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Grouping patterns and social organization in Siberian ibex (*Capra sibirica*): feeding strategy matters

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Abstract. A study on group size and composition in Siberian ibex (*Capra sibirica*) was conducted in the Eastern Tien-Shan Mountains. We found that small groups (1-5 individuals) were most common for this species. Generally, mixed-sex groups were larger than male and female groups. Since males have more ability for fiber digestion, because of their larger body size than females, they are less selective in food quality. Due to this, males gathered into larger single-sex groups in August-September, when forage was at its maximal biomass, and into smaller groups when the amount of food was limited (winter-early-spring). During birthing period, pregnant females typically separated from groups to give birth, returning to the female groups in May-June, when high-quality food was at its maximal availability, making female groups largest in this period. Similar to other sexually dimorphic species, Siberian ibex females and males stayed together in mixed-sex groups during rutting season, demonstrating sexual segregation outside of the rutting season, particularly during summer. Nevertheless, there are still a significant number of males and females that stay in mixed-sex groups throughout the year. In conclusion, the grouping pattern and social organization of Siberian ibex were closely correlated to the availability and quality of their food supply and yearly breeding cycle. Accordingly, Siberian ibexes changed their feeding strategy: being mixed feeders they behaved similar to concentrate selectors when food was scant and preferred small sized groups; while they enlarged their group sizes during seasons when the enriching of forage conditions allowed them to do that. However, group enlarging happened in different months depending on group typology (i.e. mixed-sex, male or female groups) depending on the feeding strategy of their individuals.

Key words: sexual dimorphism, group size, mean crowding value, biological events

Introduction

The most widely accepted explanation of large aggregation in ungulates is reducing the predation risk through enhanced detection of predators and dilution effect (Lima 1995, Roberts 1996). Animals which stay in foraging groups spend less scanning for risk assessment than do solitary individuals (Lipetz & Bekoff 1982, Underwood 1982, Berger & Cunningham 1988). However, most herbivores do not aggregate into a single large group in the more suitable area, but instead form numerous small groups regardless the increased risk of predation (Inglis 1976, Lott & Minta 1983). As so, other factors besides the predation risk may influence the distribution patterns, namely, environmental factors like forage quality, abundance and its distribution that can determinate group sizes (Jarman 1974, Brashares et al. 2000).

Numerous investigations have been devoted to identifying links between feeding ecology and social organization (Jarman 1974, Geist 1974, Fryxell 1991); and previous studies have confirmed that group size and group composition, which is the basic element of social organization, is related to habitat structure, spatial-temporal distribution of food, and reproductive characteristics (Barrette 1991, Raman 1997, Johnsingh et al. 1999). To benefit from gregarious, group living animals have to adjust their grouping patterns to improve foraging success and enhance fitness (Pulliam 1973, Clutton-Brock et al. 1982, Krause & Ruxton 2002). However, living in

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groups also has potential costs, such as increased competition for resources, pathogenic infections, and attracting predators (Sun 2001, Davies et al. 2012). Thus, animals make trade-offs between benefits and costs of group size to maximize individual fitness (Fryxell 1991).

The Siberian ibex (*Capra sibirica*) is classified as a Category I Protected Wild Animal Species and is listed as “Endangered” in the China Red Data Book of Endangered Animals (Wang 1998). The Siberian ibex is a gregarious species, which prefers living in rugged regions, avoiding vast flat areas without cliffs or rocks. The diet of Siberian ibex contains mainly grasses and forbs, as well as sprouts, flowers, and fruits of many herb and shrub species are willingly eaten (Johnsingh et al. 1999). The majority of ibex form mixed-sex groups during the rut from November to December, and then split into single-sex groups out of rutting season (Wang et al. 2018). Nevertheless, there are still a significant number of males and females that stay in mixed-sex groups throughout the year (Fedosenko 2003). Gestation lasts 170-180 days, and birthing peaks in May-June (Fedosenko & Blank 2001). Despite the fact that the Siberian ibex has been studied by many authors (Fedosenko & Blank 2001, Bagchi et al. 2004, Xu et al. 2012), published information, specifically on group size and composition, is still lacking (Singh et al. 2010, Zhu et al. 2016).

Social organization of various species is adapted to the abundance and distribution of resources (habitat structure and the spatial-temporal distribution of food) and to predation risk (Geist 1974, Jarman 1974, Gerard et al. 2002). Habibi (1997) found that similar to other Caprini, the Nubian ibex (*Capra nubiana*) usually forms small groups of two to seven individuals. Sparse vegetation cover and scattered plant patches are characteristics that favours small group size. Based on these facts, we suggested that the same pattern would occur in our study, and proposed as our first hypothesis that Siberian ibex would prefer to form small sized groups in dry conditions of the Eastern Tien-Shan, where food patches are relatively scarce and scattered in most seasons.

The link between the distribution and abundance of food and seasonal changes in group size has been reported for some ungulates (California bighorn sheep – *Ovis canadensis californiana*: Payer & Coblentz 1997, sika deer – *Cervus nippon*: Borkowski & Furubyashi 1998, mountain gazelle – *Gazella gazella gazella*: Geffen et al. 1999). California bighorn sheep vary their group sizes among months, and the small group sizes found in late summer reflect resource limitations (Payer & Coblentz 1997). Based on these observations, we expect to find the same phenomenon in the Siberian ibex, with largest group sizes when there is a high availability of high-quality food, and small groups when food is scarce.

Material and Methods

Study area

This study was conducted in the Eastern Tien-Shan Mountains, Xinjiang, China (43°13′-43°43′ N, 86°30′-87°29′ E). The total study area is 1700 km² and consisted of rugged ridges amid a complex of narrow and wide valleys. Elevation range between 1450 and 4479 m a.s.l. This region has semi-humid to semi-arid transition zones with a temperate continental climate, making local conditions cold and arid, typical for the entire Eastern Chinese Tien-Shan. The annual average precipitation is 663.4 mm and the annual average frost-free period is about 150 days (Zhou et al. 2010). The annual average temperature is –1 °C, with an extreme high temperature of +30.5 °C, which is common for July, and extreme low temperature of –30.2 °C, which is observed in January. In this area, habitat is dominated by coniferous forests up to the upper line of the forest zone (2100 m a.s.l.), and alpine grasslands passing to bare rocks above the forest zone line. Cyperaceae and Poaceae are relatively dominant in the local plant community, with a mixture of other families, such as Polygonaceae, Asteraceae, Fabaceae, Ranunculaceae, and Rosaceae. Siberian ibex and red deer (*Cervus elaphus*) are common ungulates in this region, and carnivores, such as snow leopards (*Uncia uncia*), wolves (*Canis lupus*), and such raptors as the cinereous vulture (*Aegypius monachus*) and golden eagle (*Aquila chrysaetos*) are also found here. A large number of livestock (mostly sheep and goats) from the town of Saerdaban stay in this area from June to October each year, and force the ibex to move to higher elevations during summer, allowing them to return to lowers slopes for autumn and winter.

Data collection

The census was conducted monthly, making a vehicle survey within the same area and along the same route from October 2014 to September 2017. Such survey was done only once per month to reduce pseudo-replication. Along the transect line, we stopped every 2-3 km and searched for ibexes using binoculars (magnification 8×) and a telescope (magnification 20-60×). We started routes at valley entrances and conducted along their bottoms. The length of transects is the full length of valley, and varied from 7 to 20 km. To avoid the possible disturbance of observed animals, the observation distance was usually more than 200 m. We defined a group as ibex having inter-individual distances of less than 50 m and showing coordinated movement during the observation period (Clutton-Brock et al. 1982). Solitary individuals were also recorded.

During our survey, we observed each group for no less than 15 min to make sure that all the individuals in observed groups were detected and recorded, decreasing the impact of the rugged terrain on detecting all animals in groups. For each group, we collected the following information: date, total number, and sex and age of each individual. For each observed group, we counted all females (adult or sub-adult) and determined the age of all males by counting horn annuli, when visible. Males ≤ 5 years old often joined female groups throughout the year and rarely participated in courting females, resulting in less opportunities to compete for copulations. Thus, we distinguished two male classes: adult males (≥ 6 years old) and sub-adult males (≤ 5 years old). We defined four types of groups: (1) female groups, which included one or more adult females, sub-adult females, sub-adult males, and kids; (2) male groups, where all individuals were males; (3) mixed-sex groups, which contained at least one adult male and one adult female; and (4) solitary individuals (Zhu et al. 2016).

Group size calculation

For the analyses of group dynamics, previous studies usually used mean group size (MGS, the arithmetic mean of group sizes averaged over groups) (Lott & Minta 1983, Wirtz & Lörscher 1983); however, this index is suitable mostly for cases when group sizes have distributions close to normal (Giraldeau & Gillis 1984). But most ungulate species have a right-skewed distribution of group sizes, where most groups are small, while large groups are rarely observed (Reiczigel et al. 2008). The Siberian ibex also had a similar right-skewed distribution in group sizes (Fig. 1). Therefore, for our study, we used another index, the crowding index (the arithmetic mean of crowding values averaged over groups) proposed by Reiczigel et al. (2008) as a way to better characterize the right-skewed distribution of group size. The definition of crowding is the size of a group in which an individual lives or the group size experienced by an individual. The crowding index equals one for a solitary individual and two for both individuals in a group of two, etc. (Reiczigel et al. 2008). For example, if we observed three groups of animals in the wild, and their group sizes were 1, 3, and 5, respectively (for a total of 9 individuals), then the crowding values would be 1, 3, 3, 3, 5, 5, 5, 5, 5, and the mean crowding value would be (1 + 3 + 3 + 3 + 5 + 5 + 5 + 5 + 5)/9 = 3.89.

Statistical Analysis

To test our predictions, a Generalized Linear Mixed Model (GLMM) with Poisson distribution was used to analyze the effects of month, group type and month: group type on the size of the groups of Siberian ibex. Date of observation was included as random factor to account for any potential temporal autocorrelation. After fitting the GLMM, model validation was performed on the residuals by checking heteroscedasticity and normality (Zuur et al. 2009). The results from GLMM are expressed as estimated means ± standard error (SE) and 95 % confidence intervals (CI), unless otherwise stated.

Chi-square analyses were used to analyze the monthly fluctuations on proportions of female groups, male groups, mixed-sex groups and solitary individuals. The statistical analyses were performed using IBM.SPSS Statistics 23 (IBM Corporation, New York, U.S.A.). All statistical tests were considered significant when $p < 0.05$.

Results

In total, we observed 3406 groups and 38118 individuals, including 6067 adult males, 6743 sub-adult males, 15658 adult females, 2308 sub-adult females and 7342 kids as part of this study.

Overall group size distribution

Group size ranged from 1 to 201 individuals over the whole study period. Groups of 1-5 animals were the most frequently observed (39.28 %), followed by 6-10

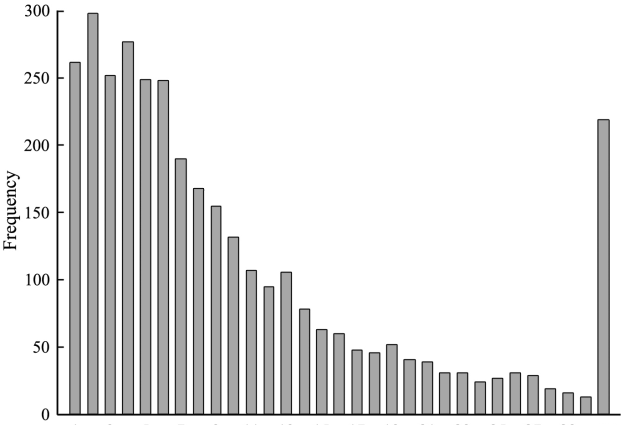

Fig. 1. Distribution of the Siberian ibex group size.

individuals (26.22 %) and 11-15 individuals (13.18 %). Groups with more than 30 individuals were rarely observed (6.44 %) (Fig. 1), with only 1-2 sightings per size.

Monthly variability in group size of different group types

The group size, quantified using the crowding index, is significantly affected by the interaction between month and group type ($F_{33,\ 38069} = 510.42$, $p < 0.01$). The estimated mean crowding value for mixed-sex groups (30.45 ± 1.15) were significantly larger than for both female groups (13.80 ± 0.52; t = 26.29, $p < 0.01$) and male groups (12.45 ± 0.48; t = 26.13, $p < 0.01$) throughout the year. Female groups were larger than male groups in January to June, while male groups were markedly larger than female groups from August to November (Fig. 2).

Mean crowding values of female groups varied significantly among months ($F_{11,\ 38069} = 9.813$, $p < 0.001$), and further analysis found this index was largest in June (26.43 ± 3.36) and smallest in December (6.51 ± 0.80) (Fig. 2).

For male groups, mean crowding values also varied significantly across months ($F_{11,\ 38069} = 12.733$, $p < 0.001$), and further analysis found the largest values in August and September (August: 22.87 ± 3.05; September: 23.94 ± 3.21), and smallest in December (5.14 ± 0.68) (Fig. 2).

Mean crowding values of mixed-sex groups again varied significantly across months ($F_{11,\ 38069} = 9.813$, $p < 0.001$), and were larger in May (54.57 ± 7.25) and smaller in July (18.75 ± 2.40) (Fig. 2).

Monthly variability in frequency of different group types

Of the 3406 groups observed during the whole study period, 52.64 % were female groups, 26.92 % were male groups, 12.74 % were mixed-sex groups and 7.70 % were solitary individuals. The female groups were most frequently observed outside the rutting season (January-October), and the frequency of female groups varied significantly over months (Chi-square test: $\chi^2 = 189.149$, df = 11, $p < 0.001$). The frequency of mixed-sex groups increased quickly during the rutting season in November and then declined gradually after the rut, and also varied significantly over months (Chi-square test: $\chi^2 = 360.748$, df = 11, $p < 0.001$). The frequency of male groups reached its maximum in July (19.8 %), and decreased to its minimum in December (6.65 %), and similarly varied significantly over months (Chi-square test: $\chi^2 = 57.556$, df = 11, $p < 0.001$). The frequency for solitary individuals also varied significantly over months (Chi-square test: $\chi^2 = 29.067$, df = 11, $p < 0.01$) (Fig. 3).

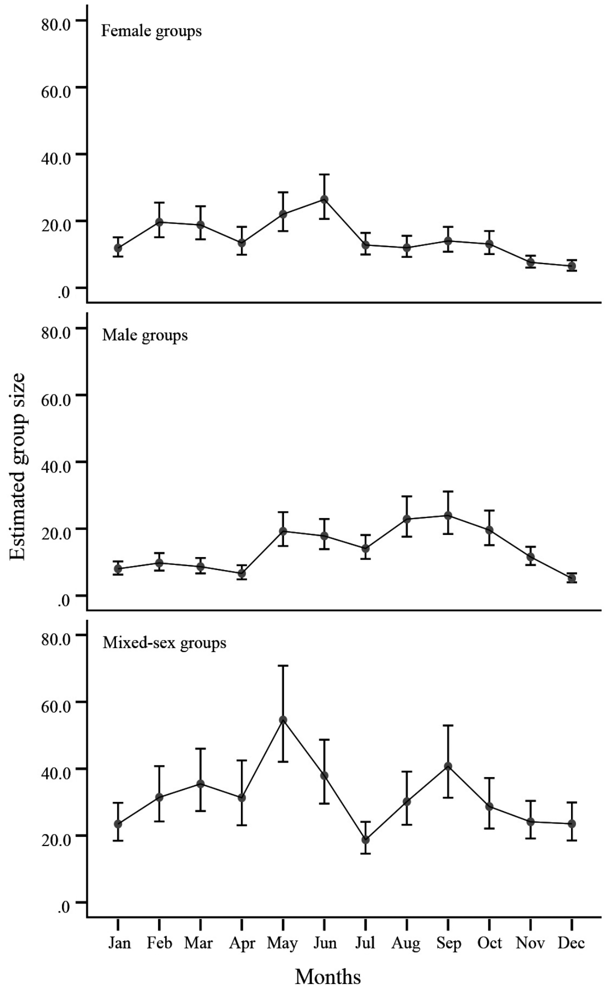

Fig. 2. Monthly variation in mean crowding values of female groups, male groups and mixed-sex groups.

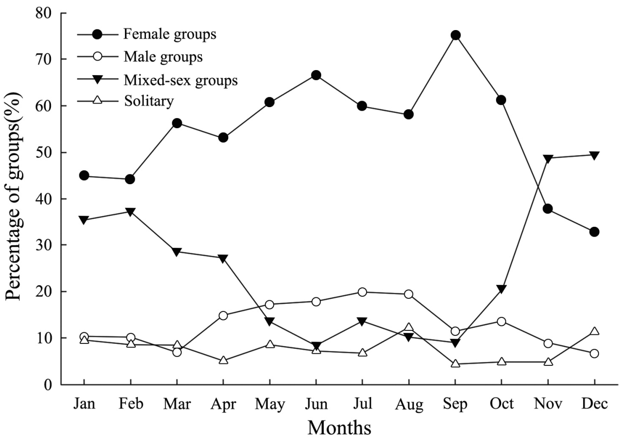

Fig. 3. Monthly changes in group composition of female groups, male groups, mixed-sex groups and solitary.

Discussion

Overall group size distribution

In accordance to our first hypothesis, although the range of group sizes in Siberian ibex could be very large, the heavily right-skewed distribution indicated that small groups were more common in this species. Groups of 1-5 members was a little lower than the hypothesized optimum of five to six animals (Berger 1978), likely as a consequence of the feeding ecology related to habitat. It has been confirmed that the Siberian ibex have the ability to alternate their diet between concentrate selectors at one extreme and grass roughage eater at other depending on seasonal changes of vegetation conditions (Owen-Smith & Novellie 1982, Zhu 2016). Since Siberian ibex inhabit in rugged mountain regions of relatively dry slopes of the Eastern Tien-Shan with unstable food supply (i.e. seasonally scarce and highly uneven food distribution), they form small groups which considerably reduces foraging competition. Our results thus indicate an association between feeding type and group size. Similarly, this phenomenon was also recorded in Japanese serow (*Capricornis crispus* – Takada & Minami 2018), Nubian ibex (*Capra nubiana* – Habibi 1997) and feral goats (*Capra hircus* – Shi et al. 2005), as they preferred to disperse in rugged terrain, where food patches were distributed unevenly.

Besides the influencing of feeding ecology, predation risk could also partly explain the grouping pattern of Siberian ibex. In general, the ibex does not move far away from the cliff areas, which were usually situated not more than 100 m from the nearest rocky area (Xu et al. 2007). These cliffs were used as a refuge from predators and provided a safer environment. As outlined above, these pastures, however, are not always rich with high quality food, and did not allow for bigger group sizes (Fedosenko & Blank 2001, Xu et al. 2007).

Our data demonstrated that adult females were twice more numerous than adult males, which is the typical sex-ratio for most Siberian ibex populations (Fedosenko & Blank 2001, Fedosenko 2003). Nevertheless, our results showed that female groups were larger than male groups only in January to June, and smaller in August to November, in spite of their multiplicity. This phenomenon maybe explained by sex-related size difference of food selection. As adult males are twice larger at least than adult females (Fedosenko & Savinov 1983), adult females, preferring the highest quality of forage with high content of nutrients, were significantly more selective in food compared to adult males (Hanley 1982, Zhu 2016). Adult males were less selective in food quality (Jarman 1974, Hofmann 1989, Zhu 2016), making forage biomass more important than its quality for them. In our study area, forage reached its maximal biomass in August-September and then decreased gradually. Therefore, males had possibility to form larger groups in August to November, taking advantage of the high availability of forage, and to form smaller groups in January to June. Similar to other studies on other ungulate species (Habibi 1997, Shi et al. 2005), mixed-sex groups of Siberian ibex were largest than the other group typologies, and are mainly formed in the pre-rut (October) or early-rutting period (November). This group type is formed throughout the year, or at least until April because of the limited areas with available forage inducing ibex to gather into larger mixed-sex groups (Johnsingh et al. 1999).

Monthly variability in group sizes and frequency of different group types

Many factors have a significant impact on the shaping of group size, such as the distribution and availability of food resources, biological events and predation risk (Fryxell 1991, Childress & Lung 2003, White et al. 2012). In our study area, the high quality forage was very scarce and highly scattered during winter (January-March), therefore the size of female groups was relatively small. The same happened in July-October, when forage quality decreased drastically as the result of a drastic increase in fiber content in plants, despite its highest biomass (Van Soest 1963, Fedosenko 2003). In contrast, vegetation began to emerge and high-quality food became more available during April-May. Fresh vegetation reached its maximum development in June, when females required high-quality food because of their relatively small body sizes and higher nutrition requirement for lactation (Ruckstuhl 1998, Alves et al. 2013). Therefore, they had the possibility to form larger aggregations. Moreover, despite of the birthing period for females in May and part of June (Fedosenko & Blank 2001), when they leave their herds and isolate themselves to give birth in sheltered locations (Fedosenko & Blank 2001), they formed the largest female groups during this time. The reason for that is females hide their kids only for 1-3 days and then return to their female herds with their offspring. It is also true that not all Tien-Shan births occur in concealment, but also on open slopes, especially in warm and dry weather (Fedosenko & Blank 2001), so we observed most mothers back in the herd after a short hiding period. During the rut in November-December, most females mate with adult males, and establish mixed-sex groups. Consequently, the number of female groups decreased drastically and their sizes reached the minimum during this period.

Mixed-sex groups reached their largest sizes in May, with a significant decreasing in its frequency of occurrence. May is the time when occurs the spring movement from the wintering grounds of lower elevations to their summer higher elevated pastures, due to the arrival of domestic livestock, which expelled wild ungulates from the best low-elevated pastures. The movement from higher to lower elevations in Siberian ibex was observed in September, when sizes of mixed-sex groups increased significantly after the minimum obtained in July. Such vertical seasonal movement is typical for Siberian ibex, when they change elevations, slopes and even ranges rising for high-elevated pastures to avoid human disturbance, high summer temperatures and midges during hot period, or descend to lower-elevated snowless slopes from deep snow cover in Alpine zone for more food resources (Savinov 1964, Johnsingh et al. 1999, Fedosenko 2003). Similar to other sexually dimorphic species (Ruckstuhl & Neuhaus 2002, Ruckstuhl 2007), Siberian ibex demonstrated significant sexual segregation during summer months with minimum number and size of mixed-sex groups. During the pre-rut period (October), large mixed-sex groups disintegrated on smaller ones after autumn movement, resulting in a sharp increase of their number. The rutting period (November-December) of Siberian ibex was characterized by the gradual decrease of group size with a subsequent increase of the number of groups. Size reduction of mixed-sex groups was likely related to the mating strategy of the Siberian ibex, leading them to form small groups to minimize male-male competition during rutting time and increasing mating success of adult males (Willisch & Neuhaus 2009). However, such tactic was also a result of the decrease of forage quantity and quality, which occurs in all breeding area supplying sufficient food for small breeding groups.

For small body-size females and young individuals, the quality of forage was more important than vegetative biomass, because their small body size allow them to make use only of high quality food with minimum fiber content, making females to shift from intermediate eaters to concentrate selector strategy. That is why, males gathered in largest groups in August-September, when forage biomass was maximal, while female groups were largest during May-June, when plant quality was higher. Mixed-sex groups were related mostly to biological events, such as movements and rutting period, and to the limited areas with available food during winter period. The movement of ibex in winter is restricted by snow, and they can feed in relatively snow-free areas in windy or sunny places (Johnsingh et al. 1999). In winter conditions, forage has low biomass and quality, and did not meet optimal demands for both males and females. Consequently, both males and females started to be opportunistic feeders (Johnsingh et al. 1999), allowing them to use the limited pastures together and to join into mixed-sex groups. Thus, forage quality and biomass and feeding strategy were primary factors, which determined group size dynamics in Siberian ibex. Regarding to the predation risk, known as the most important factor of grouping behaviour, ungulates will generally increase group size as a successful antipredator strategy (Caro et al. 2004). However, in our study area with low population density of predators, it plays a secondary role, with Siberian ibex enlarging their group sizes when there is enough amount of food of sufficient quality (Jarman 1974, Clutton-Brock et al. 1982, Shi et al. 2005). Thus, as expected, in our study area the group dynamics was primary related to forage quantity and quality.

Solitary

It is very common to observe solitary individuals in ungulate species, for example, in Tibetan antelope (*Pantholops hodgsonii*) (Lian et al. 2004), feral goats (*Capra hircus*) (Shi et al. 2005), and goitered gazelles (*Gazella subgutturosa*) (Blank et al. 2012). In our study area, solitary ibexes were observed throughout the year, but they were mainly composed of (1) males searching for receptive females; (2) females leaving for parturition; and (3) old or sick individuals abandoned by their herd (Fedosenko & Blank 2001, Zhu et al. 2016). Only 0.69 % (262 individuals) of individuals were solitary, demonstrating that most Siberian ibex individuals preferred to live in groups. Extensive research has shown that solitary individuals face a higher mortality rate than individuals in groups, due to an increase in vigilance and a decrease in foraging efficiency, resulting in a higher vulnerability to predation (Karanth & Sunquist 1995, Ramesh 2010).

Conclusion

In summary, we found that Siberian ibex formed mostly small groups, but tended to gather into larger groups when they had sufficient amounts of food of suitable quality. However, females enlarged their groups in periods when high-quality food was most abundant (May-June), while males did it in seasons of largest biomass of plants (August-September). This difference was related to different feeding strategy in females and males based on their significant difference in body size, when small-sized females selected mostly high-quality food, while males were less selective, having more abilities digesting forage with high fiber content. Dynamics of mixed-sex groups was related mostly to biological events, when they enlarged during seasonal vertical movement, reduced by size during rutting time and almost disappeared because of sexual segregation during summer time. We thus found that two main factors contributed to group sizes: primary forage conditions and related feeding strategy and secondary biological events.

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