



Suckling behavior in goitered gazelle: do females invest more in twins or singletons?



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ARTICLE INFO

Article history:

Received 11 October 2014

Received in revised form 8 February 2015

Accepted 19 February 2015

Available online 16 June 2015

Keywords:

Goitered gazelle
Maternal investment
Rearing strategy
Suckling behavior

ABSTRACT

The mother–offspring social unit is a universal feature in the social life of all mammals and nursing is the most direct and vital component of maternal investment in young. Living in diverse environments, various ungulate species have different strategies for rearing offspring, from bearing a single, relatively large newborn and supplying only limited amounts of milk, to bearing several relatively small newborns with intensive post-partum lactation. In this paper, we consider the rearing strategy of goitered gazelle with a focus on suckling behavior, which, until now, has never been a subject of special investigation. Adult females of this species in their reproductive prime typically bear twins when environmental conditions are favorable, but the proportion of singletons increases when conditions are unfavorable. We expected that in goitered gazelles suckling intensity would be maximal during the first weeks after birth, and then decrease with the growth of the young; we also expected that twins would demand more energy, but receive significantly less maternal investment per young than singletons. We found that, indeed, suckling behavior had similar dynamics as typical of all bovid species, but our expectation for less maternal investment in twins vs. singletons was wrong. In reality, female goitered gazelles suckled twins significantly more intensively and terminated suckling less often compared to singletons. We concluded that in favorable situations females of high quality have the ability to show significantly more maternal investment in each twin, while singletons are typically born to weaker females. This ability of females to produce mostly twins allows goitered gazelles to take advantage of any favorable opportunity to quickly increase their population in an environment with unpredictable and abrupt yearly changes typical of the arid regions of Central Asia.

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1. Introduction

Suckling behavior, which creates a mother–offspring social unit, is an essential and universal feature of the social life of all mammals (Eisenberg, 1981). The reproductive success in a population depends on the number and quality of young produced in each reproductive event and on the number of such events over the lifetime of each individual (Sikes, 1995). The most direct and vital component of maternal investment in offspring in mammals is lactation, which is energetically the costliest, accounting for up to 75% of all the energy expended by ungulate females on reproduction

(Millar, 1977; Oftedal, 1985; Clutton-Brock et al., 1989). Suckling itself and its progressive attenuation (weaning) are crucial elements contributing to the reproductive success of both the mother and her young (Lavigne and Barrette, 1992). Offspring survival and growth have a strong positive correlation with maternal investment of energy during late gestation and early lactation (Skogland, 1983) and depend on three factors: the quality of the milk (Oftedal, 1984), the rate of milk transfer (Loudon, 1985), and the length of the lactation period (Festa-Bianchet et al., 1994).

In general, maternal care strategy of ungulates can be roughly classified into two groups: followers, when young constantly stay close to their mother and follow her everywhere from soon after birth; and hiders, when young do not follow their mothers during the initial period after birth but instead remain hidden at a distance between suckling bouts (Lent, 1974). Ungulate species belonging to the different strategies have distinctive differences in mother–young behaviors (Ralls et al., 1986), and through

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nursing, young receive their first lessons in the social life of their kind (Eisenberg, 1981). In addition, ungulate species have to adapt to the specific environment of their habitat and suckling behavior is one of the most important parts of these adaptations, since without sufficient breeding success, population prosperity would be impossible (Rachlow and Bowyer, 1994; Byers and Hogg, 1995). Therefore, the investigation into the variability of suckling behavior in different mammal species is vital to understanding the species' sociobiology and ecological and behavioral adaptations to the natural environment from an evolutionary perspective.

In ungulates, studies of suckling behavior have been performed on a variety of species and in a wide range of captive and natural settings (Reale et al., 1999; Therrien et al., 2007; Moreno et al., 2011; Pluháček et al., 2014). These investigations, however, have been concentrated on either domestic animals or wild animals in captive or semi-captive conditions, making data on these species more widely available (Gauthier and Barrette, 1985; Ralls et al., 1986; Laviguer and Barrette, 1992; de Passille and Rushen, 2006; Bartos et al., 2001; Drabkova et al., 2008; Hejcmanova et al., 2010; Pluháček and Bartosová, 2011; Brandlova et al., 2013). In contrast, studies of suckling behavior in wild ungulates living in completely natural environments are still relatively limited (Espmark, 1969, 1971; Autenrieth and Fichter, 1975; Trillmich, 1990; Rachlow and Bowyer, 1994; Reale et al., 1999; Dalezsczyk, 2004; Zapata et al., 2009), especially for antelopes (Moreno et al., 2011). Therefore, we have devoted this paper to the consideration of nursing behavior of female goitered gazelles, which until now has never been the subject of special investigation, making this the first available data on these behaviors for this species in a totally natural environment.

The goitered gazelle (*Gazella subgutturosa*) is a medium-sized ungulate, which was originally spread widely over Middle and Central Asia, Iran, Afghanistan, Turkey, and the Caucasus (Kingswood and Blank, 1996). This species typically lives in small groups of 2–3 individuals (Blank et al., 2012). Adult males establish individual territories during the rut in November and December, as well as a “false” rut in April and May (Blank, 1998). Adult females give birth in mid-May and most (up to 75% in years with favorable environmental conditions) produce twins, while young and old females usually produce a single offspring (Kingswood and Blank, 1996). During their first weeks of life, young goitered gazelles stay alone without their mother for most of the day (Blank, 1985), with females returning to their offspring only to suckle. During these visits the young receive a number of suckles before the mothers again leave for several more hours until the next bout of suckling. As their young grow, the females stay with their offspring for longer periods of time until the young reach the age of two months, when they start to follow their mothers constantly (Blank, 1985).

It has been proven that the suckling duration is not a reliable indicator of milk transfer (Day et al., 1987; Cameron, 1998; de Passille and Rushen, 2006), and it is difficult or even impossible to measure the amount of milk transferred without weighing the young before and after each nursing session (de Passille and Rushen, 2006) or using the radioactive isotope technique (Cameron et al., 1999). However, the time spent suckling still carries information about maternal investment (Berger, 1979; Gauthier and Barrette, 1985; Trillmich, 1990; Obregon et al., 1992a; Dalezsczyk, 2004). A number of earlier detailed investigations of suckling behavior in wild sheep demonstrated that there is a close correlation between the measured suckling parameters and the growth rate of young, with an increase in suckling time having a positive effect on the growth and survival of the offspring (Geist, 1971; Reale and Bousses, 1995). This means then that mothers make an investment (either nutritive or social) in their young's growth when they allow them to suckle frequently or for longer periods of time, even if part of that time is non-nutritive, meaning young do not receive milk (Horesji, 1976; de Passille and Rushen, 2006; Cameron

et al., 2008). Some suckles are too short to be nutritive and serve mostly to strengthen the mother–offspring bond (Shackleton and Haywood, 1985). Non-nutritive suckling is still an essential part of nutritive suckling and the growth of young mammals in that the tactile stimulation of the udder induces prolactin synthesis, which in turn triggers milk production (Pedersen, 2009). In addition, since offspring often seek their mothers to suckle when they are distressed or alarmed (Clutton-Brock, 1991; Pluháček et al., 2014), suckling satisfies not only the young's nutritional needs but also their emotional and social needs (Carson and Wood-Gush, 1983; Cameron, 1998; Pluháček et al., 2014). This means that a female's maternal expenditure includes not only milk (energy), but also time spent with her young (Reale et al., 1999). So instead of limiting our research of suckling behavior to just measurements of the exact amounts of milk transferred, we considered the maternal investment in goitered gazelle as a complex of nutritive and non-nutritive suckles as well as social behaviors, which we believe are more reliable indicators of a mother's investment in her young. In addition, there have been some studies that have suggested that changes in suckling behavior (suckling duration and frequency) may also closely correlate with the amount of milk transfer (Mendl and Paul, 1989; Therrien et al., 2007; Cameron et al., 2008; Pluháček et al., 2014).

Thus, in the present paper we have quite deliberately used several nursing parameters for investigating goitered gazelle suckling behavior with the knowledge that some of the measured suckles were non-nutritive and had more of a social meaning. We have interpreted this essential complex of different nursing behaviors as the maternal investment in the rearing of young. We were also interested in the changes in maternal investment with the growth of the young and checked possible differences in suckling behaviors of mothers with single young compared to those with twins.

European mouflon ewes (*Ovis orientalis musimon*) commonly let their young suckle as long as they want during the first two weeks of lactation (Ewbank, 1967; Obregon et al., 1992b), followed by a decrease in the rate of milk transfer indicating a gradual weaning process that is very often accompanied by changes in mother–young behaviors (Martin, 1984). Based on this observation, we developed our first hypothesis that the same processes would be typical of the suckling behavior of goitered gazelles and that their young would generally receive unlimited suckles during the first two weeks of lactation, followed by a gradual weaning; additionally, all parameters of suckling behavior (suckling duration, intervals between suckles (frequency), total suckling time per bout, rate of females' termination of suckles and unsuccessful suckling attempts) would indicate a decrease in milk intake as well as maternal investment in the growth of the young.

Studies of mammalian reproductive activity have shown an increase in maternal energetic costs associated with an increase in litter size (Sikes, 1995). For example, Ruiz-Miranda et al. (1998) found that milk allocation in domestic goats was affected significantly by litter size, and that mother–young interactions were different between twins and singletons. Also, since the female's milk production did not increase for twins, her milk supply was more limited for twins, thus allowing singletons to obtain more milk and gain more weight (Figueiredo et al., 1982; Hadji-panayiotou, 1986; Alley et al., 1995). Reduced suckling frequencies and poorer growth rates in twins relative to singletons have also been reported in domestic sheep (Ewbank, 1967) and cattle (Price et al., 1984/85), because of sibling competition. Based on these findings, we proposed our second hypothesis that twins in goitered gazelles would exhibit suckling with shorter durations and longer intervals (lower frequency) compared to singletons, and that twins' suckling would be terminated by their mothers more frequently; also, cases of unsuccessful suckling would be observed more often

in twins than in singletons. In other words, a twin would receive less maternal investment than a singleton.

2. Materials and methods

We observed suckling behavior of female goitered gazelles in their natural environment of the Ili depression (southeastern Kazakhstan) during a 6-year period from 1981 to 1986. For our research, we used the continued focal animal observation method, which most accurately reflects the time spent suckling (Mendl and Paul, 1989; Cameron, 1998). All of the behaviors were recorded by one observer during the entire observation period and were recorded in the order in which they occurred and each time they occurred (all-occurrences sampling). In most cases, gazelles were observed from distances of 50–100 m using binoculars (magnification 8×) or a spotting scope (magnification 30–60×). Observation posts were usually established on elevations and in different parts of our study area to reduce pseudo-replication. Most females in the population gave birth within a period of several days starting in mid-May, which limited the movements of mothers and young during May and June (Blank, 1985). This allowed us to concentrate on 2–3 randomly selected females with young (usually the closest) for simultaneous observations from the same point for as long as possible (up to 9 h). Usually, these females had suckling bouts at different times, which gave us the possibility to observe their suckling behavior one at a time; in rare cases, when suckling occurred simultaneously, we recorded the behavior of the closest mother with young.

We measured several indices of suckling behavior: suckle duration (s), intervals between suckling bouts (min), and total suckling time per bout (s). The suckling duration was measured from when the young took a teat in its mouth and made clear suckling movements with its head until it left the teat and lifted its head, or the mother stepped or jumped forward and walked off. After birth, each twin stayed in a different resting place and suckled separately from the other. At the age of 5–7 days, the mother began to suckle them simultaneously, with both twins usually starting and finishing to suckle at the same time; in some cases, one twin started later or finished earlier than the other. Regardless of when each twin began suckling, in the cases of restricted suckles the mother stopped her nursing of both twins simultaneously (Blank, 1985). When twins started and stopped suckling together, we recorded two values of the same duration, and when they started and/or finished at different times (in the cases of non-restricted nursing), we recorded two different values. As a rule, detecting the exact time of suckling duration was not a problem with the closeness of our observation post and the help of the spotting telescope. Even when the young suckled from the far side of the female or when the twins suckled simultaneously or when the moment a teat was left could not be observed directly, it was possible to determine the end of a bout because the young lifted its head abruptly as soon as it finished suckling. If it was not possible to clearly determine when the young left the teat and/or raised its head when ending a suckling bout, these data were excluded from our calculations.

Instead of suckling frequency (number of suckles per h), the frequency characteristic of intervals between suckles was used. In goitered gazelle, the female visits her hiding offspring 2–4 times a day. During each of these visits the offspring receives a series of suckles, which we called a suckling bout, before being left alone again for several more hours (Blank, 1985). In addition to suckling duration, we measured the intervals between each separate suckle (within a bout) and summarized these suckles as the total time per suckling bout. Furthermore, we noted who terminated suckling, mother or young, and cases when females did not allow their young to suckle by terminating suckling attempts immediately. Since the

females in our study were not marked, independence of data cannot be assumed.

To analyze the changes in suckling behavior with changes in the age of the young, we pooled data for approximately every 15 days. Since goitered gazelle females give birth in mid-May, suckling behavior was observed mostly during May–August, so we defined the following periods: late May (15–31 May), early June (1–15 June), late June (16–30 June), early July (1–15 July), late July (16–31 July), early August (1–15 August), and late August (16–31 August). Even as late as September–December and as early as April, we noted separate, very short (2–3 s) suckles, but these were observed very rarely (1–2 times a month) and resembled more unsuccessful suckling attempts (quickly terminated) than real suckling. For bighorn sheep (*Ovis canadensis*), Shackleton and Haywood (1985) considered suckles shorter than 5 s as unsuccessful suckling attempts, but for goitered gazelle we defined suckles shorter than 2 s as unsuccessful, because suckles of 2 s may also be nutritive (Haley et al., 1998a). Successful suckles separated by even short interruptions (a split second) we considered as two. Aiming for a deeper analysis of changes in suckling duration during the first month after birth (late May to early June), we also tried pooling our data for every 5 days; but since this analysis gave almost the same results as our 15-day analysis, we used mostly the latter one. For the entire 6 years of our study, we had a total of 181 h of observations in April, 470 h in May, 374 h in June, 173 h in July, 50 h in August, 63 h in October, 224 h in November and 148 h in December.

According to the Shapiro–Wilk and Kolmogorov–Smirnov tests, our data had a nonparametric distribution; so we transformed our data into parametric form by using the Log 10 technique and used the general linear model (GLM; full factorial model, Type III) tests to compare several main indices (dependent variables) of suckling behavior (suckle duration, intervals between suckles, and total time suckling per bout). We used observation year, season (age of young), and litter size as fixed factors and considered their main effect on variables and interactions; the impact of observation year was insignificant. Random factors were not specified and not incorporated into our model. We also used a regression curve estimation test to investigate the relationship between suckling duration and its frequency and Pearson's correlation test for checking the relationship between the duration of restricted suckles and the general distribution of suckle duration. Proportions (percentages) of separate behavioral acts were not transformed and were analyzed with the Log-linear model and Chi-square-of-fit tests. All statistical analyses were conducted using the SPSS 17.0 software package (SPSS Inc., Chicago, IL, USA).

3. Results

Suckling duration fluctuated insignificantly over years (GLM test, $F=2.214$, $df=3$, $P>0.05$), but changed significantly over seasons for females with singles and twins (GLM test, $F=31.621$, $df=6$, $P<0.0005$). Suckling durations were longest during the first four weeks of life (late May–early June, GLM post hoc Bonferroni test, $P<0.0005$) (Table 1), though the young suckled significantly less by the beginning of June compared to May (Table 1). In late June and early July, the suckling duration decreased drastically compared to early June and late June, respectively (Table 1), and after mid-July and during August, the suckling duration was not only short, but suckling was also rarely observed. Separate cases (not bouts) of suckling could be detected until early December, but these attempts to suckle were extremely short and observed only very irregularly (Table 1).

Our analysis of the changes in suckling duration, which was checked every 15 days, demonstrated that twins and singletons had the same declining trend with the age of the young, without

Table 1
Changes in suckling duration (per half month) during May–December in females with single vs. twin juveniles.

Number of juveniles	Mean \pm SE (s)	Range (s)	N	GLM, post hoc Bonferroni test P
15–31 May				
Single	21.8 \pm 1.6	1–151	200	
Twin	28.7 \pm 0.8	2–275	1896	
01–15 June				
Single	17.7 \pm 1.4	2–133	186	0.012
Twin	27.1 \pm 1.1	2–287	1066	
16–30 June				
Single	14.0 \pm 0.9	1–92	232	0.0005
Twin	18.0 \pm 1.8	1–190	178	
01–15 July				
Single	9.8 \pm 0.6	1–25	76	0.0005
Twin	5.7 \pm 0.3	1–14	87	
16–31 July				
Single	6.5 \pm 2.1	2–16	6	
Twin	4.3 \pm 0.4	3–6	7	
01–15 August				
Single	4.0 \pm 0.6	2–6	6	
Twin	6.5 \pm 0.7	5–9	6	
16–31 August				
Single	3.6 \pm 0.7	1–6	7	
Twin	2	2	1	
01–15 September				
Single	1.5	1–2	2	
Twin	3.0	3	1	
15–30 October				
Single	2.0	2	1	
Twin				
01–15 December				
Single				
Twin	2.0	2	2	

significant differences (GLM test, $F=0.063$, $df=1$, $P>0.05$). However, the interaction between litter size and season showed that twins and singletons showed some differences in the actual decline in suckling (GLM test, $F=6.216$, $df=4$, $P<0.0005$). Indeed, in late May and early June twins suckled significantly longer than single young (Table 1), but this difference was almost absent by late June; and during July single young started to suckle longer than twins. In August and after, this difference was insignificant, because suckling was rarely observed, and the data we were able to collect was too limited for a comparison (Table 1).

According to the regression curve estimation test for May to June, the suckling duration and its frequency were interrelated in the cubic equation model, which explained 85–96% of our observation data (Table 2). This means that suckling duration was a very strong predictor of frequency, with the shortest suckles of 5–20 s observed most frequently. This was followed by an abrupt decrease in suckling duration, with the longest suckles of 2–4.5 min found only rarely. In May, most suckling events (73.8%, $n=1530$ in twins; 80.1%, $n=181$ in single young) had a duration of less than 30 s, with a suckling duration of 10 s in twins and 10–15 s in singles most often observed (log-linear model test, $Z=-11.984$ up to -2.448 , $P<0.0005$ up to $P=-0.014$ for both). During June, the proportion of short suckles (less than 30 s) started to increase even more, reaching 92% ($n=221$) in twins and 92.7% ($n=113$) in singles at the end of the month (with suckles most often lasting 5–15 s), and the maximum duration became shorter, with longer suckles observed more and more rarely.

Intervals between suckles (during suckling bouts) demonstrated significant changes with the young's age (GLM test, $F=539.470$, $df=3$, $P<0.0005$). These intervals were minimal (and frequency

was maximal) during the first two weeks after birth in late May (Table 3). In June and into early July, intervals increased significantly, by 1.4 (early June), 27.8 (late June), and 15.7 (early July) times in twins and 2, 11, and 19.4 times in single young, respectively, compared to late May (Table 3). For twins the intervals were significantly shorter than for single young during all periods (GLM test, $F=98.091$, $df=1$, $P<0.0005$) (Table 3). We did not collect data for interval durations between suckles for late July and August, since by this time mothers with young had begun making regular, daily, long-distance migrations, and the time intervals between suckles were longer than our opportunities to observe individual mothers and young.

Total suckling time within bouts also showed significant changes with the young's age (May to late June) (GLM test, $F=265.123$, $df=2$, $P<0.0005$), and for twins this value increased in early June compared to late May and then showed a drastic decrease in late June (post hoc Bonferroni test, $P<0.0005$), while in single young, a continuous decrease in total time was observed during May–June (post hoc Bonferroni test, $P<0.0005$) (Fig. 1). Similar observations regarding total suckling time were made in twins vs. single young: in late May to early June this value was significantly higher in twins compared to single young; by late June single young had larger values of total suckling time as compared to twins (GLM test, $F=59.709$, $df=1$, $P<0.0005$, Fig. 1).

During the first two weeks of life (15–31 May), young suckled as long as they wanted in most cases (84.5%, $n=1508$ in twins; 72.4%, $n=181$ in singles), and considerably less suckling was terminated by their mothers (15.5% and 27.6%, respectively) (log-linear model test, $Z=5.953$ and 6.922 , $P<0.001$ for both). Mothers with singles restricted suckling of their young more often than females with

Table 2
Regression cubic model summary and parameter estimates of interrelation between suckling duration and its frequency in single young and twins during May and June.

	Model summary					Parameter estimates			
	R ²	F	df1	df2	P	Constant	b1	b2	b3
15–31 May									
Single	0.858	38.157	3	19	0.000	43.511	−1.425	0.015	−4.814E−5
Twin	0.852	82.228	3	43	0.000	253.639	−5.389	0.035	−6.898E−5
1–15 June									
Single	0.958	106.604	3	14	0.000	60.979	−2.373	0.029	0.000
Twin	0.864	86.718	3	41	0.000	194.658	−4.115	0.026	−4.857E−5
16–30 June									
Single	0.961	82.022	3	10	0.000	85.700	−4.332	0.073	0.000
Twin	0.933	32.346	3	7	0.000	31.682	−0.323	−0.038	0.001

twins (log-linear model test, $Z=2.970$, $P=0.003$). During the next two-week period (1–15 June), females restricted suckling more and more as compared to May ($Z=8.949$, $P<0.001$), limiting single young more often (35.4%, $n=198$) than twins (20.5%, $n=1079$) (log-linear model test, $Z=9.898$, $P<0.001$). After mid-June (16–30 June), the majority of suckles were terminated by the mothers (91.9%, $n=222$ in single young; 98.2%, $n=114$ in twins), although females with single young restricted suckling less often than females with twins (log-linear model test, $Z=5.091$, $P<0.001$). By early July, all suckles were stopped by the mothers. During May and June, the frequency of suckling durations restricted by females was very closely correlated with the frequency of all (restricted and non-restricted) suckling durations (Pearson's correlation test, $R=0.925$ – 0.976 , $P<0.0005$ for all cases). This means that females restricted suckling mainly in the middle and at the end of a bout (89.5% in twins and 98.0% in single young), when suckles were shortest (less than 60 s), while they limited only 10.5% of the longest suckles (longer than 60 s, observed mainly at the beginning of a bout) in twins and 2% in singles (log-linear model test, $Z=-3.631$, $P<0.0005$). Later, this proportion was increased even further in favor of the shortest suckles (96.8% in twins and 98.5% in single young in early June and 100% and 99% in late June, respectively) (log-linear model test, $Z=-3.162$, $P=0.001$).

In some cases, females did not allow suckling at all, terminating the attempt immediately; these cases were observed less often in May compared to other months (June–August) (7.2%, $n=138$ in single young; 16.6%, $n=66$ in twins) (log-linear model test, $Z=2.346$, $P=0.019$). By the end of June, the absolute number of unsuccessful suckles observed increased to its maximum (51.4% in single young and 34.8% in twins in early July; $Z=3.027$, $P=0.001$) and then in August dropped drastically to 5–6% ($n=138$) in single young and less than 1% ($n=66$) in twins (since they had mostly been weaned). In general, the proportion of unsuccessful suckles in single young and twins fluctuated in a similar way throughout May and June

(log-linear model test, $Z=1.799$, $P=0.072$), and only at the end of June were single young rejected by females significantly more often (3.7 times) than twins ($Z=5.086$, $P<0.001$). In addition, the total number of unsuccessful suckles for single young over all months was 2.1 times as high as for twins (Chi-square-of-fit test, $\chi^2=12.960$, $df=1$, $P<0.001$). The proportion of unsuccessful suckles compared to successful ones reached its maximum in August (compared to May–July) (log-linear Model test, $Z=4.474$, $P<0.001$), when almost every successful suckle was accompanied by one unsuccessful one (57%, $n=13$ in single young; 50%, $n=12$ in twins).

4. Discussion

Our results supported our first hypothesis completely, as goitered gazelle females in most cases allowed their young to suckle as long as they wanted during the first two weeks after birth (late May). All parameters of suckling behavior testified that this was the most favorable time for young to suckle, and most likely allowed the transfer of the maximum amount of milk from mother to young. As the young grew, females gradually reduced suckling, terminating almost all suckles by late June for offspring older than one month. As a result, suckling intensity, which had a relatively smoothly decreasing dynamic in early June compared to late May, dropped abruptly by late June and especially in early July. So we found that the most intensive suckling behavior in goitered gazelles was observed during the first month of life, and then the suckling parameters showed a decrease, with an increasing trend, indicating the beginning and the quick development of the weaning process.

Goitered gazelle young began to show an interest in vegetative food (nibbling at grass) during their second or third day of life, with real grazing observed in young as early as two weeks of age; at the age of one month they consumed significant amounts of solid forage (plants) (Blank, 1990). Obviously, one month is a crucial age for goitered gazelle young, when their mothers begin to force them

Table 3
Changes in the duration of intervals between suckles during May to July in females with single and twin juveniles.

Number of juveniles	Mean \pm SE (min)	Range (min)	N	GLM, post hoc Bonferroni test P
15–31 May				
Single	2.18 \pm 0.25	0.05–25.77	145	0.0005
Twin	1.04 \pm 0.04	0.02–26.50	1325	
01–15 June				
Single	4.46 \pm 0.43	0.02–32.78	149	0.0005
Twin	1.47 \pm 0.06	0.02–26.78	994	
16–30 June				
Single	23.95 \pm 3.68	0.02–203.00	101	0.0005
Twin	28.96 \pm 5.54	3.00–118.00	24	
01–15 July				
Single	64.00 \pm 14.45	5.00–192.00	14	0.0005
Twin	16.36 \pm 3.78	2.00–45.00	14	

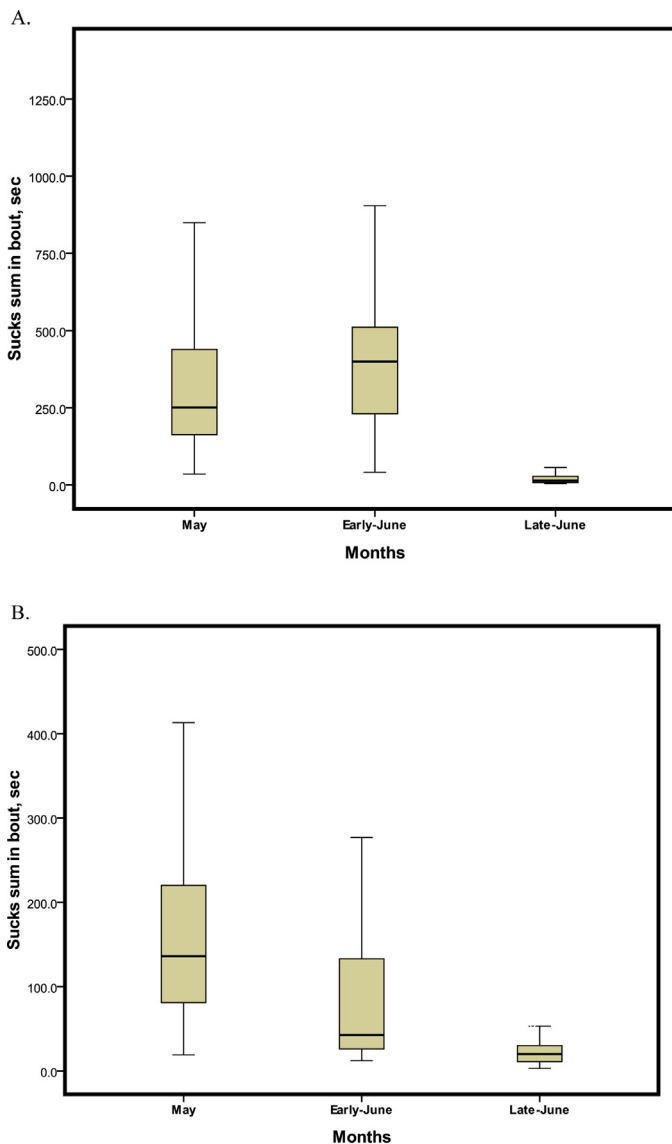


Fig. 1. Changes of the sum of suckling time in suckling bouts of (A) twins (mean \pm SE = 354.4 \pm 22.9 s, SD = 256.4, range 35–1091 s, N = 125 for May; 438.1 \pm 36.1 s, SD = 300.1, range 41–1269, N = 69 for early June; and 18.6 \pm 2.0, SD = 14.1, range 4–57 s, N = 49 for late June) and (B) single young (mean \pm SE = 169.8 \pm 26.5 s, SD = 129.7, range 19–466 s, N = 24 for May; 83.4 \pm 12.2 s, SD = 78.9, range 12–324, N = 42 for early June; and 32.1 \pm 4.5, SD = 40.2, range 3–242 s, N = 78 for late June) during May to June. The difference was significant and had confidence intervals >95% for all cases (GLM post hoc Bonferroni test, P < 0.0005).

to alternate between vegetative food and maternal milk. From this moment on, milk loses its role as the young's only nourishment and becomes a supplementary food source, the portion of which decreases quickly over the following weeks.

These results confirm the general trend typical of all bovids, with the maximal amount of milk supplied to offspring observed during the first weeks after birth (Sadleir, 1980; Clutton-Brock et al., 1982; Green, 1986; Obregon et al., 1992b). Then, as the young mature, the weaning process begins, with the mother initiating fewer and terminating more of the nursing events, while the young do the opposite (Gauthier and Barrette, 1985). Thus, the reduction of milk transfer to the offspring forces them to increase their foraging activity (Festa-Bianchet, 1988; Babbitt and Packard, 1990; Faichney, 1992). It has also been found that in years with unfavorable environment conditions offspring start to graze at a younger age than in

years with favorable conditions (Reale et al., 1999). Similar to goitered gazelle young, the lambs of mouflons, urials (*Ovis vignei*), and wild goats (*Capra aegagrus*) have been observed to nibble at grass during their first week of life (Altmann, 1970; Schaller, 1977), and young mouflon and bighorn sheep begin grazing when they are two weeks old, which coincides with the initial phase of maternal rejections, the rate of which increases with the age of the offspring (Shackleton and Haywood, 1985; Obregon et al., 1992a).

In ruminants, efficient rumen fermentation is developed by 8 weeks of age (Lyford, 1988), though there is a gradual process that starts during the first days after birth and proceeds throughout the weaning process: the decrease in the consumption of milk and increase in the consumption of vegetative food intensifies the development of rumen fermentation efficiency. It also seems that a gradual termination of milk transfer is a necessary precondition to effective rumen fermentation functioning, since it has been found that in circumstances when young are not subjected to nursing restrictions, receiving suckling without limitation, they show more behavioral signs of stress and have a more significant reduction in weight after weaning compared to young that have experienced a gradual termination (Froberg, 2008). So for goitered gazelles, as in other ungulate species (Gauthier and Barrette, 1985; Shackleton and Haywood, 1985; Obregon et al., 1992a), initial weaning behavior begins as early as two weeks of age, long before the development of an effectively functioning rumen. Clearly, a gradual weaning process prepares the young for a strictly vegetarian diet, and it is also a time when the young animal can learn about plant food from its mother (Hinch et al., 1987; Provenza and Balph, 1988). Learning about grazing habits early in life enables herbivores to develop preferences for certain plant species and to acquire the motor skills necessary to harvest and ingest those forages efficiently (Provenza and Balph, 1988). Alternating milk diet with vegetarian rations in young is accompanied by neurological (Coppersmith and Leon, 1984), morphological and physiological changes (Lyford, 1988), as well as changes in gut microflora (Hungate, 1966) and the ability to ruminate (Welch and Hooper, 1988). After weaning and during the first year of life, the willingness to accept novel foods declines steadily (Lobato et al., 1980). Thus, the early foraging experiences of young herbivores undoubtedly form their main dietary habits as adults (Provenza and Balph, 1988).

Our results did not support our second hypothesis, which stated that each twin would receive less maternal investment than singletons. In fact, we found quite the opposite was true for all suckling parameters. In our study, twin young suckled more frequently and spent more time suckling, with shorter intervals between suckles than single young. Furthermore, single young had more unsuccessful suckles, and even when successful, their suckles were terminated more frequently compared to those of twins.

On the surface, these results strongly support the hypothesis of non-nutritive suckling, which is an integral part of nursing behavior and plays an important role in the mother-offspring relationship (Cameron, 1998; Cameron et al., 1999). According to this hypothesis, not all suckling results in the transfer of milk (pigs, *Sus scrofa*: Newberry and Wood-Gush, 1985), and milk flow does not always begin immediately once the offspring begins to suckle (cattle, *Bos taurus*: Whittemore, 1980). An investigation of cattle found that a long duration of nursing in calves reflected a greater difficulty in obtaining milk rather than the young consuming a larger amount (Haley et al., 1998b). In our study, the data can be interpreted in the same way, i.e. that the higher frequency and longer suckling duration in twins demonstrates a greater difficulty in obtaining milk compared to singletons, since it seems reasonable that mothers with twins cannot produce twice the amount of milk compared to mothers with single young (Ruiz-Miranda et al., 1998). However, our results do not support this assumption. First, if the non-nutritive suckling hypothesis explained our

results, then the frequency and suckling duration would have to be greater in twins than in singletons during the entire nursing period, and might even be increased with the aging of the young. But in our study, the proportion of suckling parameters in twins compared to singletons changed over time, from twins suckling longer and with a higher frequency than singletons during the first weeks after birth to the opposite situation where singletons suckled with a higher frequency and a longer duration as they aged. Second, if twins suckled longer than singletons due to a limited amount of milk, they would have a greater number of unsuccessful suckles and their mothers would have terminated their suckling more frequently than seen in singletons. In European mouflons (*Ovis gmelini*), for example, it was found that a high frequency of unsuccessful suckling attempts was a reliable indicator of an insufficient milk supply and a good predictor of a high mortality among young (Reale et al., 1999). But our data proved the opposite was true, and in general goitered gazelle twins had significantly lower rates of unsuccessful suckling attempts compared to singletons. Third, although there was not much correlation between the measure of suckling behavior and the amount of milk actually transferred (Day et al., 1987), suckle frequency and total suckling time were significantly correlated with the estimated milk intake (Cameron, 1998). Suckle frequency and total suckling time both indicated that goitered gazelle twins actually each received significantly more milk than singletons. All these points suggest that, indeed, goitered gazelle mothers with twins provide significantly more investment in their young; at least during the first months of life, when offspring depend on milk almost completely, twins received each greater amounts of milk than singletons.

Therefore, we propose another explanation for our results. As studies on domestic sheep have suggested, ungulate females that normally bear twins can, if their nutritional status is high, produce additional milk well above the estimate for a single neonate. By completely removing the milk from the udder of a mother nursing four lambs instead of just one, the study of domestic sheep by Peart et al. (1972) showed that the ewe was able to produce more than double the regular amount of milk. Further, investigations of suckling behavior in moose (Yazan and Knorre, 1964), eland (Treas and Kravchenko, 1968), and domestic cattle (Gifford, 1953) have shown that females can produce much more milk if they are hand-milked as compared to being suckled by a neonate; and twins of white-tailed (*Odocoileus virginianus*) and black-tailed deer (*O. hemionus*) receive almost exactly twice the amount of milk that a singleton gets (Sadleir, 1980; Gauthier and Barrette, 1985). It seems clear that ungulate females are able to regulate the amount of their milk supply within a wide range rather than having to limit their neonates' milk consumption due to physiological restrictions for milk production; physiological changes in neonatal growth evidently contribute to the amount of maternal milk production (Robbins and Robbins, 1979).

Under the selective pressures of predation, hypothermia, and seasonal food restrictions, different mammalian species have different strategies for maximizing their reproductive efforts; litter size and time to weaning are likely the adaptive variables of mammalian reproduction (Millar, 1977). Some species, like African buffalo (*Syncerus caffer*) (Robbins and Robbins, 1979) and wildebeest (*Connochaetus taurinus*) (Estes and Estes, 1979), bear single neonates of relatively large size, which require more total food but can survive longer between feedings, so that the female can feed her young infrequently and spend more time foraging (Millar, 1977). This strategy demands a relatively low amount of milk that leads to a slower growth rate of their young after birth, and as a result females have to support the offspring for a longer period (Millar, 1977). Under the conditions found in the tropical African savanna, where a favorable rainy season can last for an entire four months, females have the opportunity for a longer rearing

period of their young (Spinage, 1986). Other species, like peccaries (Tayassuidae) (Frädrich, 1967) and Chinese water deer (*Hydropotes inermis*) (Dobroruka, 1970), have an opposite strategy of bearing several neonates of relatively small size and then supplying greater amounts of milk that leads to a faster growth rate after birth (Robbins and Robbins, 1979).

The strategy typical of goitered gazelles appears to be the latter one, bearing several relatively small neonates with an intensive milk supply after birth, since goitered gazelles are among the species that generally produce significantly more twins than singletons within a population (in favorable conditions, up to 75% of the whole population; Kingswood and Blank, 1996), where selection favors the survival of twins in that their mothers have the ability to supply more milk to their offspring than mothers of single young. Consequently, twins received a more intensive suckling investment (higher frequency and shorter intervals, a longer suckle duration, and a longer total suckling time) from their mothers, especially in early June, that then decreased more abruptly than for singletons. Good maternal investment allows for the rapid growth and precocious emancipation of offspring without overt mother-offspring conflict (Reale et al., 1999), with early weaning also associated with highly favorable conditions (Babbit and Packard, 1990; Lee et al., 1991). In contrast, singletons received poorer maternal investment, most likely because of a lower quality of the mother compared to the mother of twins, even if conditions generally were favorable for the rearing of young. Indeed, goitered gazelle mothers of twins were usually adult, multiparous females in good body condition giving birth to larger newborns, while mothers of singletons were typically either young, primiparous females with a smaller body size that gave birth to smaller neonates (Sludskiy, 1956; Cassinello and Gomendio, 1996), or females with poorer, weaker bodies as commonly observed in older females that also showed intensely overt conflicts with their lambs (Zhevnerov, 1984; Kingswood and Blank, 1996; Reale et al., 1999). In Cuvier's gazelles (*Gazella cuvieri*) the same phenomenon was found, with only adult mothers birthing twins, while primiparous females birthed singletons (Alados and Escos, 1994). Even in species that typically bear singletons, such as eland antelopes (*Taurotragus derbianus* and *T. oryx*), multiparous mothers make a significantly greater maternal investment (longer suckling bouts) than primiparous females (Hejzmanova et al., 2010). Furthermore, in ungulate species multiparous and older mothers generally display a higher level of maternal care than primiparous or younger mothers, because of their greater level of experience (Ozoga and Verme, 1986; Green, 1990; Cameron et al., 2000). So, maternal success in rearing young is significantly dependent on an individual's life history (Hejzmanova et al., 2010).

Maternal investment is likely to be also "environment-dependent" (Hejzmanova et al., 2010). In years with unfavorable environmental conditions, the body condition of goitered gazelle females was found to be generally poorer; and mothers in poor condition may not be able to care for their young properly or may limit their maternal expenditure in order to maintain their own reserves (Carlisle, 1982; Festa-Bianchet and Jorgenson, 1998). As a result the proportion of twins was observed to decrease significantly even among adult multiparous females through either the resorption of one of the two embryos or a higher mortality of neonates among twins after birth (Sludskiy, 1956; Carlisle, 1982; Zhevnerov, 1984). So, unfavorable conditions have a negative impact on females in reproductive prime as well, but these have a higher level of persistence so that many are strong enough to continue to bear and rear twins even in bad circumstances (Sludskiy, 1956), while very young and relatively old females, having poorer body conditions, usually birth singletons even in the most favorable environment (Zhevnerov, 1984). This correlation of litter size with environmental conditions was found for other ungulate species as

well (Fernandez-Llario and Mateos-Quesada, 1998; Moreno et al., 2011).

In unpredictable habitats, animals need to allocate a greater proportion of their resources to reproduction than animals living in predictable environments (Millar, 1977). For goitered gazelles, the ability for high reproduction may be an adaptation to the abrupt changes in their arid habitat of Central Asia. In this region, environmental conditions can change unpredictably, from years with favorable circumstances, when the survival rate of young is highest, to years with poor conditions (a late, cold spring, a dry, hot summer or an unusually severe winter with a deep snow cover, especially with an ice crust on the surface), when the mortality rate of gazelles, particularly among the young, is at its highest (Sludskiy, 1963; Zhevnerov, 1984). So to maximize reproductive output, goitered gazelles have the ability to take advantage of favorable environmental conditions to quickly increase their population (Kingswood and Blank, 1996). Saiga antelopes (*Saiga tatarica*) living in the same Central Asian environment have been found to exhibit a similar breeding behavior (Fadeev and Sludskiy, 1982), while almost all African gazelle species, inhabiting predictably favorable tropical and subtropical environments, have typically singletons. The only African species that produces twins is Cuvier's gazelle, which lives in the Atlas Mountains (Furley, 1986; Alados and Escos, 1994) with an extremely variable environment that varies from areas with frequent snowfall and very low winter temperatures to arid areas with dry, hot summers and barren vegetation; in addition, conditions in these mountains change sharply seasonally and annually in temperature and precipitation (Bencherifa and Johnson, 1991).

So in conclusion, only adult goitered gazelle females in good physical condition can bear and rear twins, since they have the ability to provide a higher maternal investment to each twin and supply them with sufficient amounts of milk for their growth and survival. In contrast, singletons are born mostly to young females or mothers of poorer quality, who lack sufficient fitness to invest in rearing twins and can only supply enough milk to support singletons.

Acknowledgments

We thank the National Natural Science Foundation of China (U1303301), Chinese Academy of Sciences (CAS) for granting our work (Visiting Professorships for Senior International Scientists – 2011T1Z42), and the West Light Foundation (CAS – Y336171) for creating all conditions for writing this paper. We are very grateful to the Institute of Zoology, former Academy of Sciences of Kazakhstan, which has given us the possibility to investigate goitered gazelles in their natural environment for 10 years. We are grateful to Ms. Patricia Johnston for her useful suggestions and remarks and constant help in English editing of this manuscript.

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