WITHIN-GROUP SPATIAL POSITION IN *SAIGA TATARICA* (BOVIDAE) IN THE STEPNOI STATE NATURE SANCTUARY, ASTRAKHAN REGION, RUSSIA

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In group-living animals, the social structure and organisation play a significant role in survival and reproduction. Understanding the social aspects of animal lives in the wild may be crucially important for effective conservation of threatened species. The fitness costs and benefits of living in a group are related to particular spatial positions individuals take within their groups. Age and sex of the individual is a major factor determining intra-group spatial position. In the present study, we investigated the within-group spatial positioning of individuals in the Critically Endangered *Saiga tatarica* (hereinafter – saiga). In saigas living under natural predation pressure in the Stepnoi State Nature Sanctuary (Astrakhan Region, Russia), we investigated the sex-age category of the first individual in the group, the inter-individual distance in the front individuals and the individuals following them, and the distribution of individuals of each sex-age category between various parts of the group. Three (summer) or four (autumn) sex-age categories of the individuals in the moving groups were recognised by direct observations in the field. In summer, adult females, accompanied by their calves, were the very first individuals in most saiga groups observed. This result agrees with the previous notion that experienced females often lead the saiga groups. However, further investigation is needed to confirm whether adult females do indeed take the role of a leader during long-distance group movements. In line with the results on other mammals, the majority of adult females moved in the central third of the group. Spatial preferences of adult females seem to be based on the risk minimisation as the central positions are likely the safest in the group. In autumn, juvenile males were moving first in the majority of the investigated groups probably because they were the most active and fast-moving sex-age category during this season. In addition, juvenile males and females were significantly more often observed in the first third of the group than in the central and the rear thirds. We suggest that despite the fact that the front edge of the group could be the most dangerous spatial position, foraging benefits may outweigh the increased risk for juvenile saigas. In contrast to some other mammals, adult males did not tend to move at the front edge and were equally often observed in the front, central and rear parts of saiga groups. Finally, our results showed that saigas closer to the front edge of the group maintained shorter inter-individual distances than the individuals positioned behind them. The tighter spacing could be used by front individuals to compensate for the increased risks associated with their within-group spatial position.

Key words: antelope, Artiodactyla, group behaviour, group structure, inter-individual distance, intra-group position, northwest pre-Caspian, spatial relations

Introduction

Saiga tatarica, Linnaeus, 1766 (hereinafter – saiga) is a migratory ungulate of the steppes and deserts of Central Asia and the pre-Caspian (Bekenov et al., 1998). Once an abundant species, the saiga faced a drastic decline in the global population which has led to a Critically Endangered listing on the Global IUCN Red List (Milner-Gulland et al., 2003). In the northwestern pre-Caspian region of Russia, a striking poaching pressure on the saiga population of the nominate subspecies (*S. t. tatarica*) in the 1990s caused a most sudden decline of the species abundance (Kühl et al., 2009; Karimova & Lushchekina, 2018). During the last decade, the local population is slowly recovering within Protected Areas, but it still remains the most threatened saiga population in the world (Karimova et al., 2021).

In group-living animals, the social structure can play a pivotal role in survival and reproduction. In case of threatened species, understanding the social aspects of animals in the wild may be critically important for effective conservation practice (Caro, 1999). Almost all our knowledge of saiga's sociality is based on the studies conducted decades ago (Zhirnov, 1977; Sokolov & Zhirnov, 1998), when the species was much more abundant and its habitat and migratory routes were considerably less disturbed by anthropogenic activities. The knowledge of saiga's social behaviour under the current conditions of very low population size and restricted migration remains very limited. In the northwestern pre-Caspian region, small (21–200 individuals) and very small (1–20 individuals) saiga groups constitute 80–90% of the population (Karimova & Lushchekina, 2018). However, little is known about the structural characteristics of these groups.

It is widely recognised that the fitness costs and benefits of living in a group differ between group members, and within-group spatial position is one of the key factors underlying this difference (Krause,

1994; Krause & Ruxton, 2002). The growing evidence indicates that variation in individual risks is related to particular spatial, which are taken by individuals within their groups. The current theoretical framework and empirical evidence indicate that individuals in front positions of their groups may be exposed to a higher general risk as they are the first ones to explore new areas and face the threats. Front individuals have considerably higher predator encounter rates than individuals in more rear positions (Balmford & Turyaho, 1992; Bumann et al., 1997; Lingle, 2001). To reduce an individual's predation risk, individuals in front positions often demonstrate increased vigilance (Di Blanco & Hirsch, 2006) and maintain smaller inter-individual distances (Hamilton, 1971; Bumann et al., 1997) than individuals elsewhere in the group. At the same time, individuals on the front are more likely to access food patches before others, i.e. they have higher foraging success than the rest of the group because of food depletion from the front to the back (Janson, 1990a; Krause et al., 1992; Rowcliffe et al., 2004). Thus, a trade-off exists for the individuals moving in a group, in which a strategy minimising predation risk by moving not in the front of the group may lower foraging success, whereas a strategy maximising food acquisition may negatively impact individual safety (Beecham & Farnsworth, 1999; Carbone et al., 2003; Teichroeb et al., 2015).

Age and sex influence both predation risk and intra-group spatial position (reviewed in Schmitt & Di Fiore, 2015; Teichroeb et al., 2015). The relative positioning of individuals of various sex and age in mixed groups can vary considerably between the species. However, in many primate species adult males tend to be at the front of moving groups, while females and juveniles typically stay closer to the group's centre (Teichroeb et al., 2015). The males' tendency to maintain front positions in the groups could be especially pronounced in sexually dimorphic primate species because larger males may be less vulnerable to predators and more actively participate in antipredator defence (Schmitt & Di Fiore, 2015). In primates, juveniles usually stay more central because they face the greatest risk of predation and have to rely on adults for vigilance (Teichroeb et al., 2015). However, in some other mammals such as *Nasua nasua* (Linnaeus, 1766), juveniles appear to choose spatial locations based on feeding success and not predation avoidance and therefore prefer the positions at the front of the group (Hirsch, 2011).

In this study, we aimed to explore the spatial position of individuals of various sex and age in saiga groups in the wild. Sexual dimorphism and synchronous calving in saigas allow clear recognition of main sex and age classes and makes this species a convenient model for this study. In saigas living under natural predation pressure, we assessed the sex-age category of the first individual in the group, the inter-individual distance for the front individuals and the individuals following them, and the distribution of individuals of each sex-age category between various parts of the group. Based on the previous reports on other mammal species, we hypothesised that the relatively more risky front positions in the groups will be predominantly occupied by adult males. With larger body size and horns as a defence, adult saiga males may be less vulnerable to predation and, therefore, benefit more from primary access to food patches associated with the front position. In females and juveniles, which may face a greater risk of predation, the costs of being in front of the group may outweigh the benefits, and therefore, they may gravitate to central positions. Alternatively, juveniles and young individuals may base their spatial choices more on feeding success than predation risk, and prefer the front positions. We hypothesised that if front positions are perceived by saigas as the riskiest ones, the individuals at the front edge will maintain shorter inter-individual distances than the individuals positioned behind them.

Material and Methods

Study subjects and site

Saiga is a harem-breeding ungulate, with an adult male typically defending a group of females during the rut in December (Bekenov et al., 1998; Sokolov & Zhirnov, 1998). Once the rut is over, group size and composition beyond the rut period are highly variable and may depend on the weather conditions, food availability, migratory activity, population size and other factors (Sokolov & Zhirnov, 1998; Karimova et al., 2020). Saigas occasionally occur in large aggregations of several thousand of individuals but the typical group size is referred to as approximately 30 individuals on average (Bekenov et al., 1998). Mixed-sex groups are common throughout the year, while male- or female-only groups and large aggregations occur seasonally (Bekenov et al., 1998). Unfortunately, to date, we have very limited knowledge of saiga social structure and organisation.

The individuals observed in the present study belong to the northwest pre-Caspian population of saigas. In the mid-XX century, the population of the saiga in this region reached over 800 000 individuals. At the early XXI century, the population dropped to about 8000–9000 individuals in re-

sponse to a combination of multiple negative factors (Neronov et al., 2012), with the most considerable effect of poaching (Kühl et al., 2009; Karimova & Lushchekina, 2018). Nowadays, the remaining population of the saiga inhabit an area of about 2000–3000 km^2, with the core habitat lying within the two contiguous Protected Areas within the northwestern pre-Caspian region of Russia, Stepnoi State Nature Sanctuary (Astrakhan Region) and Chernye Zemli State Nature Biosphere Reserve (Republic of Kalmykia) (Karimova & Lushchekina, 2018).

The present study was conducted at Stepnoi Nature Sanctuary which includes well-preserved native steppe pastures and several major watering places attracting saigas throughout the year. The sanctuary belongs to the northern subzone of the desert zone characterised by a dry continental climate and even a landscape with low vegetation. In this area, saigas exist under natural predation pressure, with *Canis lupus* Linnaeus, 1758 assumed to be a major predator (Karimova & Lushchekina, 2018). Human disturbance within the sanctuary has been kept to a minimum for the last decade. Poaching, unauthorised vehicle traffic and cattle grazing have been eliminated.

Data collection and analysis

The data for this study were collected in two various periods of the year when the majority of the groups are mixed-sex and mixed-age (single-sex/age groups were excluded) and sex-age classes can reliably be determined in the field. At late May – early June (further referred to as «summer»; Fig. 1A), mixed-sex saiga groups with recently born calves were observed and three categories of individuals were distinguished, namely adult males (more than two years old), one-year-old young males and adult females with calves. The recognition of male age categories was based on the size of the horns. Since early September, the sex of the saigas, which were born this year, can be easily distinguished from a distance. Juvenile males have short black horns, while the body size of juvenile females is noticeably smaller than that of adult females. In September (further referred to as «autumn»; Fig. 1B), four sex-age categories were recognised in saiga groups, namely adult males, adult females, juvenile males and juvenile females. The data collection was conducted during a total of 85 days in 2020, 2022, and 2023, and included observations with binoculars from a watching tower, landscape elevations and stationary hides as described elsewhere (Gilev & Karenina, 2015; Giljov et al., 2019; Fourie et al., 2021).

In mixed-sex and mixed-age groups, we recorded i) the sex-age category of the first individual at the front edge of the group, ii) the inter-individual distance in the first and second ten individuals in the group, and iii) the distribution of individuals of each category between the front, central and rear thirds of the group. Only slowly moving groups of minimally 30 and maximally 60 individuals were included in all analyses to minimise the effect of significant variations in group size and activity on the investigated parameters.

Fig. 1. Saiga (*Saiga tatarica*) groups in summer (A) and autumn (B) in the Stepnoi State Nature Sanctuary, Astrakhan Region, Russia.

Three (summer) or four (autumn) sex-age categories of the first individuals in the groups were recognised by direct observations in the field. Whether individuals of a particular sex-age category predominantly took the first front position was tested using a Chi-square test.

To assess the inter-individual spacing in front individuals and individuals moving behind them, we recorded distances between the first ten individuals and the second ten individuals in the groups. For the first ten individuals, nine distances were recorded (e.g. between the individuals one and two, two and three, three and four). Similarly, nine distances were recorded for the second ten individuals (e.g. between individuals 11 and 12, 12 and 13). The distance was scored in adult male body lengths (approximately 1 m; see Sokolov & Zhirnov, 1998) and was estimated using a marine binocular with built-in reticle scales. For this analysis, only the groups moving along the visible saiga trails in the steppe were investigated. Such long-lasting trails are common in many parts of the the Stepnoi State Nature Sanctuary regularly visited by saigas. When using a trail, saigas moved one after another in a line that helped reliable estimation of inter-individual distance. Based on the approach suggested by McDonald (2014), mean distances between the first ten individuals and the second ten individuals were compared using the Mann-Whitney U-test.

To assess the distribution of individuals of various sex and age between various parts of the group, the total number of individuals was divided into three thirds (front, central and rear). This analysis was carried out only for the data collected in autumn. For each sex-age category, the distribution of individuals between the thirds was estimated using the Kruskal-Wallis test (with a DSCF post-test). The statistical analysis was performed with Jamovi v. 2.3.18 software (Jamovi project, 2022). All statistical tests were two-tailed, and the level of p-value was less than 0.05.

Ethical statement

The study has been conducted with the approval of the Stepnoi State Nature Sanctuary authorities. The ethical permission for the study was obtained from the St. Petersburg State University (Russia) ethical committee (permit №131-03-3). The study was purely observational. A considerable effort was made to minimise the disturbance of the animals.

Results

A total of 173 groups were observed, including 93 ones in summer, and 80 in autumn. The analysis of the sex-age category of the first individual at the front edge of the group showed that in summer adult females were moving first in the majority of the groups (54 groups; $\chi^2(2) = 26$, $p < 0.001$; Fig. 1A). One-year-old young males were the first individuals in 22 groups, and adult males in 17 groups. In autumn, the first individual in most groups was a juvenile male (40 groups; $\chi^2(3) = 28.3$, $p < 0.001$; Fig. 1B). Adult females took the first front position in 18 groups, adult males in 11 groups, and juvenile females in 11 groups.

The estimation of the inter-individual spacing in front individuals and individuals moving behind them revealed that the distances between the first ten individuals were shorter than the distances between the second ten individuals both in autumn (Mann-Whitney U = 630, p = 0.005; median = 1.25 for the first ten saigas and 1.60 for the second ten ones) and in summer (Mann-Whitney U = 1308, p = 0.005; median = 1.90 for the first ten saigas and 2.20 for the second ten ones).

The distribution of individuals of various sex and age between the front, central and rear thirds of the groups showed that adult females predominantly (53.2%) moved in the central third (Kruskal-Wallis $\chi^2 = 36.3$, $p < 0.001$; DSCF post-test: $p < 0.001$ for front vs. central and central vs. rear thirds; $p = 0.120$ for front vs. rear thirds; Fig. 2). In contrast, adult males were distributed equally across various parts of the groups (Kruskal-Wallis $\chi^2 = 2.19$, $p = 0.334$; DSCF post-test: $p > 0.05$; Fig. 2). The majority of juvenile males (60.3%) were observed in the front third of their groups (Kruskal-Wallis $\chi^2 = 37.2$, $p < 0.001$; DSCF post-test: $p < 0.001$ for front vs. central and front vs. rear thirds; $p = 0.993$ for central vs. rear thirds). Similarly, juvenile females predominantly (50.6%) moved in the front third of the groups (Kruskal-Wallis $\chi^2 = 38.8$, $p < 0.001$; DSCF post-test: $p < 0.001$ for front vs. central and front vs. rear thirds; $p = 0.082$ for central vs. rear thirds; Fig. 2).

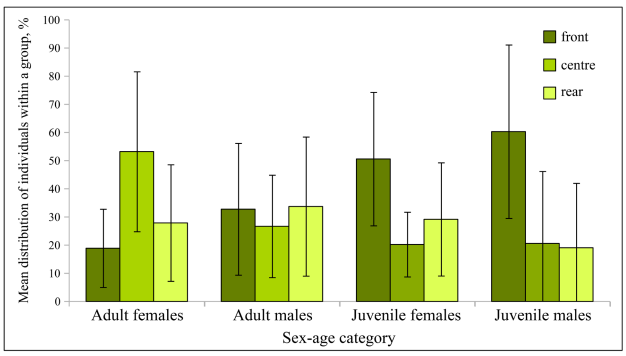

Fig. 2. Percentage distribution of individuals of each sex-age category between the front, central and rear thirds of the studied groups of saiga (*Saiga tatarica*) in the Stepnoi State Nature Sanctuary, Astrakhan Region, Russia. Bars represent standard deviation (SD).

Discussion

The present study showed some patterns of within-group spatial positioning of individuals in saigas. The analysis of the sex-age category of individuals maintaining the very first front position in moving groups showed seasonal variation in this parameter. In summer, adult females accompanied by their calves were the first individuals in the considerable majority of saiga groups observed, while in autumn juvenile males were moving first in most cases. Contrary to our prediction and the results of the previous studies on other mammals such as primates (e.g. Schmitt & Di Fiore, 2015; Teichroeb et al., 2015), adult males did not tend to be the first individuals in their groups. In addition, the analysis of the distribution of adult males within the mixed groups showed that they did not prefer to be in the first third of the group and were roughly equally distributed between the front, central and rear parts. At the front edge of the group, individuals are supposed to face a greater risk of predation and other threats. They are the first ones to explore new areas and may thereby be exposed to higher general risk. At the same time, front individuals have a higher foraging success accessing food patches before others (Balmford & Turyaho, 1992; Krause et al., 1992; Bumann et al., 1997; Lingle, 2001; Rowcliffe et al., 2004). Larger body size and horns could make adult saiga males less vulnerable to predation. Therefore, the front position is potentially less costly for them. Nevertheless, adult males did not tend to take front positions and this could be associated with their functional role within a group. Adult males often display so-called herding behaviour aimed to maintain the integrity of the group and avoid spatial separation of females and calves moving too slowly or away from the others (Sokolov & Zhirnov, 1998; Giljov et al., 2019). In this regard, it could be beneficial for adult males to move between various parts of the group and monitor other individuals. This, in turn, may result in the absence of any preference to stay in a particular part of the group in adult males.

Our results showing that adult females tend to be the first individuals in summer groups agree with the previous notions that experienced females often maintain the front position and take the role of leaders during group movements (Zhirnov, 1977; Sokolov & Zhirnov, 1998). Similarly, an adult (or old) female may take the role of a leader in the groups of feral horses (*Equus ferus* ssp. *przewalskii* Poliakov, 1881) (Bourjade et al., 2015). According to the current knowledge, the first individual in a group probably, but not necessarily, is actually a group leader (Boinski & Garber, 2000). A number of studies showed that group leaders are typically located at the front of the group. At the same time, in some species, the leader determines the direction of travelling from a central spatial position (Boinski & Garber, 2000; Couzin et al., 2005). However, it is questionable, whether the mechanisms of central leadership could efficiently be used in relatively large groups, in which visual contact between all group members is hardly possible (Hirsch, 2007). Thus, it is plausible that adult females do indeed lead the saiga groups in summer. A more focused future study may confirm this using various signs of the leadership. For example, one of the proposed ways of identifying leaders in groups of herbivores is to identify the individual that is consistently the one, which initiates long-distance spontaneous group movements toward a new feeding site (Dumont et al., 2005).

The tendency of juvenile males to be the first individuals in their groups in autumn matches the distribution of this sex-age category between various parts of the group. Juvenile males were considerably more often observed in the first third of the group than in the central and the rear thirds. The same preference was found in juvenile females. These results correspond with the previous results on juvenile *Nasua nasua*, which preferentially maintain the positions at the front of the group (Hirsch, 2011). It has been suggested that despite the front edge could be the most dangerous spatial position, foraging benefits may outweigh the increased risk of predation for juvenile *N. nasua*. The same may be true for saigas. In autumn, when nutrient-rich food becomes scarce, the possibility to reach untouched grass patches before the others may considerably increase food acquisition in juveniles. It is difficult to explain why juvenile males are typically the first individuals in the moving groups, while both male and female juveniles tend to occupy the front third of the group. It has been suggested that in some cases, the most actively moving individuals become the leaders in saiga groups (Sokolov & Zhirnov, 1998). Probably, juvenile males are the most active and fast-moving sex-age category in autumn and, as a result, they often become the very first individuals in a group.

Adult females were observed in the centre more often than at the front or rear thirds of the group. This result agrees with the general tendency of females to stay closer to the group's centre found in other mammals (Janson, 1990b; Ron et al., 1996; Hirsch, 2011; Teichroeb et al., 2015). In some species, adult dominant females aggressively defend central positions and actively exclude subordinates from the centre of the group (Hirsch, 2011; Teichroeb et al.,

2015). The cumulative evidence indicates that central spatial positions are likely the safest within a group. Central individuals typically spend less time being vigilant (Burger & Gochfeld, 1994; Di Blanco & Hirsch, 2006; Blanchard et al., 2008) and face a lower risk of predation (Balmford & Turyaho, 1992; Bumann et al., 1997; Lingle, 2001) than the individuals at the edges of the group. The preference for the central position in a group suggests that in adult female saigas, the choice of spatial positions is based on risk minimisation.

Our results showed that the distances between the first ten individuals were shorter than the distances between the second ten individuals. These differences were significant both in summer and in autumn. That is, irrespective of the groups' sex-age composition and category of individuals moving first, saigas closer to the front edge of the group maintained shorter inter-individual distances than the individuals positioned behind them. Tighter spacing between individuals is typical for animal groups facing an increased threat (Bumann et al., 1997). Staying closer to their neighbours, animals may decrease their individual predation risk by reducing their domain of danger (Hamilton, 1971; De Vos & O'Riain, 2010). Saigas moving close to the front edge may maintain shorter inter-individual distances to compensate for the increased risks associated with their spatial position. Tighter spacing in front of individuals implies that saigas likely perceive the front positions as more dangerous than the more rear ones. The comparison of the levels of vigilance between individuals in various parts of saiga groups may be a promising direction for future study.

Conclusions

The present study adds to the scarce knowledge of within-group spatial interactions of mammals in the wild. Investigation of the positioning of individuals in saigas showed that age and sex of the individual is a major factor determining intra-group spatial position. In summer, adult females were the first individuals in the majority of groups, while in autumn juvenile males maintained the very first front position in most cases. The distribution of individuals of each sex-age category between various parts of the group had the following pattern. Juvenile males and females were more often observed in the first third of the group than in the central and the rear thirds, while the majority of adult females moved in the central third of the group. Adult males were observed equally often in the front, central and rear parts of saiga groups. Some of our results followed the patterns found previously in other mammal species, while some did not. Our study emphasises the specific characteristics of spatial interactions within saiga groups. This knowledge can be used to improve our very limited understanding of saiga's sociality. Currently, when the saiga population size is critically low, such understanding may have practical implications for species conservation.

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ПРОСТРАНСТВЕННОЕ РАСПОЛОЖЕНИЕ ОСОБЕЙ ВНУТРИ ГРУППЫ У *SAIGA TATARICA* (BOVIDAE) В ГОСУДАРСТВЕННОМ ПРИРОДНОМ ЗАКАЗНИКЕ «СТЕПНОЙ», АСТРАХАНСКАЯ ОБЛАСТЬ, РОССИЯ

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У животных, ведущих групповой образ жизни, структура и организация сообществ играют важную роль в выживании и размножении. Знания об особенностях социального поведения животных в природе могут иметь большое значение для принятия эффективных мер по сохранению редких видов. Преимущества и недостатки жизни в группе для отдельных особей взаимосвязаны с тем, какое пространственное положение они занимают относительно других особей. Возраст и пол являются важными факторами, определяющими пространственное взаиморасположение членов группы. В этой работе мы исследовали пространственное расположение особей друг относительно друга в группах *Saiga tatarica* (далее – сайгак), вида, находящегося на грани вымирания. У сайгаков, живущих в условиях естественного пресса хищничества в государственном природном заказнике «Степной» (Астраханская область, Россия), была исследована половозрастная категория первых особей в группе, дистанция между особями в передней и последующей за ней частях группы и распределение особей разного пола и возраста между разными частями группы. В ходе наблюдений в природе мы выделяли три (летом) или четыре (осенью) половозрастные категории в перемещающихся группах сайгаков. Летом взрослые самки с детенышами двигались первыми в большинстве исследованных групп. Этот результат согласуется с более ранними исследованиями, предполагавшими, что группу сайгаков обычно ведет опытная самка. Для того чтобы подтвердить лидирующую роль взрослых самок необходимы дальнейшие исследования. Как и у других видов млекопитающих, исследованных ранее, большинство самок сайгака двигались в центральной части группы. Пространственные предпочтения взрослых самок, видимо, основаны на минимизации рисков, так как расположение в центре группы, скорее всего, обеспечивает наибольшую безопасность. Осенью первыми в группах чаще всего шли самцы-сеголетки, что, вероятно, связано с тем, что они были наиболее активной и быстро перемещающейся категорией особей в это время года. Сеголеток обоих полов значительно чаще наблюдали перемещающимися в первой трети группы, чем в центральной и задней. Несмотря на то, что расположение в передней части группы, вероятно, наиболее опасно, в случае с сеголетками, преимущества, связанные с приоритетным доступом к пище могут перевешивать повышенные риски. В отличие от некоторых других млекопитающих, взрослые самцы сайгака не были склонны располагаться на переднем крае группы, и их с одинаковой частотой наблюдали в передней, центральной и задней частях групп. Мы также обнаружили, что особи, перемещавшиеся у переднего края группы, располагались ближе друг к другу, чем особи позади них. Более тесное расположение передних животных может быть направлено на компенсацию повышенных рисков, связанных с их пространственным расположением внутри группы.

Ключевые слова: Artiodactyla, антилопа, групповое поведение, дистанция между особями, положение внутри группы, пространственные отношения, Северо-Западный Прикаспий, структура группы