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

David Blank[a,b,*], Weikang Yang[a]

[a] Key Laboratory of Biogeography and Bioresource in Arid Land, Xinjiang Institute of Ecology and Geography, The Chinese Academy of Sciences, Urumqi, China
[b] Institute of Zoology, Kazakh Academy of Sciences, Alma-Ata, Kazakhstan

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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.

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 (Lavigueur 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

* Corresponding author at: Key Laboratory of Biogeography and Bioresource in Arid Land, Xinjiang Institute of Ecology and Geography, The Chinese Academy of Sciences, Urumqi, China. Fax: +86 991 7885320.
E-mail address: takinserow@aliyun.com (D. Blank).

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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; Pluhácek 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; Lavigueur and Barrette, 1992; de Passille and Rushen, 2006; Bartos et al., 2001; Drabkova et al., 2008; Hejcmanova et al., 2010; Pluhácek 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; Pluhácek et al., 2014), suckling satisfies not only the youngs' nutritional needs but also their emotional and social needs (Carson and Wood-Gush, 1983; Cameron, 1998; Pluhácek 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; Pluhácek 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; Hadjipanayiotou, 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