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Temporal Dynamics of Group Size and Sexual Segregation in Ibex

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Abstract

Group size is an important variable describing behavioural ecology of animals. A variety of factors such as habitat characteristics, life history, spatio-temporal resource dynamics, population density, predation risk, competition with kin, and social learning often determine group size in large mammals. We studied temporal dynamics of group size in Siberian Ibex (*Capra sibirica*) in a protected area in Mongolia. We measured monthly and yearly variations in typical group size and used the sexual segregation and aggregation statistic to assess sexual segregation. Ibex formed the largest groups in November and smallest groups in July. However, group sizes did not significantly differ between the sexes. There was marked sexual segregation during the summer months and within all years segregation increased with temperature. We show that grouping behaviour is a complex phenomenon and is probably determined by a combination of factors, such as species' life history, habitat and environmental characteristics, and behavioural strategy against predation risk.

Keywords: ibex, SSAS, temperature, typical group size, Mongolia

1. Introduction

Many species of animals form groups (often called herds, schools, flocks, etc.). For some individuals being in a group may reduce predation risk, increase foraging efficiency, increase thermoregulation, reduce other energy costs, enhance resistance to diseases, facilitate reproduction, or set the stage for social learning (BONABEAU et al. 1999). Large mammalian herbivores often form groups of individuals located in close proximity that often engage in a common activity such as feeding, travelling, resting, and being vigilant (GERARD et al. 2002). The size and pattern of group formation varies within and between species and sexes, as well as at spatial and temporal scales. A number of factors influence group formation, including habitat openness and heterogeneity, population density, species life history, seasonal changes in forage availability, temporal variation in predation risk, body size, competition with kin, foraging patch size, and social learning (SPINAGE 1969; ESTES 1974; JARMAN 1974; WIRTZ & LORSCHER, 1983).

Despite a vast literature on grouping behaviour, we know relatively little about factors influencing ungulate grouping behaviour in low resource and highly seasonal environments (but see FESTA-BIANCHET & COTE 2008) and especially in central Asia. The Siberian ibex (*Capra sibirica*) is a sexually dimorphic, polygynous, and gregarious mountain ungulate inhabiting mountains and highlands of central Asia. Ibex frequent steep rugged cliffs, mountains, canyon, and rocky outcrop regions (FEDOSENKO & BLANK 2001; READING et al. 2007). The species exhibits a polygnous mating system and sexual segregation (VILLARET et al. 1997; RUCKSTUHL & NEUHAUS 2000). Rut occurs in late autumn and lambing occurs in spring (SCHALLER 1977, FEDOSENKO & BLANK 2001). As is typical for C*aprinae* (SCHALLER 1977), ewes separate from other animals as parturition approaches and deliver lambs in isolation. Females hide lambs for the first few days of life. Sex-ratios in both are skewed towards females (SCHALLER 1977; READING et al. 1997; FEDOSENKO & BLANK 2001). Wolves (*Canis lupus*) and snow leopards (*Uncia uncia*) are the main predators, but lynx (*Lynx lynx*) and domestic dogs (*Canis familiaris*) also kill some animals, as with argali (*Ovis ammon*) (READING et al. 2005, 2009).

We monitored the temporal dynamics of grouping behaviour and sexual segregation patterns of ibex in Ikh Nart Nature Reserve, Mongolia. Based on knowledge of species' preferred habitat we predict that typical group size should not be high (ESTES 1974; JARMAN 1974). Since the species inhabits steep rugged habitats with escape terrain, we did not expect a significant difference in group sizes between the sexes. Based on their life history and polygynous mating system ibex should form larger groups during the mating season compared to the rest of the year. If resource availability determines group size, in low density populations animals may disperse into smaller groups when forage is abundant to prevent intraspecific competition. So, under the resource availability hypothesis, group sizes should be smallest during the peak vegetation growth period and relatively larger during the rest of the year. Based on sexual body size dimorphism and polygynous mating system, we predict that ibex will display strong year-round segregation, except during the mating period, as commonly occurs in other sexually dimorphic ungulates (RUCKSTUHL & NEUHAUS 2000).

2. Study area

Ikh Nart Nature Reserve (Ikh Nart) lies within Dornogobi Aimag (East Gobi Province) of Mongolia (N 45.723º/E 108.645º). Established in 1996, Ikh Nart covers an area of about 66,760 hectares of grassland and semi-desert steppe environment and harbours one of the last remaining, large populations of argali sheep and a population of Siberian ibex (MYAGMARSUREN 2000; READING et al. 2006). Ikh Nart was established in 1996 to protect the region’s unique rocky outcrops and its wildlife on the northern edge of the Gobi (MYAGMARSUREN 2000, READING et al. 2006). The region is a high upland (~1,200 m) defined by semi-arid steppe vegetation. Permanent cold-water springs are available in some of the several, shallow valleys draining the reserve. Climate is strongly continental and arid, characterized by cold winters (January to March: minimum temperature - 43 °C), dry, windy springs (April to June: wind speed of 25 mps), and relatively wet, hot summers (July-September: Maximum temperature to 40 °C). Precipitation is low and seasonal, with most precipitation falling in summer (READING et al. 2006). Flora and fauna are representative of the semi-arid regions of Central Asia, with a mix of desert and steppe species (MURDOCH et al. 2006, READING et al. 2006). Fauna comprises of 33 mammal species, and several birds, reptiles and invertebrates. Vegetation is sparse and dominated by xerophytic and hyperxerophytic semi-shrubs, shrubs, scrub vegetation, and turfy grasses.

3. Data collection

We collected monthly data on group sizes and composition of ibex during 2000-2008. We recorded group size and composition for a minimum of 2 weeks each month, and often for the entire month. We collected most data while tracking radio collared argali and ibex (see READING et al. 2003, 2005, 2007). We defined groups as a single individual or a cluster of animals within 30 m of each other that showed co-ordinated movements. We classified animals in each group as adult males, adult females, yearlings (subadults 1-2 years in age), and lambs (newborn to 1 year in age). We usually could not determine the gender of yearlings and lambs definitively. We excluded animals that we could not classify from further analysis. We obtained daily weather data from the nearest government meteorological station (~ 50 km from Ikh Nart) and collected daily weather data at Ikh Nart. We pooled temperature (°C) and precipitation (mm) data into monthly averages of maximum, minimum, and means. To maintain the independence of groups, we did not collect data on the same group on the same day.

4. Data analyses

Group sizes and composition

We performed data analysis at monthly and yearly temporal scales. We estimated mean and JARMAN’S (1974) typical group sizes (TGS) and genders for each month per year of observation, but relied on TGS as a measure of grouping patterns in our study. While mean group size represents the average number of individuals we encountered, TGS is more animal-centred and represents the number of other members of a group in which any individual finds itself (JAR-

MAN 1974). TGS is often higher than the mean group size and collates several environmental constraints acting on group formation and therefore, we believe it represents a better descriptor of social organisation than mean group size. We followed JARMAN (1974) in calculating TGS as: $$TGS = \frac{\sum_{t=1}^{n} X_i^{\,2}}{\sum_{t=1}^{n} X_i}$$ where *x,* represents the number of individuals in each of *n* groups.

We used one way analysis of variance (ANOVA) to compare group sizes among sexes. Resource availability in seasonal environments is correlated strongly with timing and quantity of precipitation. Peak growing season in Ikh Nart occurs in summer and maximum precipitation occurs during June or July (READING et al. 2006) after the parturition period in ibex. We included precipitation as a proxy for changing resource availability in the study to identify possible relationships between resource availability and group size using generalised linear models with Poisson (random) distributions. We used generalized linear models to identify the relationship between the TGSs and mean precipitation. We tested the variables for normality. Variables were appropriately transformed in case of non-normality.

Sexual segregation

We used a derivation of the Chi-square statistic called the Sexual Segregation and Aggregation Statistic (SSAS) (BONENFANT et al. 2007) to provide a general test for segregation and aggregation patterns observed in natural populations. SSAS varies between 0 (no segregation) and 1 (complete segregation), and provides an estimate of the distance between observed and expected distributions of males and females under the null hypothesis of random association between sexes for a given number of groups and animals. Consequently, we define segregation by gender as a group that deviates from the null hypothesis and we define aggregation by gender as a group that falls close to that predicted by the null hypothesis. Segregation occurs when the sex ratio of each group deviates strongly from the population sex ratio (e.g., with many unisex groups, for instance). Conversely, aggregation occurs when each group has a sex ratio almost equal to the population sex ratio. We also assessed temporal changes in segregation for both months and years of observation with respect to changes in temperature.

5. Results

We observed 1707 ibex groups. Typical ibex group size was 7.85 ± 1.86 (mean ± S.E.). We observed the largest group in November (11.44 ± 5.02) and the smallest during July (5.49 ± 1.31) (Fig. 1). Group sizes of males and females did not differ significantly (Males = 3.26 ± 0.12, n= 780, Females = 3.36 ± 0.22=781; $F_{1,22}$ = 0.003, p = 0.97, Fig. 2) and ibex formed the largest groups in November for females and in February for males (males: 3.51 ± 1.91, females: 5.15 ± 1.94; Fig. 2). Group sizes also showed high variability by year and were typically more variable for males than females (coefficient of variation: males= 0.38, females= 0.31; Fig. 3).

We found no effect of precipitation on the grouping behaviour of ibex during the year (estimate ± S.E. = -0.19 ± 0.08; F = 5.45, df = 10, R^2 = 0.35) and across years (estimate ± S.E. = -0.23 ± 0.11; F = 4.46, df = 6, R^2 = 0.43).

Ibex show marked sexual segregation, with segregation peaking during April, May, and June (Fig. 4). The observed SSAS statistic generally fell outside the significant confidence limits of SSAS (2.5 % and 97.5 %; Table 1, Fig. 4) under the null hypothesis of random association. Segregation was more pronounced during summer months compared to other seasons (low SSAS values for January, April, November, and December). Variability in yearly SSAS values for ibex indicates that ibex did not consistently segregate from year to year. Segregation increased with an increase in mean temperature during the year (estimate ± S.E. = 0.01 ± 0.001; F = 42.35, df = 10, R^2 = 0.809).

Fig.1: Monthly variation in typical group sizes (± S.E) of Siberian ibex (*Capra sibirica*) in Ikh Nart Nature Reserve, Mongolia.

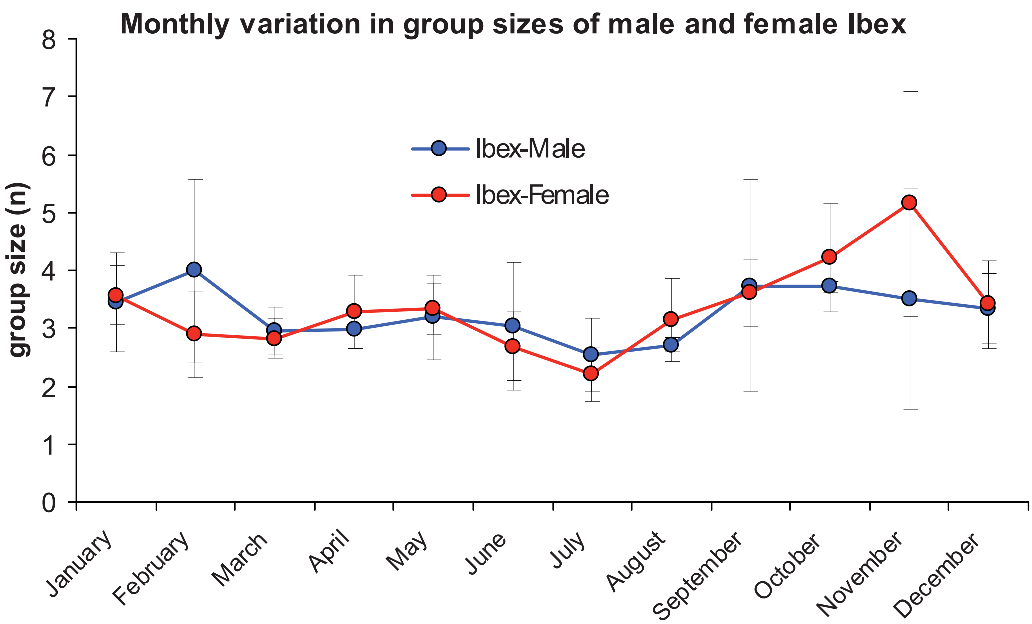

Fig. 2: Monthly variation in typical group sizes (± S.E) of male and female Siberian ibex (*Capra sibirica*) in Ikh Nart Nature Reserve, Mongolia.

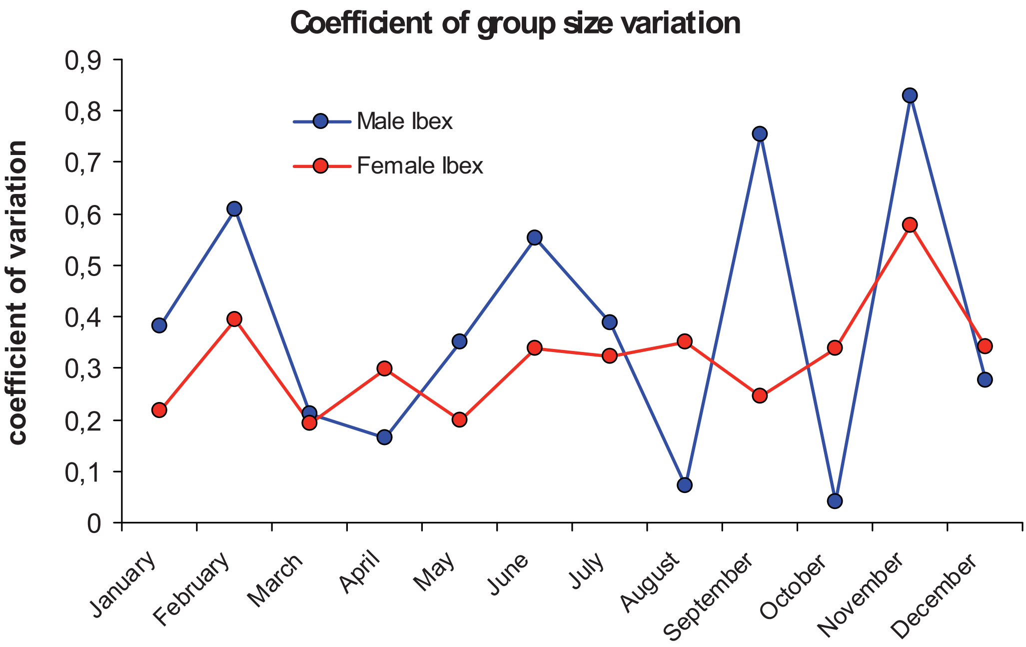

Fig. 3: Coefficient of variation of typical group sizes of Siberian ibex (*Capra sibirica*) and the sexes in Ikh Nart Nature Reserve, Mongolia.

Table 1: Sexual Segregation and Aggregation Statistic (SSAS) along with the confidence intervals for years and month

year	SSAS	2.50 %	97.50 %
2000	0.822	0.599	0.744
2001	0.292	0.109	0.125
2002	0.365	0.131	0.147
2003	0.991	0.435	0.861
2004	0.694	0.474	0.584
2005	0.644	0.533	0.616
2006	0.861	0.537	0.621
2007	0.643	0.447	0.514
2008	0.619	0.414	0.479

month	SSAS	2.50 %	97.50 %
January	0.362	0.153	0.225
February	0.282	0.180	0.255
March	0.344	0.193	0.289
April	0.413	0.216	0.325
May	0.517	0.275	0.395
June	0.613	0.284	0.366
July	0.658	0.358	0.512
August	0.575	0.332	0.467
September	0.677	0.277	0.405
October	0.297	0.155	0.246
November	0.217	0.135	0.196
December	0.456	0.214	0.306

6. Discussion

Grouping behaviour is a complex phenomenon. Ibex inhabit steep, rugged terrain and "closed" habitats that provide escape and cover from stealth predators, such as snow leopards or lynx. READING et al. (2007) found that most ibex mortalities occur due to predation. Hence, forming larger groups may not maximize energy, as it may increase the chances of being seen by predators. Our results of ibex living in relatively smaller groups all year compared to other ungulates such as argali (SINGH et al. in prep) and no significant differences in group size of females and males support this argument. We observed the largest groups in November, which is the rutting season when we expect to observe the largest groups in a polygynous species such as ibex. The higher variability in group sizes for males compared to females can be attributed to this polygynous mating system where one male may form harems and stay with many females. These harems disperse after the rut and males may form single sex groups again. In many ungulate species, different classes of males may also form separate groups (FESTA-BIANCHET & COTE 2008), perhaps explaining the higher variability in male group sizes.

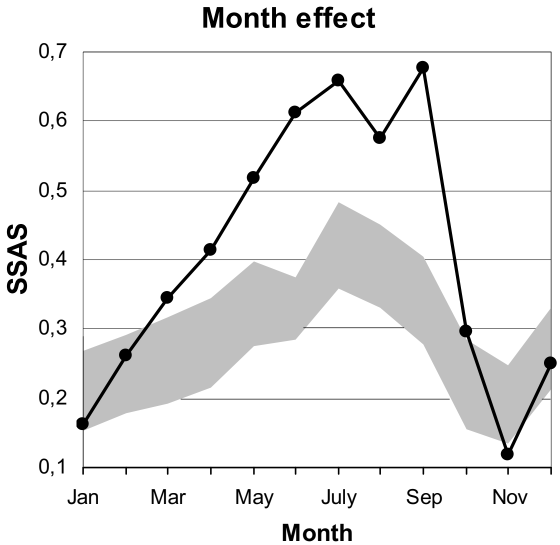

Fig. 4: Annual pattern of sexual segregation in Siberian ibex (*Capra sibirica*) in Ikh Nart Nature Reserve, Mongolia. The SSAS indicates significant sexual segregation or aggregation if the observed value falls above or below the shaded area (at the 5% error level), respectively.

The absence of an effect of precipitation indicated that the grouping behaviour did not relate to this and other correlated variables such as forage productivity. If ibex trade-off security for food, then such an observation may be valid and is confirmed by the absence of large variability in group sizes of the sexes. However, lack of data on marked animals and their precise locations in the habitat prevents further speculation.

Ibex segregated sexually during most months and years, in agreement with the 'sexual dimorphism of body size and polygynous mating systems' hypothesis (MAIN et al. 1996). Segregation peaked during spring (April-June), conforming to that found for other mountain ungulate species of similar body sizes (BONENFANT et al. 2007). Again, aggregation during winter (November to February) most likely occurred due to formation of mixed groups during the rut. The variability in gregariousness of the sexes and sexual segregation across the years suggests that gregariousness maximizes energy or reproductive success in this species, although to what extent remains unknown. As we lacked a measure of density, we were unable to predict if this resulted from a density effect. In future studies we hope to better examine the nature of sexual segregation by testing for spatial distribution of groups and assessing habitat characteristics for each group. The observation of increase in segregation with temperature (i.e., during summer) is interesting. CONRADT et al. (2000) tested a weather sensitivity hypothesis in red deer (*Cervus elaphus*), which predicts that the sexes vary in their sensitivity to harsh weather conditions. They found that bad weather (strong wind, low temperature, heavy rain) in winter and spring negatively influenced use of high quality forage habitat in all deer; that adult males responded more strongly to low temperature and strong wind than did females; and that adult males foraged on windy days at better sheltered sites than did females. If male ibex are more sensitive to the bad weather conditions that commonly characterize high altitude rangelands and mountains, we may observe stronger segregation during months with harsher weather. Lack of data on spatial distribution of groups as well as foraging and activity budgets prevents us from making strong conclusions. However, we can state that grouping behaviour and sexual segregation in ibex vary on a temporal scale and are determined by environmental factors in addition to the species' life history and habitat selection.

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