening meal. Adult males and females also preferred to play often during evening hours (after 19:00), although females played later than the others (after 20:00), when most had finished their daily suckling cycle and were quite full after the evening grazing. So, our results for goitered gazelles, both young and adult, support the surplus energy hypothesis.

Locomotor play ontogeny

Locomotor play starts at a low rate in early postnatal life, rises to a peak rate at about mid-lactation, then declines (Byers & Walker 1995). This pattern was also identified for a number of ungulate species (black-tailed deer, *Odocoileus hemionus* – Muller-Schwarze et al. 1982; piglets – Newberry et al. 1988; and cattle – Jensen & Kyhn 2000, Krachun et al. 2010), where the rate of locomotor play decreased at the same time as the start of the weaning process and a decline in milk supply. Locomotor play of goitered gazelle young had

exactly the same ontogeny (Table 3), when they sharply decreased their locomotor playing in July, concurrent with a considerable drop in the duration and frequency of suckling (Blank 1986). So, the third proposed hypothesis was supported by our data, as well.

Different play types for specific stages of aging

Investigation of play behaviour of Cuvier's gazelle (*Gazella cuvieri*), Gomendio (1988) found that locomotor play appeared at a high rate shortly after birth, reaching its peak at age two weeks, then decreasing thereafter. In contrast, social play (fighting and sexual play) for the Cuvier's gazelle started significantly later than locomotor play, reaching its peak only at the age of 4-6 months and then decreasing. According to our results, goitered gazelle young reached their peak of locomotor play in June, at the age of 4-6 weeks and then declined this kind of play in July, when they were older than six weeks (Table 3). The goitered gazelle is larger in size and body weight compared to Cuvier's gazelle (20-43 kg is weight of goitered gazelle male – Heptner et al. 1961 and 20-35 kg is weight of Cuvier's gazelle – Kingdon 1997), and the young of larger sized mammals take longer to develop than smaller ones (Blueweiss et al. 1978), denoting a difference in development time of these two gazelle species. Social play in goitered gazelle young was observed starting from the third week (Table 3), which was equivalent to what was found for Cuvier's gazelle (Gomendio 1988). However, the young of the goitered gazelle had their peak of social play simultaneously with locomotor play in June and in July and in August the social play rate decreased correspondingly with the locomotor play rate (Table 3). As a result, we did not find any difference in the proportion of locomotor play and social play in June, July and August. In other words, our results contradicted our fourth hypothesis on social play ontogeny. In contrast, object play was observed very rarely in Cuvier's gazelles at all ages (Gomendio 1988), and was also noted rarely for goitered gazelles (only three times in total). Object play is very important for juvenile development in primates (Fagen 1981) but uncommon for ungulates, for which the motor training or locomotor play is most important (Byers & Walker 1995).

Social function of play

Gomendio (1988) found that Cuvier's gazelle males participate in social play (fighting, sexual play) more often than females of the same age. This same

phenomenon was found for a number of other ungulate species as well: cattle (Vitale et al. 1986), Siberian ibex (Byers 1980), bighorn sheep (Hass & Jenni 1993), domestic sheep (Berger 1979), and domestic pigs (Dobao et al. 1985). This regularity coincides with the more general idea of the practice-exercise hypothesis, which affirms that during play animals improve their skills, which they will be needed for their survival (Bekoff & Byers 1981). According to our results, adult and sub-adult goitered gazelle males engaged in social play (fighting, sexual play), while adult and sub-adult females did not join in social play at all (Table 4). So, our data supported our fifth hypothesis.

Thus, our results for goitered gazelle supported four of our five proposed hypotheses, namely, practice-exercise and surplus energy hypotheses for adults and young, and locomotor play ontogeny and the social function of play hypotheses. Our data did not support our fourth hypothesis of different locomotor and social play types for specific stages of aging. The cause of this discrepancy may be due to the influence of the semi-captive conditions under which the Cuvier's gazelle group was observed an environment protected from carnivores and other natural negative factors and with an artificial continuous supply of food and water (Alados & Escos 1994). The goitered gazelles study group, on the other

hand, was observed in a purely natural environment, which was more changeable and unpredictable. Another possible cause in the results of the two species may have been due to the better conditions for collecting continuous data with the semi-captive Cuvier's gazelle, while collecting data in the wild environment of the goitered gazelle depended on many additional objective and subjective factors. As a result, our data may not have been as sequential and comprehensive compared to that of the Cuvier's gazelles.

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Literature

- Alados C.L. & Escos J.M. 1994: Variation in the sex ratio of a low dimorphic polygynous species with high levels of maternal reproductive efforts: Cuvier's gazelle. *Ethol. Ecol. Evol.* 6: 301–311.
- Allen C. & Bekoff M. 1997: Species of mind: the philosophy and biology of cognitive ethology. *MIT Press, Cambridge, MA.*
- Beach F.A. 1945: Current concepts of play in animals. *Am. Nat.* 79 (785): 523–541.
- Bekoff M. 1995: Play signals as punctuation: the structure of social play in canids. *Behaviour* 132: 419–429.
- Bekoff M. 2001: Social play behaviour. *J. Conscious. Stud.* 8 (2): 81–90.
- Bekoff M. 2004: Wild justice and fair play: cooperation, forgiveness, and morality in animals. *Biol. Philos.* 19: 489–520.
- Bekoff M. & Byers J.A. 1981: A critical reanalysis of the ontogeny of mammalian social and locomotor play: an ethological hornet's nest. In: Immelmann K., Barlow G.W., Petrinovich L. & Main M. (eds.), *Behavioural development: The Bielefeld Interdisciplinary Project. Cambridge University Press, New York*: 296–337.
- Berger J. 1979: Social ontogeny and behavioural diversity: consequences for bighorn sheep *Ovis canadensis* inhabiting desert and mountain environments. *J. Zool. Lond.* 188: 251–266.
- Blank D.A. 1986: Peculiarities of social and reproductive behaviour of *Gazella subgutturosa* in the Ili Hollow. *Zool. Zh.* 64: 1059–1070. (in Russian with English summary)
- Blueweiss L., Fox H., Kudzma V., Nakashima D., Peters R. & Sams S. 1978: Relationship between body size and some life history parameters. *Oecologia* 37: 257–272.
- Brownlee A. 1954: Play in domestic cattle in Britain: an analysis of its nature. *Br. Vet. J.* 110: 48–68.
- Byers J.A. 1980: Play partner preferences in Siberian ibex, *Capra ibex sibirica*. *Z. Tierpsychol.* 53: 23–40.
- Byers J.A. 1984: Play in ungulates. In: Smith P.K. (ed.), *Play in animals and humans. Blackwell, Oxford*: 43–65.
- Byers J.A. 1999: The distribution of play behaviour among Australian marsupials. *J. Zool. Lond.* 247: 349–356.
- Byers J.A. & Walker C. 1995: Refining the motor training hypothesis for the evolution of play. *Am. Nat.* 146 (1): 25–40.

- Carl G.C. & Robbins C.T. 1988: The energetic cost of predator avoidance in neonatal ungulates: hiding versus following. *Can. J. Zool.* 66: 239–246.
- Chepko B.D. 1971: A preliminary study of the effects of play deprivation on young goats. *Z. Tierpsychol.* 28 (5): 517–526.
- Chick G. 2008: Altruism in animal play and human ritual. *World Cult. eJ.* 16 (2): 1–17.
- Dobao M.T., Rodriganez J. & Silio L. 1985: Choice of companion in social play in piglets. *Appl. Anim. Behav. Sci.* 13: 259–266.
- Dugatkin L.A. & Bekoff M. 2003: Play and the evolution of fairness: a game theory model. *Behav. Process.* 60: 209–214.
- Espmark Y. 1971: Mother-young relationship and ontogeny of behaviour in reindeer (*Rangifer tarandus* L.). *Z. Tierpsychol.* 29: 42–81.
- Fagen R. 1974: Selective and evolutionary aspects of animal play. *Am. Nat.* 108 (964): 850–858.
- Fagen R. 1981: Animal play behavior. *Oxford University Press, Oxford.*
- Gazzola A., Bertelli I., Avanzinelli E., Tolosano A., Bertotto P. & Apollonio M. 2005: Predation by wolves (*Canis lupus*) on wild and domestic ungulates of the western Alps, Italy. *J. Zool. Lond.* 266: 205–213.
- Gomendio M. 1988: The development of different types of play in gazelles and functions of play. *Anim. Behav.* 36: 825–836.
- Habibi K. 1987: Mother-young interactions in aoudads, *Ammotragus lervia*. *Southwest. Nat.* 7: 111–116.
- Hass C.C. & Jenni D.A. 1993: Social play among juvenile bighorn sheep: structure, development, and relationship to adult behavior. *Ethol.* 93: 105–116.
- Heptner V.G., Nasimovich A.A. & Bannikov A.G. 1961: Persian gazelle. In: Heptner V.G. (ed.), Mammals of the Soviet Union. Ungulates, Vol. 1. *High School press, Moscow*: 423–440.
- Jensen M.B. 2001: A note of the effect of isolation during testing and length of previous confinement on locomotor behaviour during open-field test in dairy calves. *Appl. Anim. Behav. Sci.* 70: 309–315.
- Jensen M.B. & Kyhn R. 2000: Play behaviour in group-housed dairy calves, the effect of space allowance. *Appl. Anim. Behav. Sci.* 67: 35–46.
- Kingdon J. 1997: The Kingdon field guide to African mammals. *Academic Press, London and New York.*
- Krachun C., Rushen J. & de Passille A.M. 2010: Play behaviour in dairy calves is reduced by weaning and by low energy intake. *Appl. Anim. Behav. Sci.* 122: 71–76.
- McDonnell S.M. & Poulin A. 2002: Equid play ethogram. *Appl. Anim. Behav. Sci.* 78: 263–290.
- Miller M.N. & Byers J.A. 1991: The energetic cost of locomotor play in pronghorn fawns. *Anim. Behav.* 41: 1007–1013.
- Muller-Schwarze D. 1968: Play deprivation in deer. *Behaviour* 31: 144–162.
- Muller-Schwarze D., Stagge B. & Muller-Schwarze C. 1982: Play behaviour: persistence, decrease, and energetic compensation during food shortage in deer fawns. *Science* 215: 85–87.
- Newberry R.C., Wood-Gush D.G.M. & Hall J.W. 1988: Playful behaviour of piglets. *Behav. Process.* 17: 205–216.
- Pratt D.M. & Anderson V. 1979: Giraffe cow-calf relationships and social development of the calf in the Serengeti. *Z. Tierpsychol.* 51: 233–251.
- Reinhardt V. & Reinhardt A. 1982: Mock fighting in cattle. *Behaviour* 81: 1–13.
- Spinka M., Newberry R.C. & Bekoff M. 2001: Mammalian play: training for the unexpected. *Q. Rev. Biol.* 76: 141–168.
- Tacconi G. & Palagi E. 2009: Play behavioural tactics under space reduction: social challenges in bonobos, *Pan paniscus*. *Anim. Behav.* 78: 469–476.
- Unatov A.A. 1960: On some ecological and geographical regularities of vegetation cover in Xinjiang. In: Unatov A.A. (ed.), Natural conditions of Xinjiang. *Academy of Sciences USSR, Moscow*: 10–40.
- Vitale A.F., Tenucci M., Papini M. & Lovari S. 1986: Social behaviour of the calves of semi-wild Maremma cattle, *Bos primigenius taurus*. *Appl. Anim. Behav. Sci.* 16: 217–231.
- Zhevnerov V.V. 1984: Goitered gazelle of the Barsa-Kelmes Island. *Nauka of the Kazakh. SSR, Alma-Ata.*
- Zhevnerov V.V., Bekenov A.B. & Sludskiy A.A. 1983: Goitered gazelle. In: Gvozdev E.V. & Kapitonov V.I. (eds.), Mammals of Kazakhstan, Vol. 3, Part 3. Artiodactyla. *Nauka of the Kazakh. SSR, Alma-Ata*: 11–54.