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Sexual segregation in the Darwin's wild sheep, *Ovis ammon darwini*, (Bovidae, Artiodactyla), in the Mengluoke Mountains of Xinjiang, China

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Abstract. Sexual segregation has been found among many vertebrate species. Argali, like other sexually dimorphic Capridae, form sexually segregated groups outside the breeding season. The degree of sexual segregation and its seasonal changes have never been examined and quantified in Asiatic species of wild sheep. In this paper we are considering seasonal fluctuation in the degree of sexual segregation and check the activity budget hypothesis to explain this phenomenon in the Darwin's wild sheep (*Ovis ammon darwini*), a subspecies of argali sheep (*Ovis ammon*). The activity budget hypothesis states that sexually size-dimorphic males and females segregate into different groups due to incompatibilities in activity budgets and movement rates. We collected data on activity budgets in the argali sheep from 2015 to 2016, in the Mengluoke Mountains of Xinjiang Province, and used Conradt's segregation coefficient (*SC*) to measure the degree of sexual segregation outside and during the rutting seasons. Our results showed that the *SC* value was highest outside the rutting season (0.98), when argalis were almost completely segregated. During the rutting period, the segregation coefficient dropped more than twofold (0.43) compared to the non-rutting season. In addition, our data supported the activity budget hypothesis: female and male argali had different behavioural activity patterns during the non-rutting season. Female argali spent more time feeding, followed by resting, standing, moving, and other behaviours, while males spent most of their time resting, followed by feeding, standing, other behaviours, and moving. Female argali spent significantly more time feeding than males, while males spent significantly more time resting and in other behaviours than females. Activity synchronization indices for both female groups and male groups were significantly higher than in mixed-sex groups. Sexual segregation is the best behavioural strategy for sexually dimorphic ungulates and the activity budget hypothesis explained this phenomenon well in Darwin's wild sheep.

Key words: activity budget hypothesis, activity synchronization, argali, Conradt's segregation coefficient, sexual dimorphism

Introduction

Sexual segregation (by habitat or socially) has been reported across a wide range of taxonomic groups both in invertebrates and vertebrate taxa, e.g. fishes, reptiles, birds, kangaroos, carnivores, cetaceans and primates (Ruckstuhl & Neuhaus 2005). Most studies on sexual segregation have been done on social ruminants (Clutton-Brock et al. 1987, Conradt & Roper 2000, Ruckstuhl & Neuhaus 2002, Bowyer 2004, Blank et al. 2012). Sexual segregation, which is a basic component of social organization, is very important and a deeper understanding of the evolution of sociality is needed.

Many hypotheses have been proposed to explain sexual segregation, which can be classified into four categories (Beier 1987, Main et al. 1996, Ruckstuhl 1998, Barboza & Bowyer 2000, 2001, Bowyer 2004, Yearsley & Pérez-Barbería 2005, Main 2008): 1) predation-risk hypothesis, which considers the sexual differences in risk of predation and reproductive strategies; 2) social affinity hypothesis, which predicts social factors to drive segregation, such as interactions with and preference for same-sex peers, and learning fighting skills; 3) gastro-centric hypothesis, which predicts that sexual differences in energy requirements and digestive capabilities and therefore different

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choice of diet and habitat types leads to segregation; and 4) activity budget hypothesis, which explains social segregation in terms of differences in activity budgets for males and females, leading to behavioural asynchrony. These hypotheses are, however, not all mutually exclusive. The social affinity hypothesis and activity budget hypothesis mainly focus on social segregation, while the predation-risk hypothesis and gastro-centric hypothesis are predicting habitat segregation (Ruckstuhl 2007). When social segregation is found within the same habitat, then the social affinity or activity budget hypotheses can be tested (Main et al. 1996). Therefore, social segregation may be universal in explaining sexual segregation in ungulates (Yearsley & Pérez-Barbería 2005, Li & Jiang 2008).

The activity budget hypothesis has been debated since it was proposed by Ruckstuhl (1998). It states that smaller females are less efficient at digesting high-fiber forage than bigger males owing to body size digestive constraints, and females have smaller stomachs, a body size, mouth size, but higher metabolic needs (Demment & Van Soest 1985, Ruckstuhl 1998). Females thus have to compensate their lower digestive efficiency by foraging for longer than males, or females may select higher-quality forage and take more time than males, while males would spend more time ruminating or lying than females due to their digestive efficiency. The activity budget hypothesis also predicts that animals with similar activity budgets can form groups easily, while big differences in activity budgets make behavioural synchrony difficult and potentially costly (Ruckstuhl 1998). Some studies have supported this hypothesis (Conradt 1998, Ruckstuhl & Kokko 2002, Xu et al. 2012). Asiatic ibex (*Capra sibirica*) males, e.g. spent a significantly longer time standing than females, and activity synchronization indices of both female and male groups were significantly higher than those in mixed-sex groups (Xu et al. 2012). Red deer (*Cervus elaphus*) in mixed-sex groups were more likely to break up than single-sex groups due to sex differences in activity rhythm (Conradt 1998). However, the activity budget hypothesis does not work in some dimorphic species (Mooring et al. 2003, Michelena et al. 2006). For example, Mooring et al. (2003) found that in desert bighorn sheep (*Ovis canadensis mexicana*) male and female groups did not differ in foraging time, moreover time spent moving, resting, or ruminating between the sexes showed no differences as predicted by the "activity budget hypothesis". Likewise, grey kangaroos' (*Macropus fuliginosus*) differences in body size did not have an impact on the activity budget and consequently activity asynchrony: individuals of different body size did not have different transition times between feeding and resting, and synchrony was not lower among mixed-body size than same-body size groups (MacFarlane 2006). These results are inconsistent with the activity budget hypothesis; therefore, the activity budget hypothesis needs to be tested in other sexually size dimorphic species (Michelena et al. 2006, Xu et al. 2012).

The Darwin's wild sheep or Gobi argali is classified as a Category II Protected Wild Animal Species under the Wild Animal Protection Law in China (Wang 1998). Studies of this species are quite limited in subject, mainly concentrating around habitat distribution and population density (Reading et al. 1997, Schaller & Kang 2008, Yu et al. 2008), remaining relatively few in number (Harris & Miller 1995, Schaller 1998, Namgail et al. 2007, Wingard et al. 2011, Du et al. 2015). As one of the most sexually dimorphic species among wild sheep, male argali are two times larger than females (Fedosenko & Blank 2005). Therefore, sexual segregation is expected to be typical for argali (Ruckstuhl & Neuhaus 2002). Although reports that argali males and females live in separate groups outside the rutting season have been published in Russian (Fedosenko & Blank 2005), the degree of sexual segregation and activity synchrony has never been quantified. The main purpose of this study was to evaluate the degree of sexual segregation outside and during the rutting season of Darwin's argali. Based on direct observations of activity budgets, we tested the predictions of the activity budget hypothesis. In general, we predicted that male and female Darwin's argali will have different activity budgets, and females would spend more time feeding than males, males would spend more time resting than females, and the level of activity synchronization of same-sex groups would be higher than that of mixed-sex groups.

Study Area

Fieldwork was conducted in the Mengluoke Mountains (44°31′ N, 91°47′ E), located in the eastern part of the Junggar Basin, situated in the south-eastern area of the Altai Mountains (Xinjiang Province, China). The Mengluoke Mountains consist of 100 km^2 of narrow valleys and eroded rock outcrops, at an elevation of 1200-1750 m, with flora represented by desert-steppe plant communities. The climate is cold and arid, and the mean annual precipitation reaches 150 mm, the minimum of which is observed during summer. The area is inhabited by various protected animals such as the goitered gazelle (*Gazella subgutturosa*), lynx (*Lynx lynx*), wolf (*Canis lupus*), red fox (*Vulpes vulpes*) and chukar partridge (*Alectoris chukar*). The resident shepherd population included approximately 18 families with a total of 78 members, all of whom use the Mengluoke Mountains all year round for livestock grazing. The intensity of use by livestock varied seasonally: the southern parts of the mountains served as the primary pastures for eight families from October to April; the northern parts were pastures for 10 families from May to September. The total number of livestock that grazed in the Mengluoke Mountains at the time of this study was estimated as 1700 sheep, 1300 goats, 24 horses and 17 cattle during the study period.

Material and Methods

Group surveys

We carried out our surveys from July to November 2015 and from May to August 2016. Observations were carried out each month, and for at least four days in a given month. The collection of field data was based mainly on direct observations of Darwin's argali along the mountain ridges (Klich & Magomedov 2010). The survey routes were travelled on foot during all daylight hours, and all Darwin's argali were recorded along these transects.

We distinguished female, male, mixed-sex, and sub-adult groups. Females become sexually mature at the age of 2.5-3 years, males at the age of 4-4.5 years. We identified the sex and age of Darwin's argali according to the length, thickness and shape of horns (Fedosenko & Blank 2005). Herds of sub-adult males and females were uncommon, and thus merged with adult groups according to their sex (yearling-female groups typically merged with female groups, yearling-male groups with male-only groups, and very rarely yearling groups of both sexes joined mixed-sex groups). Female groups contained one or more adult females plus young or/and sub-adult females (yearlings). Male groups contained one or more adult males plus sub-adult males (yearlings). Mixed groups consisted of one or more adult males and one or more adult females plus sub-adults (yearlings of both sexes) or/and young of the year (Blank et al. 2012).

Behavioural records

Our observations were conducted during the daytime from 7:00 a.m. to 8:00 p.m. Groups were video recorded using a video camera (Sony HDR- XR150E, Sony Corporation, Tokyo, Japan), with a distance > 300 m away from the group to minimize disturbance (Rieucau et al. 2012). Although the individuals were not marked, we tried to avoid re-sampling same individuals during the day by filming groups spaced by distance of > 2 km from each other.

Group size was recorded at the beginning of each observation period and we noted all changes of group size during recording. We recorded the date, time, location, total herd size and group composition by age and sex. We recorded the following five behaviours: feeding, standing, moving, bedding, and other. Feeding was defined as biting, chewing, browsing, grazing, or swallowing. Standing was defined as standing still, standing alert, and standing ruminating. Bedding was defined as sternal recumbency with or without rumination and includes sleeping with eyes closed. Moving was defined as travelling and walking. Other behaviours were defined as all other activities not included in the above categories such as grooming, defecating, and lactating (Shi et al. 2003, Li & Jiang 2008, Xu et al. 2012).

Using the video recordings, we sampled data using the focal animal sampling method and group scan sampling method (Martin & Bateson 2007). Focal animal sampling method was used to sample five to eight individuals which are the most common group size in our study area.

Individual vigilance was estimated by the focal animal sampling rule (Martin & Bateson 2007). Focal individuals were randomly selected from the herd based on their age-sex class. The duration of each category of behaviour by the focal animal was recorded and used for calculations of time budget proportions. Argali activity synchronization was recorded by scanning animal groups at 3-min intervals. All data were collected by the same person during the entire observation period (Martin & Bateson 2007). We recorded the behaviour of each individual in observed groups as long as we could, until the group ran away or group size changed. The observation time of each group usually ranged from 15 to 30 min.

Statistical analyses

We pooled our group survey data into two physiological periods: non-rutting season (May-August) and rutting season (September-November) (Fedosenko 2000, Fedosenko & Blank 2005). We used the Condradt's segregation coefficient (*SC*) to quantify the degree of sexual segregation (Conradt 1998). However, we included singletons for our calculations of *SC* values, as suggested by Bonenfant et al. (2007). This is important because singletons are very commonly observed in argali and omitting those

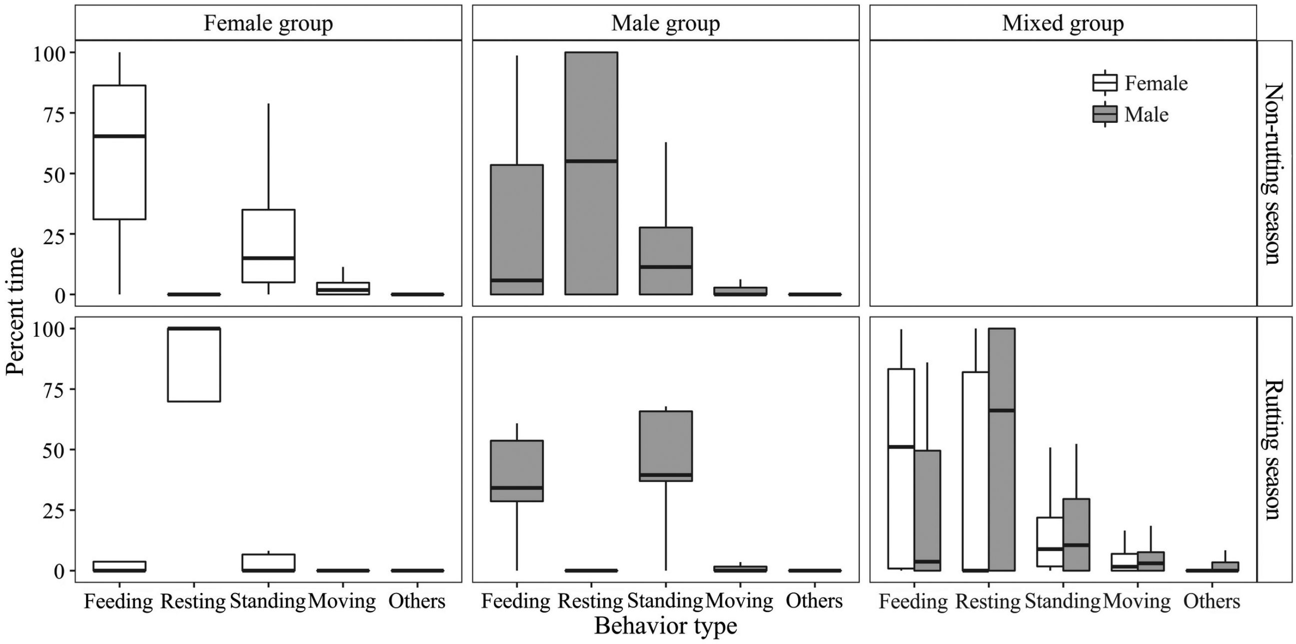

Fig. 1. Activity time budgets in argali sheep, *O. ammon darwini*, in the Mengluoke Mountains of Xinjiang, China. Percent time are displayed with quartiles and 95 % confidence intervals in each behavioural category.

individuals would considerably bias the segregation index (Bowyer 2004). Conradt's *SC* was calculated according to the following formula:

$SC_{social} = 1 - [(N - 1)/X \times Y] \times \sum[x_i \times y_i/(n_i - 1)]$

where x_i is the number of adult males in *i*th group, y_i is the number of adult females in ith group, n_i is the number of adults in *i*th group ($n_i = x_i + y_i$), *X* is the total number of adult males sampled, *Y* is the total number of adult females sampled, *N* is the total number of adults sampled ($N = X + Y$). *SC* ranges from 0 (no segregation) to 1 (complete segregation).

The degree of activity synchronization was measured using the behaviour synchronization index (*S*) proposed by Ruckstuhl (1999). The synchronization factor (S_f) was calculated for each group, when more than 50 % of individuals in the group had the same activity ($S_f = 1$), otherwise $S_f = 0$. The mean synchronization S_i for *i*th behavioural observation sample was $S_i = \sum(S_f)/n$, where *n* is the number of scans. The mean group synchronization index *S* was $S = \sum(S_i)/k$, where *k* is the number of the observed groups. The group *S* varies from 0 to 1, with a high *S* value meaning high behavioural synchronization. Because the data were not normally distributed, we used the Mann-Whitney U-tests to compare sexual differences in the synchronization index of female, male, and mixed-sex groups. To control the effect of group size on feeding behaviour, we excluded groups below five individuals (Risenhoover & Bailey 1985, Ruckstuhl 1999). All significance levels were set at $P = 0.05$. Data were analyzed with the IBM SPSS 22.0 statistical package.

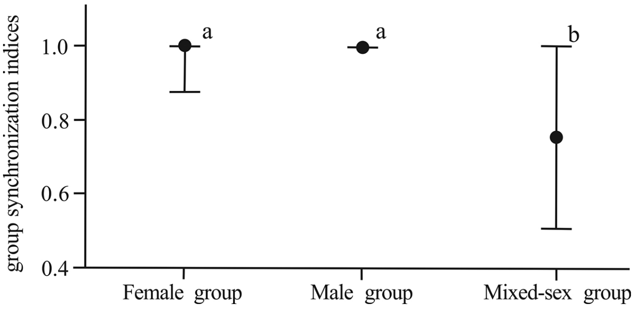

Fig. 2. The index of synchronization of three kinds of groups (median with 95 % confidence intervals). Different letters above each plot indicate significant differences in values.

Results

During our observations, we identified 685 argali individuals from 205 groups. Among them, we found 107 female groups (52.71 % from all herds), which contained 359 argali (52.72 % of all identified individuals). We found 74 male groups, which made up 35.41 % of all groups, and contained 126 argali or 17.91 % of all individuals. We also observed 24 mixed-sex groups, which were rare compared to female and male groups, and represented only 11.82 % of all herds (they contained 200 argali or 29.37 % of all individuals). We found 134 groups (mean group size: 2.98 ± 3.74) during non-rutting season, with 92 female groups (mean group size: 3.46 ± 4.35), 41 male groups (mean group size: 1.90 ± 1.36), and only one mixed group (group size: 3). We observed 71 groups (mean group size: 4.03 ± 3.75) during rutting season, with 33 male groups (mean group size: 1.90 ± 1.36), 23 mixed groups (group size: 8.57 ± 3.19) and 15 female groups (mean group size: 2.73 ± 1.22). The *SC* value was highest during the non-rutting season (0.98), when argali were almost completely segregated. During the rutting period, this coefficient dropped to 0.43 and was significantly lower than during the non-rutting season.

Female and male argali had different behavioural patterns in mixed groups during the rutting season. Argali females spent most of their time feeding, followed by resting, standing, moving, and other behaviours, while males spent most of their time resting, followed by feeding, standing, other behaviours, and moving (Fig. 1). Female argali spent significantly more time feeding than males (Mann-Whitney U-tests, Z = –3.50, $P < 0.01$), while males spent significantly more time resting (Mann-Whitney U-tests, Z = –2.15, $P = 0.032$) or were engaged in other behaviours (Mann-Whitney U-tests, Z = –3.54, $P < 0.01$), than females. There were no significant differences in standing (Mann-Whitney U-tests, Z = –0.38, $P = 0.71$) and moving (Mann-Whitney U-tests, Z = –0.674, $P = 0.493$) between females and males. In non-rutting season, there was only one mixed group and the data remained unrecorded, and behavioural data of single-sexed groups are mostly valued and analysed in rutting seasons.

Independent of season, group synchronization indices were the highest in male groups, followed by female and mixed-sex groups (Fig. 2). The index of synchronization was statistically the same in male and female groups (Mann-Whitney U-tests, Z = –0.811, $P = 0.417$), but they both were significantly different from mixed-sex groups (Mann-Whitney U-tests: female groups, Z = –2.963, $P < 0.01$; male groups, Z = –2.269, $P = 0.023$).

Discussion

As predicted by the activity budget hypothesis, argali, which have a highly distinctive sexual size dimorphism, were sexually segregated into three group types (males, females and mixed sex groups; (Ruckstuhl & Neuhaus 2002). Moreover, our argali were highly sexually segregated in the non-rutting season, while the level of segregation dropped considerably during the rutting period, which is consistent with that observed in other wild sheep species [Rocky mountain bighorn sheep (*Ovis canadensis canadensis*): Ruckstuhl 1998; desert bighorn sheep: Mooring et al. 2003; Alaskan moose (*Alces alces*): Spaeth et al. 2004; Tibetan argali (*Ovis ammon hodgsonii*): Singh et al. 2010].

Sexual and age related body size dimorphism is a driving factor leading to sexual differences in activity budget (Ruckstuhl & Neuhaus 2002, Yearsley & Pérez-Barbería 2005). As mentioned earlier, argali have a high degree of sexual size dimorphism, with males being two times as heavy as females (Fedosenko & Blank 2005). Thus, as we predicted, the activity budget between females and males was significantly different. Large body-sized males are predicted to be better at digesting low-quality food due to a larger rumen size. As predicted males spent less time feeding and more time resting (Ruckstuhl & Neuhaus 2002). In contrast, high-quality food (high in protein and low in fiber) demands less time for rumination and digestion, but more time for collection. Consequently, females compensated their lower digestive efficiency by spending more time feeding (Van Soest 1994).

Individuals from the same sex group are expected to have similar demands in regards to food and activity patterns (Ruckstuhl 1998). In our study, females and males had a considerably higher index of synchronization in single-sex groups than in mixed-sex groups, which is in accordance with the activity budget hypothesis. Surprisingly, even in mixed-groups, the index of synchronization remained high during the mating season. This suggests that male and female argali in mating groups synchronized activities, consistently with the idea that behavioural synchrony may be important in maintaining group cohesion even during the mating season (Ruckstuhl & Neuhaus 2000, Tettamanti & Viblanc 2014).

Predation holds potential to cause sexual segregation in ungulates (Bleich et al. 1997, Bowyer 2004). Males select high-risk, high-energy gain habitats, whereas females trade off food quality of the habitat in favour of safety to their offspring (Bowyer 1984, Main et al. 1996, Lingle & Wilson 2001). Habitat segregation is thus ultimately due to sexual differences in reproductive strategies and predation risk. Lynxes and wolves were observed in this study area with quite a small population and only one observed appearance in the two years. Therefore, the impact of predators on the argali was neglected.

The activity budget hypothesis explains many cases of sexual segregation for sexually dimorphic species, such as bighorn sheep, red deer (Conradt 1998), merino sheep (*Ovis aries*) (Michelena et al. 2004), Tibetan gazelle (*Pantholops hodgsonii*) (Li & Jiang

2008) and Asiatic ibex (Xu et al. 2012). However, the activity budget hypothesis fails to explain sexual segregation if males and females show the same activity patterns but lived segregated or if they differed greatly in their activity budgets but stayed in mixed-sex groups (Ruckstuhl & Neuhaus 2002). Although we found support for the activity budget hypothesis in our study on argali, other hypotheses of sexual segregation cannot be excluded. The predation-risk, gastro-centric hypothesis and social affinity hypothesis invoke functional explanations involving ecological factors, body size dimorphism, feeding behaviour, and energy requirements (Bon & Campan 1996, Stokke & du Toit 2002, Bowyer et al. 2004, Xu et al. 2010, 2012). Mooring et al. (2003) found that, in desert bighorn sheep, ram and ewe groups did not differ in foraging time or selectivity, nor did they differ in time spent moving, reclining, or ruminating as would be predicted by the activity budget hypothesis. In this study, males sought more abundant forage to build up body condition needed and to maximize mating success, while females chose rugged terrain that minimized predation risk to themselves and their offspring. These results are in accordance with the predictions of the predation-risk hypothesis. Furthermore, merino sheep males and females differed in their speed of movement and/or higher social affinity between same-sex than opposite-sex peers, which can be explained by the social affinity hypothesis (Michelena et al. 2004). Barboza & Bowyer (2001) assumed that gastro-centric hypothesis could explain sexual segregation according to the difference of seasonal metabolism of energy and protein among nonreproductive female, reproductive female and male reindeer (*Rangifer tarandus*). Further they pointed that differences in feeding activity between the sexes might be a consequence of metabolic demands rather than the cause of sexual segregation.

Sexual segregation is a complex phenomenon, with multiple ultimate and proximate causes, and as stated by many, no single hypothesis is able to fully explain this phenomenon. Though the activity budget hypothesis explains sexual segregation in some cases, including ours, it does not explain all segregation. Further research on social and habitat segregation is warranted.

Our study in Darwin's wild sheep showed that males and females had a high degree of sexual segregation outside the rutting season and a low degree of sexual segregation during the rutting period. Differences in body size between sexes lead to dissimilar patterns of foraging and resting behaviour, resulting in behavioural strategies driving sexual segregation through modification of activity budgets and synchronization in all group types (all male, all female and mixed sex groups). Therefore, activity budget differences between the sexes may play an important role in driving adult individuals to segregate into single-sex groups.

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