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Social arenas in the open habitat: the social role of waterholes for saiga antelope

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In wild animals, specific locations may function as 'social arenas' playing a significant role in various aspects of intraspecific interactions. The emergence of such social arenas is assumed to be particularly important under conditions of low visibility and density of individuals typical for forest dwelling species. In the forest, open areas with a high probability of meeting conspecifics such as waterholes and mineral licks can favor socialization. The paucity of studies on the open-habitat species limits our understanding of whether forest habitat is an essential condition for the emergence of social arenas. Here we address this issue by investigating whether resource hotspots function as social arenas in a species adapted to open habitat. The social behaviour in groups of saiga antelopes (*Saiga tatarica tatarica*) was recorded at large permanent waterholes (serving also as mineral licks) and away from them in the steppe environment. The frequency and variety of social interactions between the group mates were compared with a special effort made to minimize the potential impact of other factors besides the location. Also the focal individuals, interacting or not interacting with conspecifics at the waterholes, were traced continuously to explore the duration of their visit at the waterhole area. Finally, we recorded the number of individuals in the groups entering and leaving the waterhole. Active social interactions between group members occurred more often and were more varied near the waterholes as compared to the areas away from them. The participation in social interactions influenced the duration of individual waterhole visits. Males that interacted with others shortly after arrival stayed significantly longer compared to those who did not. Females whose calves engaged in social interactions with age-mates spent more time at the waterholes than females whose calves did not. The comparison of mean group sizes showed that saigas left waterhole areas in larger groups than they entered them. Our findings, together with previous studies, suggest that resource hotspots can function as social arenas in mammals regardless of the habitat type (open or closed). The emergence of specific locations having particular social significance may be especially important for highly dispersed species with large home ranges. The results of the study emphasize the significance of large permanent waterholes and mineral licks used by many individuals year after year for the social behaviour of saiga antelopes.

Para animales silvestres, sitios específicos pueden funcionar como "arenas sociales" que desempeñan un papel importante en varios aspectos de las interacciones intraespecíficas. Se sugiere que el surgimiento de tales espacios sociales es particularmente importante en áreas de baja visibilidad y con una densidad baja de individuos, condiciones típicas en especies que habitan en los bosques. En el bosque, las áreas abiertas con una alta probabilidad de encontrarse con congéneres, como pozos de agua y saladeros de minerales, pueden favorecer la socialización. La escasez de estudios sobre especies de hábitat abierto limita nuestra comprensión de si el hábitat forestal es una condición esencial para el surgimiento de espacios sociales. Aquí abordamos este tema investigando si los puntos críticos de recursos funcionan como arenas sociales en una especie adaptada al hábitat abierto. El comportamiento social en grupos de antílopes saiga (*Saiga tatarica tatarica*) se registró en grandes pozos de agua permanentes (que sirven también como fuentes de minerales) y lejos de ellos en las estepas. Se comparó la frecuencia y variedad de interacciones sociales entre los compañeros del grupo con un esfuerzo especial para minimizar el impacto potencial de otros factores además de la ubicación. También, los individuos focales, que interactuaban o no con sus congéneres en los pozos de agua, fueron rastreados continuamente para explorar la duración de su visita al área del pozo de agua. Finalmente, registramos el número de individuos de los grupos que entraban y salían del pozo de agua. Las interacciones sociales activas entre los miembros del grupo ocurrieron con mayor frecuencia y fueron más variadas cerca de los pozos de agua en comparación con las áreas alejadas de ellos. La participación en interacciones sociales influyó en la duración de las visitas individuales a los pozos de agua. Los machos que interactuaron con otros poco después de su llegada permanecieron significativamente más tiempo en comparación con los que no lo hicieron. Las hembras cuyas crías participaban en interacciones sociales con sus compañeros de edad pasaban más tiempo en los abrevaderos que las hembras cuyas crías no lo hacían. La comparación de los tamaños medios de los grupos mostró que los saigas abandonaron las áreas de los pozos de agua en grupos más grandes de los que entraron en ellas. Nuestros hallazgos demuestran que los puntos críticos de recursos pueden funcionar como arenas sociales en los mamíferos independientemente del tipo de hábitat (abierto o cerrado). La aparición de lugares específicos que tengan un significado social particular puede ser especialmente importante para especies muy dispersas con grandes áreas de distribución. Los resultados del estudio enfatizan la importancia de los grandes pozos de agua permanentes y saladeros de minerales utilizados por muchos individuos año tras año para el comportamiento social de los antílopes saiga.

Keywords: mineral lick; open landscape; social behavior; socialization; ungulate; waterhole.

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Introduction

In many animals, the social interactions between conspecifics are not evenly distributed throughout the species' habitat (*e. g.*, Fishlock *et al.* 2008; Brightsmith and Villalobos 2011). There are specific places providing the enhanced probability of meeting conspecifics, maximizing social opportunities for both solitary (Klaus-Hügi *et al.* 2000) and group-living species (Turkalo and Fay 1995). For example, leks and resource hotspots are strategically used to increase the possibility of encountering opposite-sex individuals in the mating context (Hardenberg *et al.* 2000; Klaus-Hügi *et al.* 2000; Bro-Jørgensen 2003). Some of these areas may serve as so-called 'social arenas', *i. e.* social hotspots promoting inter-individual interaction and playing a significant role not only in mating but in various aspects of social behaviour. Social arenas are supposed to emerge in places which provide limited and highly dispersed nutritional resources, such as specific food (*e. g.*, Egbert and Stokes 1976) or mineral-rich soil and water (*e. g.*, Fishlock *et al.* 2008). Apart from nutritional benefits, resource hotspots have been found to function as lodestones for social contacts and communication in birds (Brightsmith and Villalobos 2011; van Overveld *et al.* 2020) and mammals (Couturier and Barrette 1988; Klaus-Hügi *et al.* 2000; Fishlock and Lee 2013). Social opportunities may motivate visits to the salt licks on a par with mineral consumption (van Strien 1985; Turkalo and Fay 1995; Clayton and MacDonald 1999; Brightsmith and Villalobo 2011). Potential social benefits of licks and other resource hotspots used as gathering places include the establishment of new relationships or the maintenance of the existing ones, exchange of social information between individuals and different social units, socialization of younger individuals, etc. (Fraser and Hristienko 1981; Fishlock *et al.* 2008, Gilev and Karenina 2015). For researchers, such places provide unique opportunities for detailed investigation of social behaviours which are difficult to observe otherwise (Clayton and MacDonald 1999; Fishlock and Lee 2013; Hii 2017; Giljov *et al.* 2019).

Places with a high probability of meeting conspecifics, such as resource hotspots, may be particularly important for forest dwelling species (*e. g.*, moose, *Alces alces*, Couturier and Barrette 1988; forest elephants, *Loxodonta cyclotis*, Turkalo and Fay 1995; babirusa, *Babyrousa babyrussa*, Clayton and MacDonald 1999; bongo antelope *Tragelaphus eurycerus*, Klaus-Hügi *et al.* 2000; forest buffalo, *Syncerus caffer nanus*, Melletti *et al.* 2007; Asian elephants, *Elephas maximus,* Fishlock *et al.* 2008, Fishlock and Lee 2013, Hii 2017; Baird's tapir, *Tapirus bairdii,* Reyna-Hurtado and Arias-Domínguez 2024). Under conditions of low visibility and low density of individuals in the forest environment, animals can use open areas as social arenas facilitating interactions among individuals. For example, forest elephants form large, dynamically changing social gatherings in natural forest clearings offering nutritional resources (Klaus *et al.* 1998; Fishlock and Lee 2013). Forest clearings can be used by elephants to interact, to establish and maintain the dominance hierarchy, and learn social skills (Turkalo and Fay 1995; Turkalo *et al.* 2013). Individual elephants maximize their social opportunities in the clearing and significantly increase their mean visit duration when they take the opportunity to associate with individuals outside their ranging party. Both inter-and intrasexual interactions occur within the clearing. Social benefits are further maximized by joining large groups, often including older elephants, or, for males, parties with females (Fishlock and Lee 2013).

On the other hand, little effort has been made to investigate the presence of social gathering places in species inhabiting open landscapes. Mineral licks are supposed to have some social significance for large herbivores in African savanna landscapes (Weir 1969; Ruggiero and Fay 1994; Merte *et al.* 2010) but no focused research has been conducted to test this. It is widely assumed that the social function of waterhole/mineral lick clearings can be explained by the high visibility contrasting with dense forest (Klaus *et al.* 1998; Melletti *et al.* 2007). It is proposed that in areas with high visibility, visual contact between herd members is easier and probably more group members can see each other simultaneously. Greater choice of partners for interaction may also play some role. The paucity of studies on the open landscape species restricts our understanding of whether closed habitat is, in fact, a necessary condition for the emergence of social arenas. In the present study, we tested the alternative hypothesis by investigating whether resource hotspots function as social arenas in open landscapes, particularly for saiga antelope (*Saiga tatarica tatarica*) – an ungulate strongly adapted to the open habitat.

The saiga antelope is a nomadic bovid inhabiting arid areas of central Asia and the northwestern pre-Caspian (Bekenov *et al.* 1998). A drastic decline in the global population has led to a Critically Endangered listing on the 2002 IUCN Red List (Milner-Gulland *et al.* 2003). There are two subspecies, *S. t. tatarica* (in the present study), the nominate subspecies studied, in Kazakhstan and Russia, and the morphologically distinct *S. t. mongolica* in Mongolia.

In the middle of the 20th century, the population of the saiga antelope in the northwestern pre-Caspian region reached over 800,000 individuals. At the beginning of the 21st century, the population dropped to only 8,000 to 9,000 individuals in response to a combination of multiple negative factors (Neronov *et al.* 2012). Nowadays, the remaining population of the saiga antelope inhabit an area of about 2000 to 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 in Astrakhan Oblast and Biosphere Reserve "Chernye Zemli" in the Republic of Kalmykia (Karimova and Lushchekina 2018).

An adult male saiga typically defends a harem of about 10 to 30 females during the rut which takes place in December (Bekenov *et al.* 1998; Sokolov and Zhirnov 1998). Once the rut is over, the social structure of saigas becomes loose and highly variable. Group size and composition can vary significantly depending on the weather conditions, food

availability, migratory activity, population size and other factors (Sokolov and Zhirnov 1998; Karimova *et al.* 2020). Saigas occasionally occur in large aggregations of several thousand but the typical group size is referred to as 30 individuals on average (Bekenov *et al.* 1998). Within the study area in the northwestern pre-Caspian region of Russia, small (21 to 200 individuals) and very small (1 to 20 individuals) saiga groups constitute 80 to 90 % of the population (Karimova and Lushchekina 2018). Mixed-sex groups are common throughout the year, while male- or female-only groups and large aggregations occur seasonally (Bekenov *et al.* 1998). The current knowledge of group composition, stability, and hierarchy in saigas remains very limited.

The comparability between the open and closed habitat species studied is especially important considering the very small number of species investigated in terms of the presence of social arenas so far. Most extensively, the social arenas at resource hotspots have been studied in forest elephants (Fishlock and Lee 2013). The saiga has similar behavioral characteristics that resemble those of the forest elephants, such as fluid social structure and large range areas (Bekenov *et al.* 1998; Sokolov and Zhirnov 1998). Thus, saiga antelope can serve as a model to compare with closed habitat species the social function of resource hotspots between different types of environments.

In the arid steppes of the northwestern pre-Caspian region, during the warm season, natural water bodies are scarce and surface water is mainly found in artificial waterholes fed by artesian wells drilled more than two decades ago. Moreover, many of them became fenced for the livestock use in the recent. The remaining large permanent waterholes are extensively used by the local saiga population for drinking, geophagia (deliberate soil ingestion) and cooling down during the summer heat (Gilev and Karenina 2015). Concentration around permanent water sources is typical behaviour of antelopes living in arid areas (Blank and Li 2022).

We conducted a study to determine if large permanent waterholes, which also serve as mineral licks, act as social arenas for saigas. We compared the frequency and variety of social interactions within saiga groups at waterholes versus away from them. We hypothesized that if waterholes promote social interactions, we would see more varied social behaviors at these sites. Additionally, we explored whether engaging in social interactions influenced the length of time saigas spent at waterholes. We aimed to understand if saigas adjust their behavior based on social cues, with individuals who enter interactions staying longer at waterholes to maximize their social opportunities. Finally, to test whether visiting waterholes favors social grouping in saigas, the sizes of the groups entering and leaving a waterhole area were compared.

Material and methods

Study area. The data for this study were collected at Stepnoi Nature Sanctuary (45° 57' 28.8" N, 46° 33' 6.1" E) which includes well-preserved native pastures and several major watering places attracting saigas throughout the year. The sanctuary includes semi-desert steppes characterized by a dry continental climate and even landscape with low vegetation. In this region, saigas exist under natural predation pressure, with wolves assumed to be a major predator (Karimova and Lushchekina 2018). Human disturbance within the sanctuary has been kept to a minimum for the last decade. Poaching, vehicle traffic and cattle grazing have been eliminated.

Saigas display a variety of active social interactions on the banks of the waterholes that inspired this study. Flat areas lacking vegetation which surround waterholes provide good visibility and enable continuous observations of focal individuals (Gilev and Karenina 2015). For conservation and research purposes, small (2.4 x 1.5 m) observation hides have been built by the main saiga watering places (Figure 1). The construction of partly underground hides (only 50 cm above the ground level) covered by camouflage nets minimizes disturbance and saigas casually approach them at very close distances even when there are humans inside. The data for the present study were collected from the hides at the two largest permanent waterholes in the sanctuary (perimeters 1,200 m and 460 m), which are situated more than 14 km away from each other. On average, about four hundred saigas including single individuals, same-sex and mixed-sex groups visited the waterholes daily. On particularly hot days, more than 1,500 individuals per day have been recorded. As a nomadic species, saigas almost constantly move around the sanctuary and the nearby territories (Karimova and Lushchekina 2018); therefore, many different individuals visited the study sites during the period of data collection. Study areas away from the waterholes (at least 1 km away) were flat steppe grasslands dominating in the sanctuary. Because of the flat nature of the steppe in this saiga habitat, saiga antelopes were visible with binoculars up to approximately 10 km away from the hide.

Data collection and analysis. The data collection was carried out at the beginning of summer (May-June) when social activity in saiga groups is prominent and diverse for several reasons: daytime heat is still moderate, food has been plentiful for a while, and the most of the groups are mixed-sex and mixed-age. Social interactions were recorded during the peak period of saiga activity in the morning (between 5:30 and 11:00 a.m.) in 2019 (31 days) and 2020 (20 days). Morning hours were used for the data collection because this is when the great majority of saiga visits to the waterhole occur (Gilev and Karenina 2015). Two researchers entered the hide well before the beginning of data recording (before dawn) to minimize the potential disturbance of animals.

Several questions were addressed to investigate the social significance of waterholes for saiga antelopes, and the process of data collection varied accordingly.

The comparison of within-group social behaviour at waterholes and away from waterholes. Since waterholes attract many groups of saiga antelopes, the general level

of social activity at the waterholes may be increased simply because of a higher number of individuals and/or antagonism and competition between strangers. This potential confounding factor was avoided by studying only within-group interactions.

Within-group social behaviour of saigas was investigated by the waterholes (within a 30-m perimeter from the shoreline) and more than 1 km away from them. The procedure of data collection was similar at the waterholes and away from them. The groups with similar characteristics were investigated to minimize the potential impact of other factors besides the location. The typical size of saiga groups is supposed to be around 30 individuals (Sokolov and Zhirnov 1998); therefore, we chose the groups consisting of 25 to 35 adults for the data collection. Mixed-sex and mixed-age groups were observed as the most socially active. Basic parameters of the group composition were balanced: each group included at least three males (more than one year old) and at least 70 % of females with calves. In addition, for these observations, we applied a narrower time window between 5:30 and 8:30 a.m. (which is the saiga activity peak at the waterhole) to avoid the influence of the rising air temperatures on the intensity of social activities. Overcast and rainy days (very rare) when saiga activity at the waterholes significantly decreased were excluded. To avoid any systematic impact of the changing weather (*e. g.*, increasing average air temperatures as the summer progressed), data recording at the waterholes and away from them were alternated (one day the 'waterhole' observations followed by one day 'away', etc.).

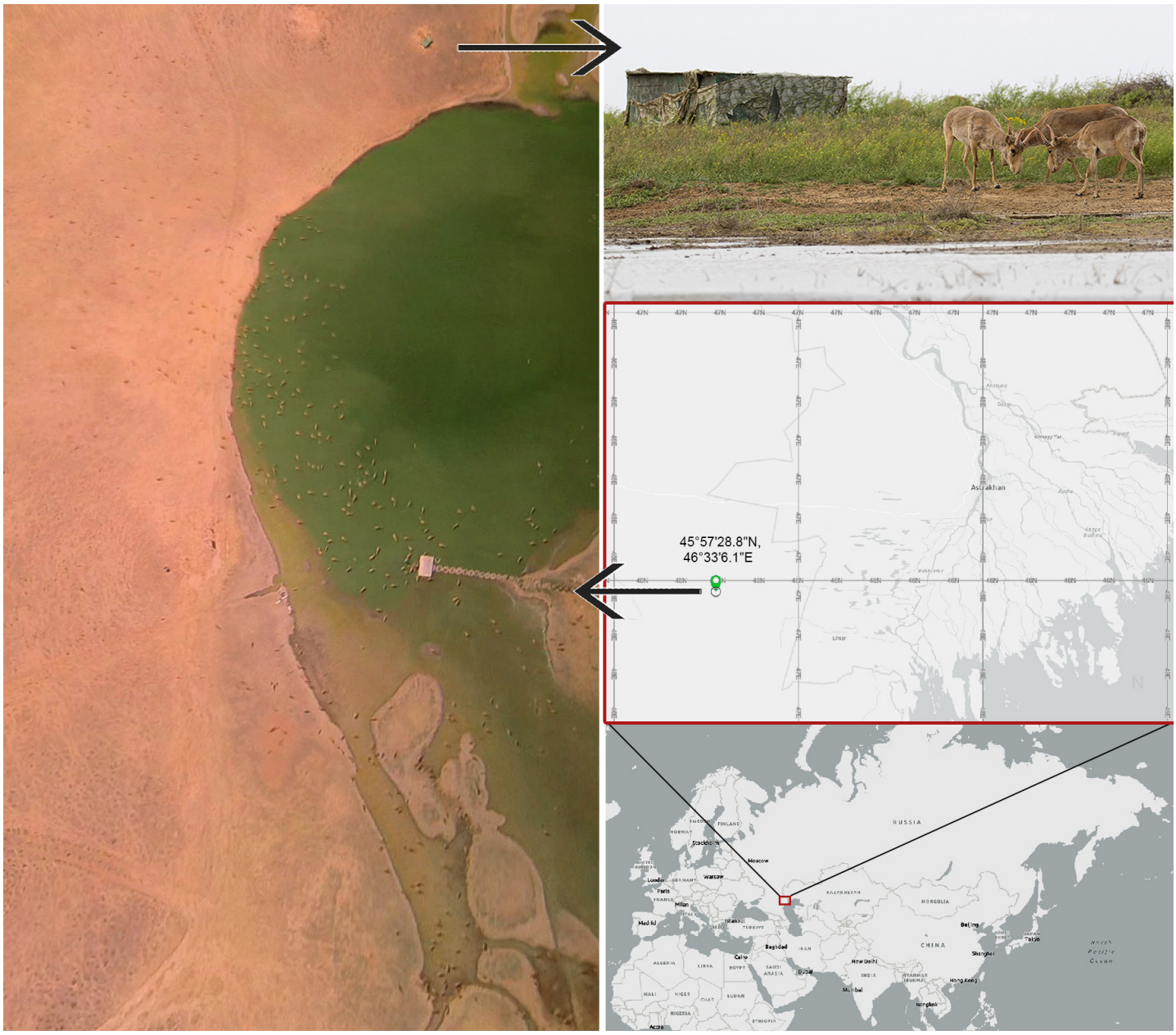

Figure 1. Study site. Bottom right: a digtal map of the northwestern pre-Caspian with a map marker showing the position of the Stepnoi Nature Sanctuary. Top left: an aerial view of the WH1 waterhole. Top right: a camouflaged observation hide.

For further comparison, the behaviour of saiga groups at the waterholes and away from them was video recorded for standardized periods of time. At both types of locations, the groups of antelopes which were at least 100 m away from other saigas were filmed continuously for 10 minutes. Each group was filmed just once. The groups were defined as individuals moving in the same direction and staying together longer than 20 minutes before the beginning of data recording (Sokolov and Zhirnov 1998, Karimova and Lushchekina 2018). In addition, only the animals arriving at the waterhole together were considered as a group (in the case of observations at the waterholes). The distance between the closest individuals within a group typically did not exceed 50 m, except for a short-term separation of adult males chasing each other.

Both at the waterholes and away from them, we only filmed saiga groups showing no signs of disturbance, *i. e*. not running, walking fast or jumping in a particular manner (Sokolov and Zhirnov 1998). Calm slow movement was the most common type of activity recorded. In addition, data recording started at least 10 minutes after the arrival of the group at the waterholes to minimize the impact of arousal associated with drinking. During the further analysis, all clearly distinguishable active interactions between the group members, *e. g*., male fights, male–female chases, and playful interactions between calves were recorded (Figure 2; see Table 1 for a full list of interactions). The number of occurrences of each social interaction was recorded. Non-obvious subtle social interactions (*e. g*., approaching, sniffing, side-by-side walking) which cannot be accurately recorded in relatively large and tight groups typical for saigas were excluded. To test whether waterholes facilitate active social interactions within groups, we compared the frequency and variety of social interactions at waterholes and away from them. No interactions between the antelopes from different groups were included in the analysis to avoid the impact of the concentration of unfamiliar individuals at the waterholes.

The impact of social interactions on the staying time at waterholes. Another question we aimed to address was whether utilizing social opportunities influences the duration of saiga visits to waterholes. The focal individuals at the waterholes were traced continuously and their active interactions with conspecifics (Table 1) were recorded. The data were collected only when 60 or more saigas and all sex/age classes (adult females, one-year-old males, adult males and calves) were present at the waterhole, that is, the individual's social opportunities were abundant. In the case of males, each observed individual was photographed using a camera with a long-focus lens for individual identification to avoid repeated observations of the same individuals. Photo-identification was based on a set of natural markings such as scars, and individual features in colouration, shape and size of horns as described elsewhere (Giljov *et al.* 2019). Younger (one-year-old) and adult (≥ 2 years old) males recognized by the horn size were considered separately because of the likely differences in their social behaviour. In females, reliable individual identification was not possible except for a few individuals with remarkable colouration features. Only females with calves were included as they significantly prevailed in the population during the study period. Females with calves rarely engaged in active social interactions with other individuals besides their calves, therefore we recorded not their own interactions but the interactions of their calves.

To test the influence of the social experience on the visit duration we compared the time spent at the waterhole in males which interacted and did not interact with others during the first three minutes at the waterhole. It is plausible that the longer the individual stay the more chances to interact. We, in contrast, aimed to test whether the individuals interested in socializing choose to stay longer. Therefore, the time for the recording of the social interactions was standardized (three minutes) to avoid the effect of the duration of the stay on the probability of social interactions. However the total time spent at the waterhole by focal individuals was scored. In the case of females, the duration of the visit was compared between the females whose calves interacted with other calves and the females whose calves did not interact with age-mates during the first three minutes after arrival at the waterhole.

The comparison of group sizes when entering and leaving the waterholes. Finally, we tested whether visits to the waterholes favor social grouping. The number of individuals in the groups entering and leaving the waterhole area was recorded. The group sizes were compared. The cases when only one group was present at the waterhole were not included in the analysis as there was no opportunity to form a larger group.

In addition, we investigated whether the drinking itself works as a factor favoring spatial aggregation of individuals at waterholes. Solitary individuals may be particularly vulnerable during drinking when they are not able to monitor the surroundings and must group with mates

Table 1. The types of active social interactions recorded within saiga groups.

Behaviour	Interactors
Fight	male-male
Chase	male-male
Jump	male-male
Snout touch	male-male
Displace from the resting place	male-male
Jump	female-female
Snout touch	female-female
Displace from the resting place	female-female
Play-chase	calf-calf
Jump	calf-calf
Inspection	calf-calf
Chase	male-female
Snout touch	female-calf
Inspection	male-calf

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to rely on their vigilance. We recorded whether a single individual approached a group prior to starting drinking or stayed alone. The following situations were observed: a single individual arrived at the waterhole when a group of 15–35 individuals was already present by the water. Smaller groups could potentially be not enough for social attraction, while larger groups may occupy a significant part of the shoreline and leave the arriving individual not much spatial choice. We included only the single individuals who approached the waterhole from a different direction (the movement directions of the group and the solitary individual forming 90 to 270° angle) than did the already present group to minimize the chances that this individual is a member of the same group. Approaching was defined as drinking at 20 m or less from the closest individual. Whether single individuals preferentially started drinking near the group of saigas was tested with a binomial *z* test.

The normality of continuous data was assessed using a Shapiro-Wilk test. Since the data deviated significantly from normality, a non-parametric Mann-Whitney U test was used for comparisons. The statistical analyses were conducted in JAMOVI v2.3.28 software https://www.jamovi.org (Gallucci 2019). The α level was set at $P < 0.05$.

This purely observational study was conducted in several study sites in the protected nature reserve using long-lasting stationary camouflaged hides for animal observation and population monitoring.

Ethical statement. The ethical permission for the study was obtained from the St. Petersburg State University ethical committee (permit no. 131-03-3). Work was conducted with the approval of Stepnoi State Nature Sanctuary authorities. The study was purely observational. The observations were conducted from the hide that kept the disturbance of the antelopes to a minimum.

Results

For the comparison of saiga social behaviour by the waterholes (two sites) and more than one km away from them (two sites), 2 513 within-group social interactions were recorded in 204 groups of saiga antelopes (see Supplementary material Tables). Analysis of the frequency and variety of active social interactions between the group members near the waterholes (112 groups) and away from them (92 groups) revealed significant differences. Interactions occurred more often near the waterhole (WH) than away from it (*near*: median = 15, *IQR* = 24.0, *away*: median = 5, *IQR* = 7.25; Mann-Whitney $U = 2263$, $P < 0.001$). This difference was revealed for both waterholes (*near*: median = 18, *IQR* = 27.0 vs. *away*: median = 4, *IQR* = 8.0, Mann-Whitney $U = 621$, $P < 0.001$, WH1; and *near*: median = 7.5, IQR = 5.5, *away*: median = 5, IQR=6.0, Mann-Whitney $U = 479$, $P = 0.028$, WH2). Similarly, a greater variety of social interactions were recorded near the waterholes than away from them (Mann-Whitney $U = 2629$, $P < 0.001$) with both waterholes showing the same pattern (WH 1: Mann-Whitney $U = 784$, $P < 0.001$; WH 2: Mann-Whitney $U = 512$, $P = 0.039$). Male-male fights were the predominant form of social interaction observed, both in proximity to waterholes (WH 1: $W = 3160$, $P < 0.001$; WH 2: $W = 276$, $P < 0.001$) and at a distance from them (WH 1: $W = 595$, $P < 0.001$; WH 2: $W = 780$, $P < 0.001$, one-sample Wilcoxon rank test).

Continuous observations of focal individuals showed that engagement in active social interactions affected the duration of saiga visits to the waterhole. One-year-old males ($n = 114$) which interacted with conspecifics stayed at the waterhole significantly longer (median time = 13 min, *IQR* = 14.5) than those who did not (median time = 7 min, *IQR* = 9.5, Mann-Whitney $U = 1000$, $P = 0.002$). In adult males (n = 72) also, the individuals which engaged in social interactions spent more time at the waterhole (median time = 10 min, *IQR*=17.0) than males who did not interact with others (median time = 6.5 min, *IQR* = 6.3; Mann-Whitney $U = 394$, $P = 0.030$). In females with calves ($n = 53$), the influence of calves' social involvement was found. Females whose calves participated in social interactions with other calves stayed at the waterhole significantly longer (median time = 8.0 min, *IQR* = 6.0), than the females whose calves did not interact with age-mates (median time = 5.5 min, *IQR* = 4.5; Mann-Whitney $U = 183$, $P = 0.028$).

The comparison of the number of individuals in any group entering ($n = 214$) and leaving ($n = 141$) the waterhole area showed significant differences. The groups of leaving saigas were larger than the groups of arriving individuals at both WH1 (arriving: median group size = 29 individuals, *IQR* = 55.3: leaving: median group size = 75 individuals, *IQR* = 132.0; Mann-Whitney $U = 5517$, $P < 0.001$) and WH 2 (arriving: median group size = 4 individuals, *IQR* = 10.0, leaving: median group size = 8 individuals, *IQR* = 10.0; Mann-Whitney $U = 636$, P = 0.033).

Analysis of the behaviour of solitary saigas coming at the waterholes showed that, in the presence of a group of conspecifics by the water, such individuals did not demonstrate a preference to approach the group for drinking (WH 1: 39 out of 52, binomial $z = 1.26$, $P = 0.208$; WH2: 16 out of 23, $z = 0.96$, $P = 0.337$).

Discussion

The results of the present study suggest that in saiga antelopes, large permanent waterholes serving also as mineral licks facilitate social interactions, at least among group mates. Both the frequency and variety of active social interactions within groups were increased at the waterholes, as compared to the steppe environment away from the water. A special effort was made to minimize the potential impact of other factors besides the location: data collection at the waterholes and away from them was conducted in the same season and time of the day, while the social opportunities were balanced. The greater frequency and variety of interactions between the individuals cannot be explained by the novel or increased social opportunities at the waterholes as only intragroup interactions, *i. e.* interactions

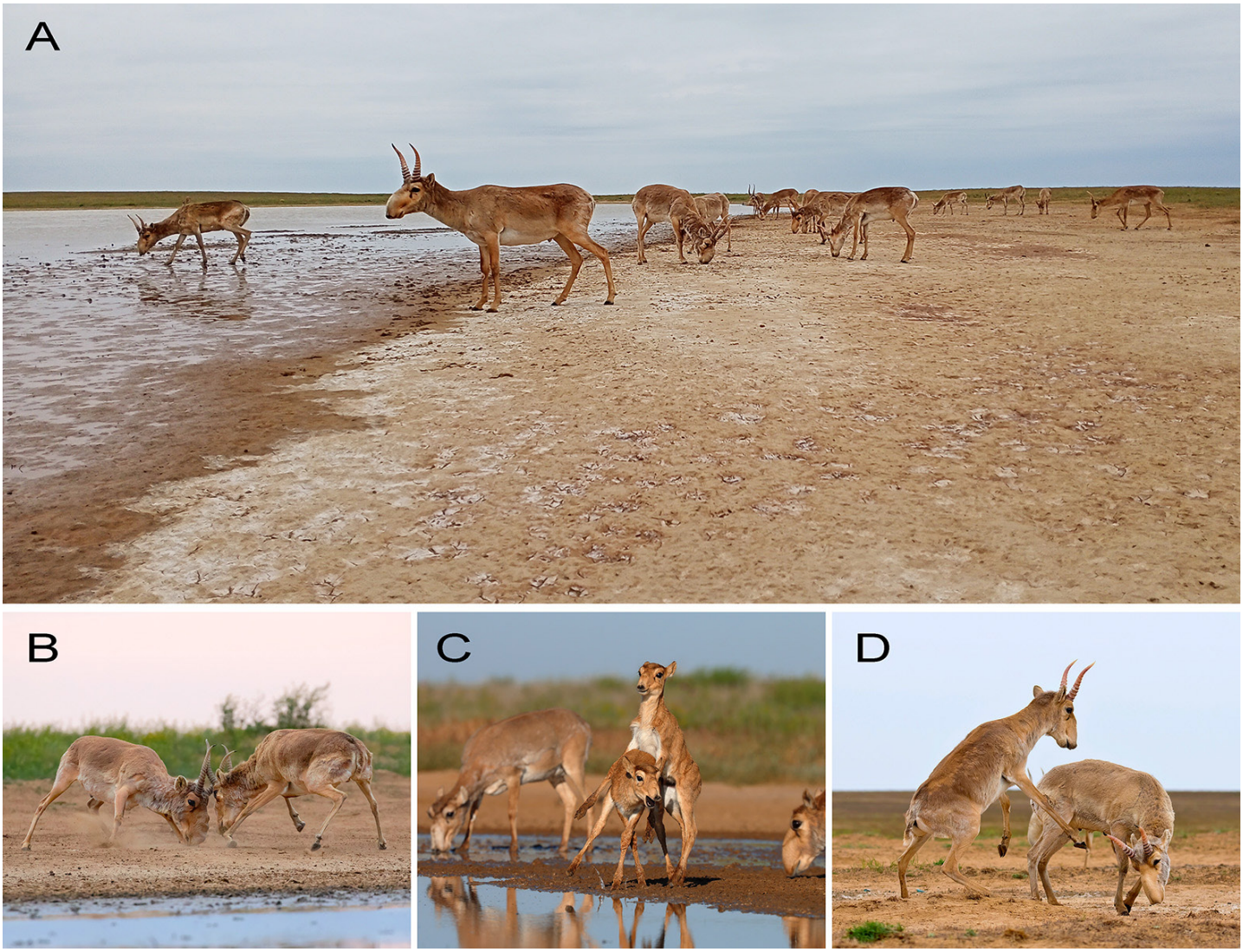

Figure 2. Saiga antelopes at the waterhole (A) A group of males drinking and licking mineral-rich soil on the lacking vegetation banks of the waterhole. B) 'Male-male fight': two males fighting with their horns crossed. C) 'Calf-calf jump': a calf standing on its hind limbs and trying to jump on the other calf's back. D) 'Male-male jump': a male standing on its hind limbs and trying to jump on the other male's back.

between group members, were included in the analysis. The groups of similar size and composition were observed at the waterholes and away from them, that is, the revealed difference in the social activity is not a result of the greater number and variety of social partners at the waterholes. Since we only analyzed the interactions between saigas which came to the waterhole together as a group, the elevated frequency of interactions cannot be explained by the antagonism between strangers or competition between different groups.

There are several plausible explanations for why waterholes facilitate social interactions between group members. First, the physical characteristics of the steppe waterholes may provide the optimal conditions for the manifestation of social behaviours. The water mirror is surrounded by relatively large areas of flat hard ground lacking vegetation (due to the soil salinity), which provide good visibility of both conspecifics and potential predators. In addition, hard substrate lacking obstacles facilitates fast movements, such as running and bouncing, common during saiga interactions. Another positive factor may be the physical condition of the saigas themselves. Arriving at the waterhole, saigas usually drink and lick minerals first and then start interacting while keeping drinking and licking from time to time until leaving. Having satisfied the need for water and minerals and staying close to their source (to get more if needed), saigas may be more prone to participate in active physically demanding social interactions. The artesian well water coming from the underground and the breeze over the water surface could help saigas to lower body temperature in the absence of shade. This could serve as an additional positive factor for the manifestation of social activity.

Whether the individual entered into social interactions may influence the duration of saiga visits to the waterholes. Both young and adult males that interacted with others during the first three minutes at the waterhole stayed significantly longer than those who did not. In females with calves, a more sophisticated version of this tendency was

found: the mothers whose calves engaged in social interactions with age-mates in the first three minutes after arrival stayed at the waterhole significantly longer than the mothers whose calves did not interact with other calves during this time interval. All individuals were observed in contexts with abundant social opportunities, that is, the absence of interaction cannot be explained by the absence of social opportunities. Therefore, our results suggest that saigas modify their visit duration according to their social incentives, *i. e.* the individuals that are prone to participate in social activity stay longer to maximize their social opportunities, while those who do not – leave earlier. In the case of females with calves, mothers may choose to stay longer to favor their calves' socialization.

Much like saiga antelopes, forest elephants form social gatherings at places offering them scarce nutritional resources (Klaus *et al.* 1998; Turkalo *et al.* 2013). In line with the results on saigas, forest elephants modify the duration of their visits to forest clearings to facilitate their involvement in social interactions. Thus, despite ecological and behavioural differences, saigas and forest elephants display a similar tendency to the management of social opportunities at resource hotspots. In elephants, the novelty of the social opportunities plays a key role: individuals increase their visit duration when they associate with conspecifics outside their ranging party (Fishlock and Lee 2013), while in saiga antelopes, the participation in social interactions with members of their group may be enough to motivate the individuals to stay longer. Intriguingly, recent study on Baird's tapir, *Tapirus bairdii*, revealed that water bodies (aguadas) serve as important place for various social interactions of this predominately solitary species. Taking into account that Malayan tapirs gather near salt licks which facilitate male-female social behaviour (Tawa *et al.* 2021), further research is needed to determine whether these watering/salt-licking sites can be utilized by tapirs as social arenas (Reyna-Hurtado and Arias-Domínguez 2024).

During the period of study, saigas visited the waterholes intensively and, in many cases, several groups were simultaneously present, providing the opportunity to form larger aggregations. The comparison of mean group sizes showed that saigas left waterhole areas in larger groups than they entered them. That is, group merging took place at the waterholes. In nomadic species with large home ranges, such as saiga antelope, places with a high probability of meeting conspecifics could be particularly important providing aggregation opportunities. Long-lasting resource hotspots such as waterholes and mineral licks may potentially play an important role in the fission-fusion social dynamics of otherwise highly dispersed groups.

The tendency for social attraction was not evident in individuals coming to the waterholes alone. In the presence of a group of conspecifics, many solitary individuals did not approach the group for drinking. As saiga antelope is a highly social species with most individuals in the study population living in groups (Karimova and Lushchekina 2018), the absence of social attraction in solitary individuals could be a byproduct of a specific condition and/or status of these animals. For example, a significant portion of individuals coming at the waterholes alone could be sick or exhausted which prevents them from joining the group. Alternatively, their low social status may explain their hesitance to interact with others. Unfortunately, too little is known about the saiga social hierarchy to provide a more confident interpretation of this result.

Social benefits provided by social arenas can vary according to species-specific social requirements. If saigas visiting social arenas may potentially benefit from both socialization and group merging, forest elephants appear to use gatherings at forest clearings specifically to develop important social relationships that would otherwise be lacking. Groups formed in the clearing were larger than ranging groups, and individuals were specifically attracted to these large groups (Fishlock and Lee 2013). However, unlike saiga antelopes, forest elephants did not form larger groups when leaving the clearing, as most animals exited the clearing with those same conspecifics with whom they arrived. This could be explained by the difference in social organization, in particular a greater stability of group composition in forest elephants.

Our findings support the hypothesis that resource hotspots may function as social arenas in species inhabiting open landscapes. Among mammals, resource hotspots such as mineral licks have been found to be used for socialization in, *e. g.*, moose (*Alces alces*) in the forests of North America (Couturier and Barrette 1988), Asian elephants (*Elephas maximus*) in the forests of South East Asia (Hii 2017), babirusa (*Babyrousa babyrussa*) in the forests of Sulawesi (Clayton and MacDonald 1999), bongo antelope (*Tragelaphus eurycerus*; Klaus-Hügi *et al.* 2000), forest elephants (Turkalo and Fay 1995, Fishlock *et al.* 2008; Fishlock and Lee 2013) and forest buffalo (*Syncerus caffer nanus*; Melletti *et al.* 2007) in the forests of Central Africa. Since such social arenas have been found predominantly in forest dwelling species, it may be hypothesized that the social significance of mineral licks and other resource hotspots, typically situated in the forest clearings, is specifically associated with higher visibility, contrasting with the forest environment and favoring interactions between conspecifics. Our results in saiga antelopes emphasize that a closed habitat is not a necessary condition for the emergence of such social arenas. The emergence of specific locations having particular social significance may be important for highly dispersed species with large home ranges irrespective of the habitat type (open or closed). In addition, the increased level of social activity at waterholes and mineral licks may be associated with the improved physical and emotional condition of animals, which has satisfied their needs for water and minerals.

The results of the study emphasize the significance of large permanent waterholes and mineral licks used by many individuals year after year for the social behavior of

saiga antelopes and likely many other nomadic ungulates inhabiting open landscapes. Their presence and condition should be considered as important factors for the success of conservation efforts such establishment and management of protected areas for threatened species (Klaus-Hügi *et al.* 2000; King *et al.* 2016).

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Supplementary material

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