ISSN 2079-0961, Arid Ecosystems, 2023, Vol. 13, No. 3, pp. 305–313. © Pleiades Publishing, Ltd., 2023.
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SYSTEMATIC STUDY
OF ARID TERRITORIES

Interference Competition between Wild and Domestic Ungulates at Watering Sites of Gobi Desert, Mongolia

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Received March 28, 2023; revised April 1, 2023; accepted April 3, 2023

Abstract—Desertification processes in Central Asia are largely dependent on soil degradation induced by excessive livestock grazing, besides climate changes. Desertification represents a threat to wildlife species living in arid environments, since reduced accessibility to water strongly affects their distribution and behavior. Moreover, livestock presence exacerbates competition with wildlife for scarce water resources. Given their crucial importance to wildlife persistence, water sources in arid environments are critical to the study of wildlife behavior and interspecific competition. The Small Gobi A is one such environment of Mongolia, characterized by high grazing pressure despite low human presence. Between September and October 2017, we conducted camera trapping surveys at two waterholes identified as potential drinking sources for wildlife. We aimed to explore the spatio-temporal interactions among large domestic ungulates (*e.g.*, Bactrian camel *Camelus bactrianus*), and wild ungulates (*e.g.*, Asian wild ass *Equus hemionus,* and goitered gazelle *Gazella subgutturosa*), which are among the most iconic and threatened ungulates of Mongolia. The results showed a complete spatial segregation between domestic and wild ungulates, and a high temporal segregation among wild ungulates. This study confirms spatial and temporal niche partitioning as a strategy adopted by wild species to reduce competition and allow species coexistence. We recommend enhanced management measures of free-roaming livestock to reduce the pressure on wild species at drinking sites.

Keywords: spatio-temporal overlap, water sources, arid ecosystems, Asiatic wild ass, Goitered gazelle, Gobi Desert

DOI: 10.1134/S2079096123030101

Water availability is becoming increasingly limited in the arid regions of Central Asia, as a result of climate changes and of increased human activities such as herding and mineral extraction (Kaczensky et al., 2011; Ito et al., 2013). Particularly, large-scale patterns of livestock management necessitate extensive water resources, hindering their use on behalf of wildlife (Kaczensky et al., 2016; Wakefield, Attum, 2006). As a result, wild and domestic species compete for food and territory, and wildlife is often displaced from areas occupied by livestock (Rovero et al., 2020; Salvatori et al., 2021). In particular, wild ungulates are among the species most impacted by livestock due to their wide dietary and habitat overlap (Berger et al., 2013). Previous studies (Zhang et al., 2015; Nandintsetseg et al., 2016) demonstrated that human and livestock disturbance induces changes in spatio-temporal activity patterns of wild ungulates. Studies on the interactions between feral horses and native ungulates showed that interference competition occurs at watering sites, especially in periods of water scarcity (Kaczensky et al., 2016; Hall et al., 2016). Thus, reduced accessibility to water in desert ecosystems exacerbates competition between domestic and wild ungulates, inducing both spatial and temporal niche segregation (Ostermann-Kelm et al., 2008; Hall et al., 2016; Gooch et al., 2017) to avoid direct competition at waterholes (Xue et al., 2018). Segregation could be a successful strategy to limit interactions, minimizing strife among species, thus enabling coexistence in shared habitats (Edwards et al., 2015; Torretta et al., 2016; Nagy-Reis et al., 2019).

In Central Asia, Mongolia has steadily suffered from desertification during the last decades (Dorj et al., 2013; Meng et al., 2021). Since the 1990s, economic reforms and a growing demand for cashmere

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led to an increase in livestock numbers (Berger et al., 2013; Meng et al., 2021), which resulted in overgrazing and soil degradation (Liu et al., 2018; Wang et al., 2020), enhancing the process of desertification (Zolotokrylin et al., 2016). Poaching, exploitation of natural resources and development of infrastructures represent additional critical threats that increased the pressure on wild ungulates and their habitat (Mallon, Zhigang, 2009; Ito et al., 2013). Indeed, human disturbance and competition with livestock for pastures and water is leading to a decrease in the availability of habitat for wild ungulates (Reading et al., 2001; Buuveibaatar et al., 2016). Presence of households is known to affect the distribution of wild ungulates. For example, K.A. Olson et al. (2011) found that the density of Mongolian gazelle *Procapra gutturosa* in the eastern steppe of Mongolia was significantly lower within areas in which human settlements were present. Hence, wild ungulates range is often limited to strictly protected areas where human presence is negligible, as observed in the Great Gobi A and Great Gobi B (Kaczensky et al., 2017; Nasanbat et al., 2016).

The Small Gobi A Strictly Protected Area (hereafter, SGA) represents a significant hotspot of biodiversity in the South Gobi and provides an important refuge for wild ungulates (Augugliaro et al., 2019). The area supports important populations of ungulates under protection at a global level, such as the Asian wild ass *Equus hemionus* (Reading et al., 2001; Kaczensky et al., 2015), categorized as Near Threatened by the IUCN Red List (IUCN, 2020) and the goitered gazelle *Gazella subgutturosa* (Reading et al., 2001; Buuveibaatar et al., 2017) categorized as Vulnerable by the IUCN Red List.

Previous studies conducted in other areas of the Mongolian Gobi observed both spatial and temporal segregation at water sources among wild ungulates (Nasanbat et al., 2016). However, that study considered only interactions among wild species due to the absence of humans and livestock in the area. Exploring the interactions between wild and domestic ungulates is pivotal where both occur, since wild ungulates could avoid livestock, influencing their distribution and behavior, and leading to habitat contraction (Michler et al., 2021). For instance, reduction and degradation of habitat due to livestock presence may limit the chances of accessibility to water sources for wild ungulates, especially in an arid environment. Hence, a better comprehension of how livestock distribution around waterholes could affect wildlife is essential in the SGA. Among the most iconic ungulates of the SGA, the Asian wild ass and the goitered gazelle were observed to positively co-occur at waterholes, since the two species do not compete in normal circumstances in a shared habitat. Since water represents a considerable limiting factor in the SGA, a better understanding of its usage by these two threatened species is mandatory for their proper management and conservation.

In this study, we aimed to assess the interactions among the Asiatic wild ass, the goitered gazelle, and the livestock at water sources of the SGA. We predicted absence of direct competition in favour of niche partitioning in order to enable coexistence among the different species (Xue et al., 2018). Considering the small dimension of the waterholes, we expected a marked spatial segregation between wild ungulates and the livestock. Moreover, as the presence of the Asian wild ass is known to be positively related with the presence of the goitered gazelle (Nandintsetseg et al., 2016), we did not expect spatial segregation between these two wild ungulates, but instead a temporal segregation allowing both species to rely on these small water sources.

MATERIALS AND METHODS

Study Area

The study was conducted in the Small Gobi A Strictly Protected Area (42°39′ N, 105°79′ E, datum WGS84), South Gobi province, Mongolia. The SGA cover an area of approximately 11,500 km^2 in the southernmost part of Mongolia, at the border with China. The Mongolian Gobi is part of the Central Asian dryland region and represents the easternmost desert in the Palearctic realm (Von Wehrden et al., 2009). The climate of the region is arid with cold winters (January mean value −17.5°C) and short hot summers (July mean value 22.5°C; Weischet, Endlicher, 2020). The annual rainfall ranges from 33 to 100 mm (Von Wehrden et al., 2009). The vegetation is sparse and dominated by desert and desert-steppe plant communities, mainly including *Artemisia* spp., *Allium* spp., *Stipa* spp., and *Anabasis* spp. The plant community of the driest areas is dominated by Chenopodiaceae (*Haloxylon* spp.), while trees species, such as *Haloxylon ammodendron* (C.A. Mey.) Bunge ex Fenzl, *Ulmus pumila* L., and *Populus euphratica* Olivier, are restricted to river valleys and large basins (von Wehrden et al., 2009). As the other mammal spots in the Mongolian Gobi, such as the Great Gobi A (Nasanbat et al., 2016), the SGA hosts rare and globally threatened species such as the goitered gazelle, the Asian wild ass, and the snow leopard *Panthera uncia*, among others (Augugliaro et al., 2019). The area is scarcely inhabited, with less than 10 households breeding domestic Bactrian camels *Camelus bactrianus* as well as small herds of sheep *Ovis aries* and goats *Capra hircus* in the north-eastern side of the protected area. Few rare natural and artificial water springs are sparse across the area and visited by both wild and domestic species. Mining activity is widely spread through North and East areas adjoining the SGA. Therefore, the area between the SGA and the easternmost Small Gobi B Strictly Protected Area is intensively crossed by trucks carrying extraction materials from the South Gobi to China.

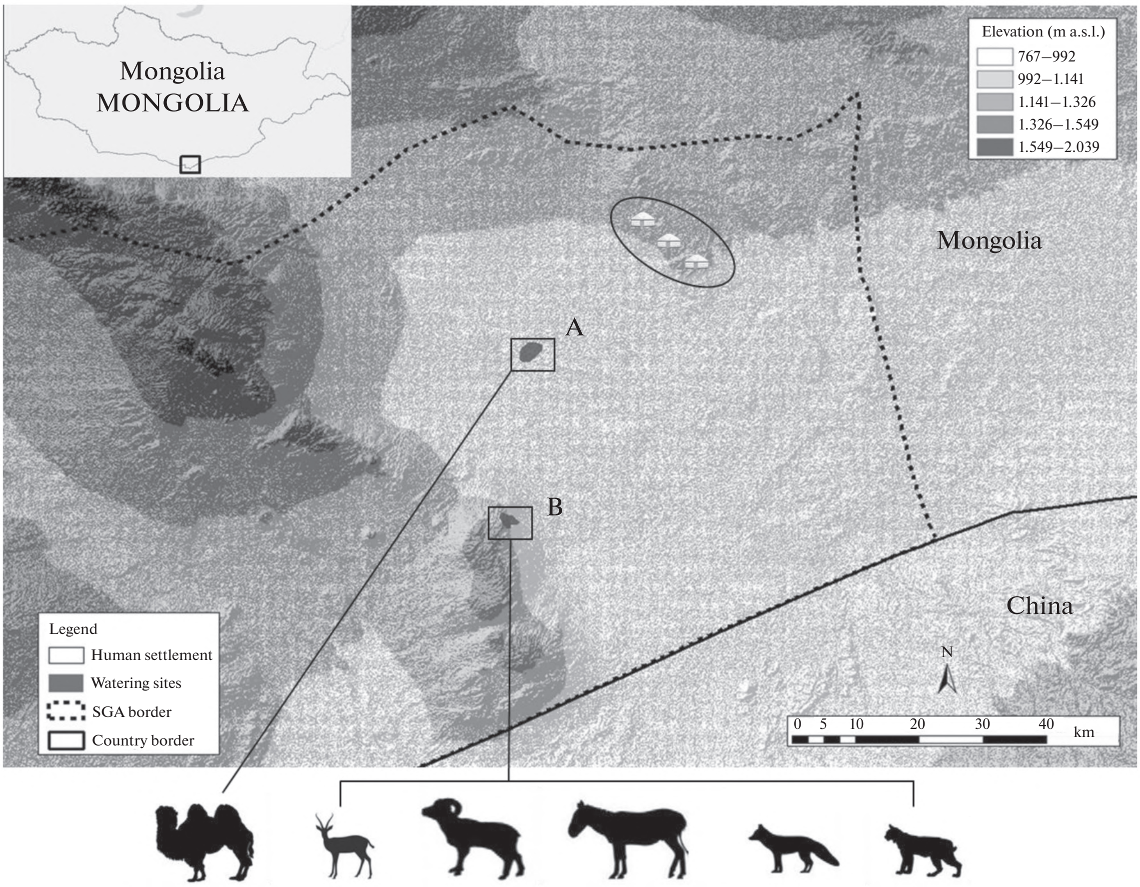

Fig. 1. Overview of the study site (Small Gobi-A Strictly Protected Area, SGA). Site A and site B represent the watering sites. For each location, a schematic representation of the sighted species is provided (Augugliaro et al., 2019).

Data Collection

As part of a larger project (Augugliaro et al., 2019), we placed camera traps on the only two water sources lying in the SGA easternmost area (Fig. 1). All the camera traps were placed on 24th September 2017, left unattended in the field until 20th October 2017, and were set to work h24 without time delay among photos. The northernmost camera site (hereafter, "site A") was placed 20 km west from the closest herder settlement and approximately 24 km from the protected area northern border. In site A, we placed two camera traps on either side of an artificial pond with a diameter of approximately 20 m (at positioning time). The pond diameter had shrunk to approximately 10 m when the cameras were removed (Fig. 2). The pond was located at 910 m above sea level (a.s.l.) surrounded by open flatland. We set a single camera trap at the southernmost site (hereafter, "site B"). Site B was located approximately 21 km south from site A, 22 km from the Chinese border, at 1120 m a.s.l. on a low mountain foothill. The camera at site B was set in front of a natural water source with a diameter of approximately 6 m (at positioning time), which was reduced to approximately 2 m when the camera was retrieved (Fig. 2). We used two Reconyx HC600 (one each site) and a Cuddeback Black Flash E3 at site A, placing the camera traps on big rocks at an average height of 40 cm above the ground (Tobler et al., 2008). We identified all species from photographic records using the book by N. Batsaikhan et al. (2014). Since we detected only domestic ungulates at the site A, and only wild ungulates at the site B, we did not proceed with further spatial analysis.

Assessment of Temporal Activity Patterns and Overlap

For each species and site, the dataset was filtered by collapsing all detections spaced less than 30 minutes in one single event, to reduce pseudo-replication (Meredith, Ridout, 2021). Target species (i.e., Bactrial camel, Asian wild ass and goitered gazelle) provided us with more than 20 independent detections, thus we could proceed with the analyses (Ridout, Linkie, 2009). Temporal activity patterns of the different species were analysed through the R package *overlap* (Meredith, Ridout, 2021). To estimate whether a random activity pattern was exhibited by each species (Viviano et al., 2021), we used the Hermans–Rasson

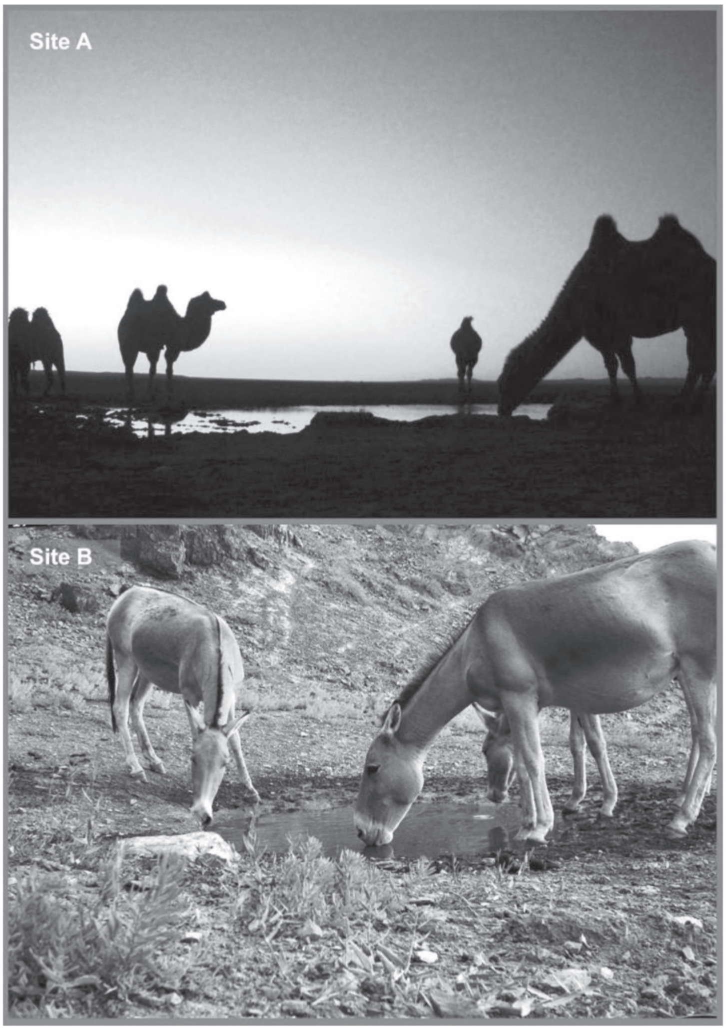

Fig. 2. Site A—Bactrian camels at water source, site B—Asian wild asses at water source within the Small Gobi-A.

uniformity test (*r*) using the function *HR_test* in the package *CircMLE* (Fitak, Johnsen, 2017). Through the R package *overlap*, we also quantified the overlap in activity patterns between the Asian wild ass and the goitered gazelle using the coefficient of overlap (Δ), measured non-parametrically using kernel density estimates (Schmid, Schmidt, 2006). Owing to the complete spatial segregation between wildlife and livestock we did not analyse the activity overlap between wild ungulates and Bactrian camel. Overlap coefficient is defined as the area under the two kernel density curves and it varies between 0 (i.e., no overlap) and 1 (i.e., total overlap; Ridout, Linkie, 2009). We used the "Δ_1 estimator" for the pairwise comparison since the goitered gazelle provided us with less than 75 records (Ridout, Linkie, 2009; Meredith, Ridout, 2021). Temporal overlap was considered as "very low" with $\Delta \leq 0.35$, "low" with $0.35 < \Delta \leq 0.50$, "moderate" with $0.5 < \Delta \leq 0.75$, "high" with $\Delta > 0.75$ (Monterroso et al., 2014; Sogliani et al., 2021). The 95% confidence intervals (hereafter, 95% CIs) of the overlap coefficients were estimated through bootstrap resampling (10 000 replicates; Meredith, Ridout, 2021). Owing to the purely descriptive nature of these estimators (no associated *p*-value; Monterroso et al., 2014) we used the Mardia-Watson-Wheeler test (*W*). The MMW test was applied through the R package *circular* (Mori et al., 2021; Panzeri et al., 2021), to assess whether the activity times of the two species were significantly different. An additional bootstrap test was calculated to estimate "*the probability that two sets of circular observations come from the same distribution*" (Rowcliffe et al., 2014), using the function *compareCkern* in the R package *activity*. A chi-square test was used to assess if records of each species were evenly distributed throughout the lunar phases (Viviano et al., 2021), assessed for each camera-trap day through the R package *suncalc*, using the function *getMoonIllumination* (Simmons et al., 2021). Moon phases were classified as follows: phase (1) from new moon to 1/4 (retrieved value of lunar phase [LP]: $0 < LP \leq 0.125$ or $0.875 < LP \leq 1$); phase (2) from 1/4 to 1/2 ($0.125 < LP \leq 0.250$ or $0.750 < LP \leq 0.875$); phase (3) from 1/2 to 3/4 ($0.250 < LP \leq 0.375$ or $0.625 < LP \leq 0.750$) and phase (4) from 3/4 to full moon ($0.375 < LP \leq 0.5$ or $0.5 < LP \leq 0.625$). The darkest nights include phases (1) and (2), while phases (3) and (4) the brightest ones (Panzeri et al., 2021; Viviano et al., 2021). Finally, using the function *getSunlightTimes* of package *suncalc*, we calculated sunrise and sunset mean values for our camera trap survey period; useful in the classification of the species as nocturnal, diurnal, crepuscular, or cathemeral depending on the percentage of observations recorded at day, night, and twilight period (Azevedo et al., 2018; Houngbégnon et al., 2020). All the analyses were implemented in the software R, version 4.1.1 (R Development Core Team 2021).

RESULTS AND DISCUSSION

The total camera trapping effort was 56 camera-trap days (i.e., *N* of camera-traps × *N* days they were active). At site B, we detected only wild mammal species (Fig. 1): the Asian wild ass, the goitered gazelle, the argali (*Ovis ammon*), the red fox (*Vulpes vulpes*) and the Eurasian lynx (*Lynx lynx*). Whereas the Bactrian camel was the only species detected at site A (Fig. 1). The Bactrian camel was the most detected species ($N = 812$, where *N* is the number of independent detection events), followed by the Asian wild ass ($N = 172$) and the goitered gazelle ($N = 25$). At water sources, the Bactrian camel was cathemeral (34% of diurnal, 23% of crepuscular, and 43% of nocturnal detections) and the goitered gazelle was mostly diurnal (80% of diurnal detections; Fig. 3). In addition, the Bactrian camel showed a marked peak of activity at dusk. On contrary, the Asian wild ass was mostly nocturnal (72% of nocturnal detections; Fig. 3).

Throughout the survey period, the Hermans-Rasson test indicated a non-random activity pattern at water sources for all the species ($p < 0.001$; Asian wild ass: $r = 31.38$; goitered gazelle: $r = 29.12$; Bactrian camel: $r = 456.70$). We detected a "very low" temporal overlap between the Asian wild ass and the goitered gazelle, sympatric at site B (Fig. 3). In addition, the MWW test showed significant differences for the comparison between wild ungulates' activity times ($p < 0.001$; Asian wild ass-Goitered gazelle: $W = 31.83$). At water sources, the temporal activity of the Asian wild ass differed significantly among lunar phases, with the species being most active during bright nights (phases 3 and 4; $\chi^2 = 11.57$, df = 1, $p < 0.001$). Conversely, the temporal activity of both the goitered gazelle and the Bactrian camel at water sources seemed not to be influenced by moon illumination ($\chi^2 = 1.01$, df = 1, $p = 0.31$; $\chi^2 = 0.38$, df = 1, $p = 0.53$, respectively).

Our findings highlighted a complete spatial segregation between wild and domestic ungulates. Instead,

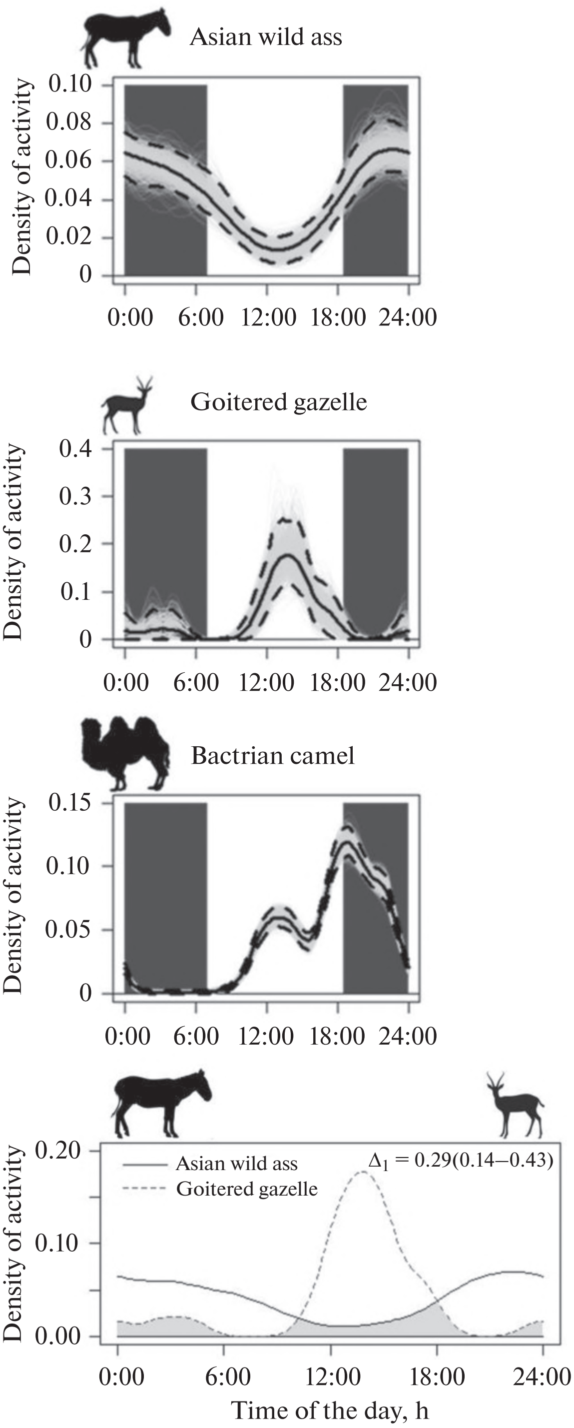

Fig. 3. Density estimates of daily activity patterns of the three ungulate species at water sources in the Small Gobi-A Strictly Protected Area, Mongolia; sunrise is approx. at 07:00, while sunset is approx. at 18:30 (solar time). *Leged:* dark rectangles—dark hours, faded lines around and inside the dashed lines—bootstrapped estimates of activity patterns, dashed lines—95% CIs. Bottom picture shows the overlap in temporal distribution of water use between the Asian wild ass and the goitered gazelle, the overlap coefficient (shaded area) is reported along with the 95% CI.

wild species coexisted in the same site adjusting their diel temporal activity patterns to reduce their overlap and thus competition for water resources. Spatial segregation between wild and domestic ungulates around waterholes was also observed in other studies conducted in arid environments (Ostermann-Kelm et al., 2008; Gooch et al., 2017). However, results from previous research are contrasting, since spatio-temporal segregation may depend on the topographic characteristics of the sites, as well as the dimensions of the waterholes across seasons. For instance, feral horses and native ungulates exhibited spatial segregation at water sources in areas devoid of human settlements (Hall et al., 2016). In the Western Gobi Region, the Asian wild ass and the livestock are known to use the same waterholes, thus allowing coexistence by means of temporal partitioning (Payne et al., 2021).

We speculate that Bactrian camel colonization of waterhole at site A have induced a complete spatial segregation of wild ungulates, indicating a case of high level of interference competition (Hennig et al., 2021). These findings support our initial prediction of low level of direct competition dictated by avoidance behavior, and it underlines how the constant presence of a large domestic competitor at waterholes can lead to wildlife exclusion from a precious resource in such a harsh environment. Our results are supported by previous studies, which documented evidence that Asian wild asses and goitered gazelles are negatively impacted by human activities and livestock presence in the Gobi Desert (Kaczensky et al., 2011; Buuveibaatar et al., 2016), especially in Autumn (Tsendjav, Purevsuren, 2007) due to the reduction of waterholes dimension and scarce availability of snow, as we assessed during our research period.

In our study area, Bactrian camels at site A occupied the water resources in proximity to herders' settlements, although within the protected area's border. As a consequence, wild ungulates seemed to prefer the waterhole at site B, which is sheltered by mountain outcrops and located farther from human settlements (Yoshihara et al., 2008; Sheehy et al., 2010). Further investigation should be related to the distribution of wild ungulates around water sources previously occupied by herder families, taking into the account the rotational grazing system adopted by Mongolian nomadic families for their livestock.

In contrast with other studies, the goitered gazelle showed a clear diurnal pattern at watering sites, as observed elsewhere in China (Xue et al., 2018). This temporal pattern may be due to the small size of the waterhole concomitant with the presence of a bigger competitor such as the Asian wild ass at night-time. Being the site B among the few rare water sources available in the east SGA, the goitered gazelle may have adapted its behavior to access this resource undistrubed.

Our results concerning the Asian wild ass temporal activity are also in contrast with those found in previous studies, which described the absence of specific diurnal or nocturnal pattern, that may be altered only when external threats occur (Kaczensky et al., 2010, 2021). Our study area is located in the proximity of the Chinese border, an area devoid of legal wildlife protection management, and possibly representing a critical migration route for wild ungulates. Poaching episodes are known to occur also through the SGA in Mongolia (Stubbe et al., 2012), a fact that may have affected the temporal patterns of the Asian wild ass, by peaking its activity during bright nights at waterpoints. Whereas human presence may represent a potential threat mostly during the daytime, the Asian wild ass activity rhythm could be potentially affected by large predators such as the grey wolf *Canis lupus*, which however appears to be present at a very low density in the area (Augugliaro et al., 2019). Unlike other smaller mammals which are more active during the darkest nights to avoid natural predators (Kotler et al., 2010; Panzeri et al., 2021), the Asian wild ass has not many risks to face during brighter nights, when poaching activities are likely negligible.

As we hypothesized, we observed co-existence among wild ungulates by means of temporal segregation. Although very little is known about the activity interactions between the Asian wild ass and the goitered gazelle, temporal segregation among other wild ungulates have been observed at the watering sites in arid environments. Y. Zhang et al. (2015) observed a high degree of spatial overlap between Asian wild asses and Przewalski's horses, which approached waterholes at different times during the day. It was also observed that, although the encounters between these species were rare, Przewalski's horses have priority access to drinking sites respect to Asian wild assess with the latter species waiting apart to avoid direct competition (Zhang et al., 2015). This behavior was also observed by J.D. Hennig et al. (2021), who reported how the more aggressive and dominant species had priority in accessing water resources. However, this does not represent a temporal segregation at a landscape level, but rather a temporal partitioning (Hall et al., 2016). Differences in temporal use of watering sites were also observed within a guild of wild ungulates in an arid region of the Altun Mountains in China, where smaller ungulates modified their temporal patterns in order to avoid direct competition (Xue et al., 2018). There is evidence of spatial overlap around water sources between the Asian wild ass and the goitered gazelle, in line with our results (Buuveibaatar et al., 2016; Nandintsetseg et al., 2016; Payne et al., 2021). In the Altyn-Emel National Park (Kazakhstan), D.A. Blank (2020) found that the goitered gazelle did not perceive the Asian wild ass as a threat, thus did not alter its behavior. This suggests that the two species do not compete in normal circumstances in a shared habitat with adequate resources. In our study case, the small water sources could have exacerbated competition. We believe temporal segregation is an effective strategy to limit interspecific competition, allowing the coexistence of sympatric wild ungulates whenever water resources have a limiting extent.

Owing to the scarce number of waterholes in the SGA, this study evaluated only two distant waterholes across a limited gradient of ecological conditions, which could determine the species behavior. For a better understanding, the ungulates' activity patterns should be evaluated over a larger area including a higher number of waterholes beyond the protected zone and distributed in a variety of biological and topographic characteristics.

CONCLUSIONS

In conclusion, we suggest a more integrated and systematic approach in assessing activity patterns and behavior of desert ungulates in SGA, and in desert environments in general, by focusing on connections among water sources.

Finally, we believe that education campaigns can be put in place to sensitize the herders, specifically on managing free-roaming animals (e.g., free-roaming camels or domestic apex predators such as dogs). We suggest restricting livestock access to a limited number of artificial water points located nearby the human settlements, in order to reduce the competition with wild ungulates at waterholes and to favorite the spatial segregation with domestic animals in order to reduce the pathogen transmission.

ACKNOWLEDGMENTS

We thank the government of Bayan Ovoo district for assisting us in the field. We thank the Small Gobi-A Special Protected Area administration, and the Ministry of Environment and Tourism for their support.

We thank Mr. Batkhuyag (Wildlife Initiative) for his contribution to data collection. We are also grateful to the Department of Ecology and Evolution of the University of Lausanne that supplied some of the camera traps and to Munkhoyon Suvarga who provided fundings.

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare that they have no conflicts of interest.

AUTHORS CONTRIBUTIONS

FR and DS wrote the first draft; DS analyzed data and produced figures; MC conducted the GIS analysis and produced figures; CA conceived and supervised the research and acquired funding. CA and LA revised and edited the first draft.

REFERENCES

Augugliaro, C., Paniccia, C., Janchivlamdan, C., Monti, I.E., Boldbaatar, T., and Munkhtsog, B., Mammal inventory in the Mongolian Gobi, with the southeasternmost documented record of the snow leopard, *Panthera uncia* (Schreber, 1775), in the country, *Check List*, 2019, vol. 15, no. 4, pp. 565–578. https://doi.org/10.15560/15.4.565

Azevedo, F.C., Lemos, F.G., Freitas-Junior, M.C., Rocha, D.G., and Azevedo, F.C.C., Puma activity patterns and temporal overlap with prey in a human-modified landscape at Southeastern Brazil, *J. Zool.*, 2018, vol. 305, no. 4, pp. 246–255. https://doi.org/https://doi.org/10.1111/jzo.12558

Batsaikhan, N., Buuveibaatar, B., Chimed, B., Von Wehrden, H., and Whitten, T., Conserving the world's finest grassland amidst ambitious national development, *Conserv. Biol.*, 2014, no. 28, pp. 1736–1739. https://doi.org/10.1111/cobi.12297

Berger, J., Buuveibaatar, B., and Mishra, C., Globalization of the cashmere market and the decline of large mammals in Central Asia, *Conserv. Biol*, 2013, vol. 27, no. 4, pp. 679–689. https://doi.org/10.1111/cobi.12100

Blank, D.A., Behavioral responses of goitered gazelles to potential threats, *Mammal Research*, 2020, vol. 65, no. 4, pp. 141–149. https://doi.org/10.1007/s13364-019-00457-y

Buuveibaatar, B., Mueller, T., Strindberg, S., Leimgruber, P., Kaczensky, P., and Fuller, T.K., Human activities negatively impact distribution of ungulates in the Mongolian Gobi, *Biol. Conserv.*, 2016, no. 203, pp. 168–175. https://doi.org/10.1016/j.biocon.2016.09.013

Buuveibaatar, B., Strindberg, S., Kaczensky, P., Payne, J., Chimeddorj, B., Naranbaatar, G., and Fuller, T., Mongolian Gobi supports the world's largest populations of khulan *Equus hemionus* and goitered gazelles *Gazella subgutturosa, Oryx*, 2017, vol. 51, no. 4, pp. 639–647. https://doi.org/10.1017/S0030605316000417

Dorj, O., Enkhbold, M., Lkhamyanjin, S., Mijiddorj, K., Nosmoo, A., Puntsagnamil, M., and Sainjargal, U., Mongolia: Country features, the main causes of desertification and remediation efforts, in *Combating Desertification in Asia, Africa and the Middle East*, Dordrecht: Springer, 2013, pp. 217–229. https://doi.org/10.1007/978-94-007-6652-5_11

Edwards, S., Gange, A.C., and Wiesel, I., Spatiotemporal resource partitioning of water sources by African carnivores on Namibian commercial farmlands, *J. Zool.*, 2015, vol. 297, no. 1, pp. 22–31. https://doi.org/10.1111/jzo.12248

Fitak, R.R. and Johnsen, S., Bringing the analysis of animal orientation data full circle: Model-based approaches with maximum likelihood, *J. Exp. Biol.*, 2017, vol. 220, no. 21, pp. 3878–3882. https://doi.org/10.1242/jeb.167056

Gooch, A.M., Petersen, S.L., Collins, G.H., Smith, T.S., McMillan, B.R., and Eggett, D.L., The impact of feral horses on pronghorn behavior at water sources, *J. Arid Environ.*, 2017, no. 138, pp. 38–43. https://doi.org/10.1016/j.jaridenv.2016.11.012

Hall, L.K., Larsen, R.T., Westover, M.D., Day, C.C., Knight, R.N., and McMillan, B.R., Influence of exotic horses on the use of water by communities of native wildlife in a semi-arid environment, *J. Arid Environ.*, 2016, no. 127, pp. 100–105. https://doi.org/10.1016/j.jaridenv.2015.11.008

Hennig, J.D., Beck, J.L., Gray, C.J., and Scasta, J.D., Temporal overlap among feral horses, cattle, and native ungulates at water sources, *J. Wildl. Manage.*, 2021, no. 85, pp. 1084–1090. https://doi.org/10.1002/jwmg.21959

Houngbégnon, F.G.A., Cornelis, D., Vermeulen, C., Sonké, B., Ntie, S., Fayolle, A., Fonteyn, D., Lhoest, S., Evrard, Q., Yapi, F., Sandrin, F., Vanegas, L., Ayaya, I., Hardy, C., Le Bel, S., and Doucet, J.-L., Daily activity patterns and co-occurrence of duikers revealed by an intensive camera trap survey across Central African rainforests, *Animals*, 2020, vol. 10, no. 12, p. 2200. https://doi.org/10.3390/ani10122200

Ito, T.Y., Lhagvasuren, B., Tsunekawa, A., Shinoda, M., Takatsuki, S., Buuveibaatar, B., and Chimeddorj, B., Fragmentation of the habitat of wild ungulates by anthropogenic barriers in Mongolia, *PLoS ONE*, 2013, vol. 8, no. 2, p. e56995. https://doi.org/10.1371/journal.pone.0056995

IUCN, The IUCN Red List of Threatened Species, 2020. www.iucnredlist.org. Accessed March 30, 2022.

Kaczensky, P., Dresley, V., Vetter, D., Otgonbayar, H., and Walzer, C., Water use of Asiatic wild asses in the Mongolian Gobi, *Exploration into the Biological Resources of Mongolia*, 2010, vol. 11, pp. 291–298.

Kaczensky, P., Kuehn, R., Lhagvasuren, B., Pietsch, S., Yang, W., and Walzer, C., Connectivity of the Asiatic wild ass population in the Mongolian Gobi, *Biol. Conserv.*, 2011, vol. 144, no. 2, pp. 920–929. https://doi.org/10.1016/j.biocon.2010.12.013

Kaczensky, P., Lkhagvasuren, B., Pereladova, O., Hemami, M., and Bouskila, A., *Equus hemionus*. The IUCN Red List of Threatened Species, 2015, p. e.T7951A45171204. https://doi.org/10.2305/IUCN.UK.2015-4.RLTS.T7951A45171204.en

Kaczensky, P., Sheehy, D.P., Johnson, D.E., Walzer, C., Lhkagvasuren, B., and Sheehy, C.M., Room to roam? The threat to khulan (wild ass) from human intrusion, in *Mongolia Discussion Papers*, Washington, D.C: World Bank, 2016.

Kaczensky, P., Enkhsaikhan, N., Ganbaatar, O., and Walzer, C., Identification of herder-wild equid conflicts in the Great Gobi B strictly protected area in SW Mongolia, *Exploration into the Biological Resources of Mongolia*, 2017, vol. 10, pp. 99–116.

Kaczensky, P., Payne, J., Ganbaatar, O., Altansukh, N., and Walzer, C., Water use by khulan in the Dzungarian Gobi in SW Mongolia, in *Exploration into the Biological Resources of Mongolia*, Halle/Saale, Germany, 2021, vol. 14, pp. 27–38.

Kotler, B.P., Brown, J., Mukherjee, S., Berger-Tal, O., and Bouskila, A., Moonlight avoidance in gerbils reveals a sophisticated interplay among time allocation, vigilance and state-dependent foraging, *Proceedings of the Biological Sciences*, 2010, vol. 277, no. 1687, pp. 1469–1474. https://doi.org/10.1098/rspb.2009.2036

Liu, Q., Liu, G., and Huang, C., Monitoring desertification processes in Mongolian Plateau using MODIS tasseled cap transformation and TGSI time series, *Journal of Arid Land*, 2018, vol. 10, no. 1, pp. 12–26. https://doi.org/10.1007/s40333-017-0109-0

Mallon, D.P. and Zhigang, J., Grazers on the plains: Challenges and prospects for large herbivores in Central Asia, *J. Appl. Ecol.*, 2009, no. 46, pp. 516–519. https://doi.org/10.1111/j.1365-2664.2009.01654.x

Meng, X., Gao, X., Li, S., Li, S., and Lei, J., Monitoring desertification in Mongolia based on landsat images and Google Earth Engine from 1990 to 2020, *Ecol. Indic.*, 2021, no. 129, p. 107908. https://doi.org/10.1016/j.ecolind.2021.107908

Meredith, M. and Ridout, M., Overview of the overlap package, 2021. https://cran.r-project.org/web/packages/overlap/vignettes/overlap.pdf. Accessed March 30, 2022.

Michler, L.M., Kaczensky, P., Ganbaatar, O., and Treydte, A.C., On the move-do domestic and wild ungulate species distributions overlap in the Mongolian Gobi?, in *International Grassland Congress Proceedings, XXIV Int. Grassland Congress / XI Int. Rangeland Congress,* 2021.

Monterroso, P., Alves, P.C., and Ferreras, P., Plasticity in circadian activity patterns of mesocarnivores in Southwestern Europe: Implications for species coexistence, *Behav. Ecol. Sociobiol.*, 2014, vol. 68, no. 9, pp. 1403–1417. https://doi.org/10.1007/s00265-014-1748-1

Mori, E., Paniccia, C., Munkhtsog, B., Cicero, M., and Augugliaro, C., Temporal overlap among small- and medium-sized mammals in a grassland and a forest-alpine meadow of Central Asia, *Mamm. Biol.*, 2021, vol. 101, no. 2, pp. 153–162. https://doi.org/10.1007/s42991-020-00085-z

Nagy-Reis, M.B., Iwakami, V.H.S., Estevo, C.A., and Setz, E.Z.F., Temporal and dietary segregation in a neotropical small-felid assemblage and its relation to prey activity, *Mamm. Biol.*, 2019, no. 95, pp. 1–8. https://doi.org/10.1016/j.mambio.2018.12.005

Nandintsetseg, D., Kaczensky, P., Ganbaatar, O., Leimgruber, P., and Mueller, T., Spatiotemporal habitat dynamics of ungulates in unpredictable environments: The khulan (*Equus hemionus*) in the Mongolian Gobi desert as a case study, *Biol. Conserv.*, 2016, no. 204, pp. 313–321. https://doi.org/10.1016/j.biocon.2016.10.021

Nasanbat, B., Ceacero, F., and Ravchig, S., A small neighborhood well-organized: Seasonal and daily activity patterns of the community of large and mid-sized mammals around waterholes in the Gobi Desert, Mongolia, *Front. Zool.,* 2016, no. 18, p. 25. https://doi.org/10.1186/s12983-021-00412-1

Olson, K.A., Mueller, T., Kerby, J.T., Bolortsetseg, S., Leimgruber, P., Nicolson, C., and Fuller, T.K., Death by a thousand huts? Effects of household presence on density and distribution of Mongolian gazelles, *Conserv. Lett.*, 2011, vol. 4, pp. 304–312. https://doi.org/10.1111/J.1755263X.2011.00180.X

Ostermann-Kelm, S., Atwill, E.R., Rubin, E.S., Jorgensen, M.C., and Boyce, W.M., Interactions between feral horses and desert bighorn sheep at water, *J. Mammal.*, 2008, vol. 89, pp. 459–466. https://doi.org/10.1644/07-MAMM-A-075R1.1

Panzeri, M., Mazza, G., Bisi, F., and Mori, E., Patterns of spatiotemporal activity of an alien lagomorph inferred through camera-trapping, *Mammalian Research*, 2021, vol. 66, no. 2, pp. 281–288. https://doi.org/10.1007/s13364-021-00557-8

Payne, J.C., Buuveibaatar, B., and Bowler, D.E., Hidden treasure of the Gobi: Understanding how water limits range use of khulan in the Mongolian Gobi, *Sci. Rep.*, 2021, vol. 10, no. 1, pp. 1–13. https://doi.org/10.1038/s41598-020-59969-2

Reading, R.P., Henry, M., Lhagvasuren, B., Feh, C., Kane, D.P., Dulamtseren, S., and Enkhbold, S., Status and distribution of khulan (*Equus hemionus*) in Mongolia, *J. Zool.*, 2001, vol. 254, no. 3, pp. 381–389. https://doi.org/10.1017/S0952836901000887

Ridout, M.S. and Linkie, M., Estimating overlap of daily activity patterns from camera trap data, *Journal of Agricultural, Biological, and Environmental Statistics*, 2009, vol. 14, no. 3, pp. 322–337. https://doi.org/10.1198/jabes.2009.08038

Rovero, F., Augugliaro, C., Havmøller, R., Groff, C., Zimmermann, F., Oberosler, V., and Tenan, S., Co-occurrence of snow leopard *Panthera uncia*, Siberian ibex *Capra sibirica* and livestock: Potential relationships and effects, *Oryx*, 2020, vol. 54, no. 1, pp. 118–124. https://doi.org/10.1017/S0030605317001685

Rowcliffe, J.M., Kays, R., Kranstauber, B., Carbone, C., and Jansen, P.A., Quantifying levels of animal activity using camera trap data, *Methods in Ecology and Evolution*, 2014, vol. 5, no. 11, pp. 1170–1179. https://doi.org/10.1111/2041-210X.12278

Salvatori, M., Tenan, S., Oberosler, V., Augugliaro, C., Christe, P., Groff, C., and Rovero, F., Co-occurrence of snow leopard, wolf and Siberian ibex under livestock encroachment into protected areas across the Mongolian Altai, *Biol. Conserv.*, 2021, vol. 261, no. 3, p. 109294. https://doi.org/10.1016/j.biocon.2021.109294

Schmid, F. and Schmidt, A., Nonparametric estimation of the coefficient of overlapping-theory and empirical application, *Computational Statistics & Data Analysis*, 2006, vol. 50, no. 6, pp. 1583–1596. https://doi.org/10.1016/j.csda.2005.01.014

Sheehy, D., Sheehy, C., Johnson, D., Damiran, D., and Fiamengo, M., *Mongolia: Livestock and Wildlife in the Southern Gobi Region, with Special Attention to Wild Ass*, World Bank, Washington, DC, 2010.

Simmons, O.M., Gregory, S.D., Gillingham, P.K., Riley, W.D., Scott, L.J., and Britton, J.R., Biological and environmental influences on the migration phenology of atlantic salmon *Salmo salar* smolts in a chalk stream in Southern England, *Freshwater Biol.*, 2021, vol. 66, no. 8, pp. 1581–1594. https://doi.org/10.1111/fwb.13776

Sogliani, D., Cerri, J., Turetta, R., Crema, M., Corsini, M., and Mori, E., Feral rabbit populations in a peri-urban area: Insights about invasion dynamics and potential management strategies, *European Journal of Wildlife Research*, 2021, vol. 67, no. 3. https://doi.org/10.1007/s10344-021-01505-2

Stubbe, A., Stubbe, M., Batsaikhan, N., and Samjaa, R., Long-term ecology of Asiatic wild ass (*Equus h. hemionus* Pallas) in Central Asia, *Exploration into the Biological Resources of Mongolia*, 2012, vol. 12, pp. 61–76.

Tobler, M.W., Carrillo-Percastegui, S.E., Pitman, L.R., Mares, R., and Powell, G., An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals, *Animal Conservation*, 2008, vol. 11, pp. 169–178. https://doi.org/10.1111/j.1469-1795.2008.00169.x

Torretta, E., Serafini, M., and Puopolo, F., Spatial and temporal adjustments allowing the coexistence among carnivores in Liguria (N-W Italy), *Acta Ethologica*, 2016, no. 19, pp. 123–132. https://doi.org/10.1007/s10211-015-0231-y

Tsendjav, D. and Purevsuren, S., Some information on the ecology of the khulan *Equus hemionus* (Pallas 1775) in the western part of the South Gobi province, Mongolia, *Exploration into the Biological Re-sources of Mongolia (Halle/Saale)*, 2007, no. 10, pp. 61–8.

Viviano, A., Mori, E., Fattorini, N., Mazza, G., Lazzeri, L., Panichi, A., Strianese, L., and Mohamed, W.F., Spatiotemporal overlap between the European brown hare and its potential predators and competitors, *Animals*, 2021, vol. 11, no. 2, p. 562. https://doi.org/10.3390/ani11020562

Von Wehrden, H., Wesche, K., and Miehe, G., Plant communities of the southern Mongolian Gobi, *Phytocoenologia*, 2009, vol. 39, no. 3, pp. 331–376. https://doi.org/10.1127/0340-269X/2009/0039-0331

Wakefield, S. and Attum, O., The effects of human visits on the use of a waterhole by endangered ungulates, *J. Arid Environ.*, 2006, vol. 65, no. 4, pp. 668–672. https://doi.org/10.1016/j.jaridenv.2005.08.007

Wang, J., Wei, H., Cheng, K., Ochir, A., Davaasuren, D., Li, P., and Nasanbat, E., Spatio-temporal pattern of land degradation from 1990 to 2015 in Mongolia, *Environ. Dev.*, 2020, vol. 34, p. 100497. https://doi.org/10.1016/j.envdev.2020.100497

Weischet, W. and Endlicher, W., *Regionale Klimatologie*, vol. 2*: Die Alte Welt (Europa, Afrika, Asien)*, Teubner Stuttgart-Leipzig, 2020.

Xue, Y., Li, J., and Sagen, G., Activity patterns and resource partitioning: Seven species at watering sites in the Altun Mountains, China, *Journal of Arid Land*, 2018, vol. 10, pp. 959–967. https://doi.org/10.1007/s40333-018-0028-8

Yoshihara, T., Ito, T.Y., Lhagvasuren, B., and Takatsuki, T., A comparison of food resources used by mongolian gazelles and sympatric livestock in three areas in mongolia, *J. Arid Environ.*, 2008, vol. 72, no. 1, pp. 48–55. https://doi.org/10.1016/j.jaridenv.2007.05.001

Zhang, Y., Cao, Q.S., Rubenstein, D.I., Zang, S., Songer, M., and Leimgruber, P., Water use patterns of sympatric Przewalski's horse and khulan: Interspecific comparison reveals niche differences, *PLoS ONE*, 2015, vol. 10, no. 7, p. e0132094. https://doi.org/10.1371/journal.pone.0132094

Zolotokrylin, A.N., Gunin, P.D., Titkova, T.B., Bazha, S.N., Danzhalova, E.V., and Kazantseva, T.I., Diagnosis of the desertification dynamics of arid pastures in Mongolia from observation in key areas and modis data, *Arid Ecosyst.,* 2016, vol. 6, no. 3, pp. 149–157. https://doi.org/10.1134/S2079096116030100