University of Natural Resources
and Life Sciences, Vienna

Space-time characterization of Przewalski's horse movement in the Great Gobi B SPA in SW Mongolia

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Declaration in lieu of oath

I herewith declare in lieu of oath that this thesis has been composed by myself without any inadmissible help and without the use of sources other than those given due reference in the text and listed in the list of references. I further declare that all persons and institutions that have directly or indirectly helped me with the preparation of the thesis have been acknowledged and that this thesis has not been submitted, wholly or substantially, as an examination document at any other institution.

Date	Signature

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I could not have accomplished this project without the positivity and encouragement I received from my wonderful friends Anja, Benni, and Maxi. I also want to thank my family for their great support and for trying to understand what I spend my time on.

ABSTRACT

This study pursues an explorative approach to elucidate Przewalski's horses (*Equus ferus przewalskii*) utilization distribution with special regard to time-use metrics in the Great Gobi B Special Protected Area in SW Mongolia.

Three individuals from three different social groups were equipped with a new generation of GPS-Iridium collars in June 2013 and have been collecting regular GPS locations at hourly intervals for almost two years allowing for a new analysis approach.

Time-Local Convex Hull (T-LoCoH), a novel method of empirical home range estimation was selected to best describe ranging behaviour, habitat selection and resource selection of collared animals by means of adding a temporal dimension to nearest-neighbour convex-hull constructions. This is the first application of this novel method to a species of such a major conservation concern.

Precise definitions and differentiation of important resources was hampered by spatiotemporal overlap of foraging and drinking behaviour. However, important directional movement (e.g. corridors) between valuable resources and around demanding topographical features could be detected. Range shifts could be visualized in some cases, but their relatedness to seasonal resources could not be confirmed. Oasis and water points were identified to be central regarding utilization distributions and their importance as habitat constituting most productive vegetation communities could be confirmed. Utilization of confined space-use was illustrated with high precision by multiple tools of the algorithm. Except for day-night variation regarding average speed, no 24-hour patterns could be detected from time-use metrics.

T-LoCoH proofs to be a valuable implement to elucidate and characterize spatiotemporal movement of Przewalski's horses in the Great Gobi B SPA. Depending on the research question, the toolset of this algorithm works all the better in combination with other metrics and home range estimating tools rather than simply by itself.

Keywords: GPS, Mongolia, monitoring, movement ecology, Przewalski's horse *(Equus ferus przewalskii)*, time use, T-LoCoH, utilization distribution

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1 INTRODUCTION

Progressive advances of satellite wildlife tracking tools have remarkably increased the volume, precision, affordability, and the availability of ancillary variables integrated with movement data (Kaczensky et al., 2011; Lyons et al., 2013; Tomkiewicz et al., 2010). These technical and analytical improvements hold both opportunities and challenges for ecologists (Cagnacci et al. 2010) but ultimately allow deeper insights into activity budgets and goal-related trajectories of animals without affecting their natural behaviour (Powell and Mitchell, 2012).

Przewalski's horse (*Equus ferus przewalskii* Poljakov, 1881) is one of seven recent equid species in the world and the only true representative of wild horses (Wakefield et al., 2002). Following its extinction in the wild in the 1960's, it survived as a species solely due to captive breeding programs (Mohr and Volf, 1984). Of multiple efforts to reintroduce the species in the wild, only three projects in Mongolia and China managed to establish free-ranging populations (Kaczensky et al., 2016). This has resulted in small populations of Przewalski's horses, 113 of which live in the Great Gobi B Special Protected Area (SPA) in SW Mongolia (Ganbaatar et al., 2015). The increase in numbers of free-ranging Przewalski's horses subsequently lead to the down-listing from Extinct in the Wild to Critically Endangered in 2008 and to Endangered in 2011 by the IUCN Red List of Threatened Species (King et al., 2016). The Gobi areas arguably provide a marginal, rather than an optimal habitat for Przewalski's horses (Kaczensky et al., 2008; Van Dierendonck and Wallis de Vries, 1996). Since equids are non-ruminant hind gut fermenters, they dependent on processing large quantities of low-quality forage (bulk feeders) and on the availability of free water (Wakefield et al., 2002). Van Dierendonck and Wallis de Vries (1996) suggest that Przewalski's horses can only survive under arid conditions as long as they have continued access to water points.

Classical home range analysis and resource selection function (RSF) analysis have determined that Przewalski's horses (*Equus ferus przewalskii*) in the Gobi have annual home range of 152–826 km² and select for the most productive habitat types (Kaczensky, et al. 2008), 'a strategy generally expected when dealing with resource selection by animals in stable environments' (Manly, et al., 2002). However, these analyses did not incorporate the temporal aspects of space- or habitat use, apart from down-weighting the importance of points which were less than 24 hours apart in order to minimize spatial autocorrelation. Incorporating time in these past analyses was partly hampered by irregular sampling intervals, differences in sampling intervals, und missing data (Kaczensky et al., 2011). However, in June 2013, three Przewalski's horses from three different social groups were equipped with a new generation of GPS-Iridium collars, which collected GPS locations at hourly intervals for almost 2 years, thus allowing for new analysis approach.

In the past, temporal aspects have often been incorporated by using a priori defined and potentially arbitrary (from the perspective of the animal) time periods (e.g. months, seasons). An alternative approach is to look for obvious changes in the movement data (e.g. step length, velocity, density, degree of directionality) and subdivide the data post priory. This second approach allows to potentially identify species- and area specific relevant time periods and important life history stages (e.g. phases of territoriality, dispersal, denning).

A new analysis became recently available with the Time Local Convex Hull (T-LoCoH) toolset (Lyons et al., 2013). The T-LoCoH package for R 'provides functions designed to help the user select and evaluate parameter values appropriate for the species, system, and study question' (Lyons et al., 2013). The algorithm incorporates both the temporal and spatial distance between locations for building non-parametric local hulls (Lyons, 2013). 'By taking hulls, rather than individual points, as samples for analysis, T-LoCoH produces areas of high use, so called utilization distributions (UDs) with high spatiotemporal fidelity and can differentiate internal space either with a traditional density gradient or alternately various behavioural metrics' (Lyons et al., 2013), e.g. directionality of movement, average speed, revisitation or duration. Such time-use properties can be important delineators for different types of resources and were able to identify waterhole use and temporal territoriality in a springbok *Antidorcas marsupialis* dataset from Namibia (Lyons et al., 2013). The geometry of the hulls further allowed identifying time consistent movement corridors and directionality of movement for springbok (Lyons et al., 2013) or illustrated foraging trips of leopard seals *Hydrurga leptonyx* in Antarctica (Krause et al., 2015). Basically, the algorithm allows a lot of flexibility for data exploration, can be run in program R, and is compatible with GIS for additional or further spatial analysis. 'This flexibility places T-LoCoH in a growing family of methods responding to the demand for more questionbased home range methods' (Lyons et al., 2013).

The goal of this Master thesis is to explore space-time characteristics of Przewalski's hores movement in the Great Gobi B SPA, using high-resolution GPS data collected over a period of 21-23 months from three different individuals representing three social groups.

The main aims within the scope of this thesis were:

(1) To identify areas which likely constitute important time-specific habitat for each group:

- (1.1) Do all individuals use all parts of their range equally throughout the year or can time-specific differences be identified?
- (1.2) If so, what periods can be identified and do they relate to any known climatic or biological parameters?

(2) To identify areas which likely constitute different resources based on revisitation rate and duration of stay for each group:

- (2.1) Does differentiation into important seasonal resources (e.g. “winter range”) and year-long resources (water points) occur?
- (2.2) If so, where are these areas and how are they characterized?

(3) To identify potential movement corridors used by each group:

- (3.1) Are there distinct movement corridors?
- (3.2) If so, where are these areas and how can they be characterized?

(4) To reveal common patterns among the three groups:

- (4.1) Do the groups exhibit similar spatiotemporal patterns?
- (4.2) Are certain habitat types underlying specific time-space use types and do sympatric groups utilize the same corridors and time-space use types (e.g. water holes, “winter range”)?

2 METHODS

2.1 STUDY AREA

The Great Gobi B SPA was established in 1975 and includes approximately 9000 km² of desert steppes and semi-deserts. The climate is continental and highly seasonal with long cold winters and short, hot summers at average monthly temperatures ranging from 14 to 19°C in summer (May–September) and 4 to −20°C in winter (October–April). Average annual rainfall is 96 mm peaking during summer and snow cover lasts for an average of 97 days (Kaczensky et al., 2008). The area is generally considered to follow a non-equilibrium dynamics as biomass production, and as a consequence, ungulate population fluctuations are driven by the amount and timing of rainfall events (von Wehrden and Wesche, 2007).

Plains dominate the east of the park, while rolling hills constitute its western portion. Except for more accessible areas at the international border, the park is not encompassed or sectioned by fences. Open water sources are sparse but if multiple springs occur together they are often inundated by periodic swamps and form oases. Human presence within the SPA is insignificant, especially during summer and winter. For more detailed information and features regarding the Great Gobi B SPA please refer to Kaczensky et al. (2007 and 2008) and Zhirnov and Ilyirsky (1986).

2.2 STUDY SPECIES

The species forms stable harem groups, exhibits non-exclusive home ranges and selects strongest for the most productive habitat types in the B SPA, which are typically associated with watercourses and oasis (Kaczensky et al., 2008). Przewalski's horses seem to drink at least once per day, preferably in the early morning or the late afternoon (Ganbaatar, 2003; Zhang et al., 2015). Their mean distance to nearest water source in the B SPA was estimated to be approximately 9 km and revealed reduced mean distance to the nearest water source during the summer months (Kaczensky et al., 2008). Group size and sex are ignored in this study, since behaviour – especially foraging and resting - of all herd members was shown to be highly synchronized (Boyd 1988; Boyd 1998; Souris et al., 2007; van Dierendonck et al., 1996).

April is the time when mares are starting to give birth, which leads to stallions chasing out older offspring and harems to move a lot (Ganbaatar, pers. comm.). Foals are more vulnerable to wolf predation than adults, especially when foals are small (Kaczensky, pers. comm.). Birth rate is highest in May and oestrus/breeding time last from June to August. The most recently released harems, including the Erkhes harem, receive hay as supplementary forage during the harshest periods of winter (e.g. the Erkhes harem was fed in Janurary, February and March at Chonin Us since January 2014; Ganbaatar, pers. comm.).

The Erkhes harem and the Bachelor West group were both consisted of animals recently translocated to the B SPA, whereas the Bundan harem primarily consisted of animals born in the area (Table 1). The Erkhes harem consisted of five individuals including the collared mare 7215 (Boroo), Bundan harem consisted of 25 individuals including the collared mare 7209 (Khatan), and the isolated Bachelor West group consisted of seven individuals including collared stallion 6092 (Oidov; Ganbaatar 2014).

2.3 DATA ANALYSIS

Animals were equipped with GPS-Iridium collars (VECTRONIC Aerospace, Berlin, Germany) programmed to obtain one GPS fix every hour over a two year period from June 2013 to May 215 (Table 1, Figure1). These locations were transmitted via the Iridium satellite phone connection every 10-20 hours. The estimated lifespan of these collars was two years and for animal welfare reasons and to allow collar retrieval, all collars were equipped with pre-programmed drop-off devices (CR-2a, Telonics). Due to its death, the monitoring period of animal 6092 of the Bachelor West group was slightly shorter and already ended at end of March 2015 (Table 1).

MCP size was shown to be independent from the length of the monitoring period, sex and sensor type (Kaczensky et al., 2008). Two subsets of locations per individual were generated to allow comparison of metrics between years and to detect shifts in range or other space-time use behaviour (Table 1). High fix success rate (FSR) was achieved due to high performance of GPS Iridium Satellite Collars and exposition on a large mammal species roaming in an open habitat lacking canopy.

Name	ID	Sex	Born	Origin	Monitoring period		N	1st year	01.06.2014	FSR [%]	Group	Capture location	Fate
					from	to		31.05.2014	2nd year				
Boroo	7215	f	08.06.2008	Doebritzer Heide, Germany	07.06.2013	01.05.2015	16,535	8519	8013	99.4	Erkhes	enclosure	collar dropped
Khatan	7209	f	21.05.2006	Gobi, Mongolia	08.06.2013	01.05.2015	16,580	8547	8030	99.8	Bundan/Bars	near Shirin Us	collar dropped
Oidov	6092	m	07.09.2006	Jimsar, China	10.06.2013	26.03.2015	15,021	8494	6518	95.7	Bachelor West	near Takhi Us	died
							Sum	48,136					

Table 1. *Individual information of all three individuals, including the total number of locations (N) collected during the entire monitoring period (and its annual subsets as well as Fix Success Rate (FRS). First year's data of was collected from respective starts of monitoring until 31.05.2014; "second year" lasts from 01.06.2016 until the end of respective monitoring periods.*

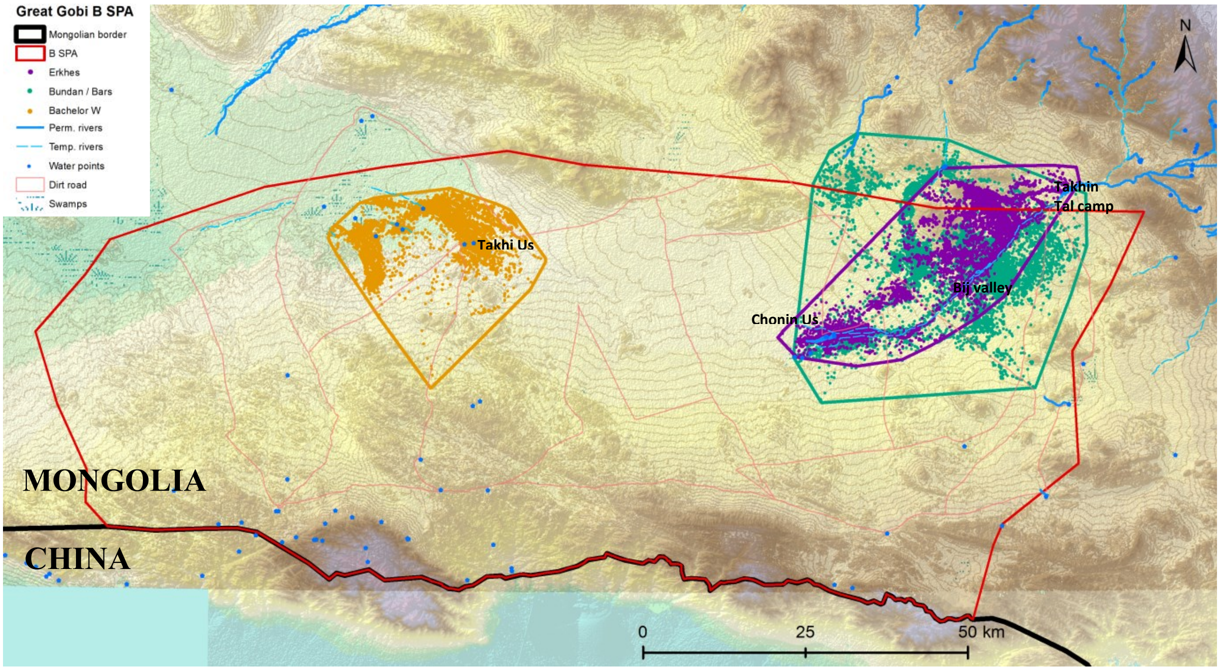


Figure 1. *Overview of group distribution in the B SPA (red frame) in SW Mongolia bordering China (black frame). 6092/Bachelor W (yellow) at Takhi Us, sympatric 7215/Erkhes (purple) and 7209/Bundan/Bars (green) around Chonin Us; 100% MCP's indicated in frames of respective colour.*

Following a tutorial provided by Lyons (2013), the T-LoCoH (version 1.40.00) package for R (version 3.2.3, 2015-12-10) was applied to each Przwalski's horse GPS data set (including yearly subsets, Table 1, Table 2) and reviewed to ensure even time-sampling interval of locations. Duplicate points were off-set by 1 meter to avoid bias. T-LoCoH map locations were plotted in a Universal Transverse Mercator (UTM) zone 46N projection. In reference to elucidating 24h-foraging patterns, s-values were determined via the 'lxy.plot.sfinder'-function. They vary between individuals and subsets as they are constituted by the time term being approximately equal to the distance term of the time-scaled distance (TSD) metric (Lyons, 2015, Table 2, Fig. A1).

7215 - Erkhes - Boroo	s	k	a
all	0.0115455	40	30,000
1st year	0.0097422	40	30,000
2nd year	0.0144868	40	30,000
7209 - Bundan/Bars - Khatan			
all	0.0085370	40	30,000
1st year	0.0081996	40	30,000
2nd year	0.0148675	40	30,000
6092 - Bachelor W - Oidov			
all	0.0068686	35	25,000
1st year	0.0072932	35	25,000
2nd year	0.0073868	35	25,000

Table 2. *Selected values of s, k and a determined for each individual's dataset and respective subsets.*

Subsequently, hulls were created which are essentially minimum convex polygons (MCPs) constructed around a number of locations defined by different algorithms “fixed-a-method” and “fixed-k-method”. The values of “a” and “k” were determined by minimizing “spurious holes” in the UDs (for each individual and their subsets) with remaining holes primarily excluding unsuitable habitat features or larger areas obviously not used by the animals.
Sorting the hulls by point density produced colour-coded UDs reflecting the overall frequency of occurrence (Lyons et al., 2013, Table 3, e.g. Fig. 2). Analogically, sorting hulls by eccentricity produced elongation distributions (Krause et al., 2015) reflecting movement corrridors. Resulting isopleths were visualized by a decreasing five-level colour scale (0.1, 0.25, 0.5, 0.75, 0.95) ranging from red (i.e. 0.1, likely highest intensity of use or greatest elongation) to light blue (i.e. 0.95, less heavily utilized regions or little directionality). To illustrate directionality of movement at a more explicit scale, the hulls were sorted by their elongation to extract ‘directional routes’ by connecting temporally contiguous hull parent points of the top 15% of hull elongation.
For creating the hulls the “fixed-a-method” algorithm was used to obtain elongation, whereas the “fixed-k-method” was to obtain UDs and for further examination of other time-use metrics.
To compute the time-use metrics of revisitation (nsv) and average visit duration (mnlv), an inter-visit gap period (IVG) of ≥21 hours was defined to examine 24-hour foraging patterns under the assumption that horses need to drink at least once a day. This IVG value was used consistently for all three individuals. To explore the relationships among the distribution of hulls in time-use space, hull scatter plots (hsp) of hull revisitiation and were produced. Manually defined and colour-coded regions of interest in the hsp space could then be used to visualize hull parent points of matching colours in space as well as in date-hour scatterplots (Lyons et al., 2013). For detailed terminology of metrics, fucntions and parameters used in T-LoCoH please refer to the Glossary in Appendix I of Lyons (2013).
Graphic T-LoCoH outputs (i.e. isopleths, directional routes, manually defined hsp-regions) of all individuals and respective subsets were exported into ArcMap and Google Earth (images from 04.10.2013) to examine metrics spatially more explicit and for subsequent analysis of habitat use. For data analysis digitized rivers, springs and elevation from Russian 1:100,000 topographic maps were imported into ArcMap 10.1 (ESRI, Environmental Systems Research Institute, Inc., Redlands, California, USA) with the Spatial Analyst extensions. Permanent rivers and permanent water points were combined to water points in a more general sense.

Rangers provided GPS locations of supplementary feeding sites from January and February 2015.

Main plant communities within the wild equid range were ranked by their estimated productivity following methods described in Kaczensky et al. (2008): Riparian vegetation > *Nitraria s.* > *Stipa* grassland > *Nanophyton e.* > *Caragana l.* > *Reaumuria s.* and *Anabasis b.* > *Haloxylon a.* (Kaczensky et al., 2008). Vegetation were subsequently clipped with the the 100% minimum convex polygon (MCP) and UD's for levels 95%, 75%, 50%, 25%, and 10% and the elongation utilization isopleths at levels 95%, 75%, 50%, and 25% to check for possible selection based on the intensity of use or movement.

3 RESULTS

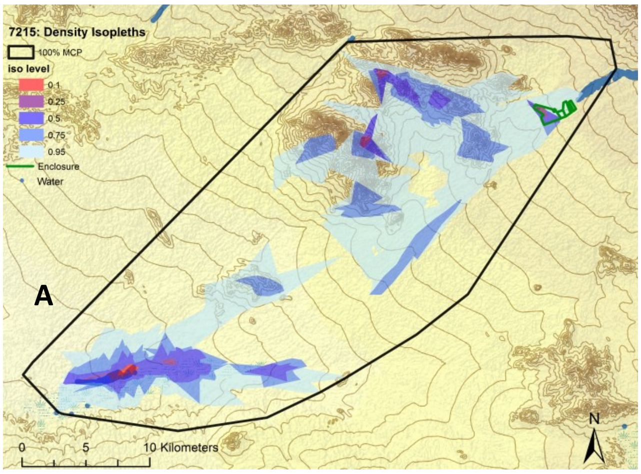
3.1 Area size and distribution of high intensity use areas

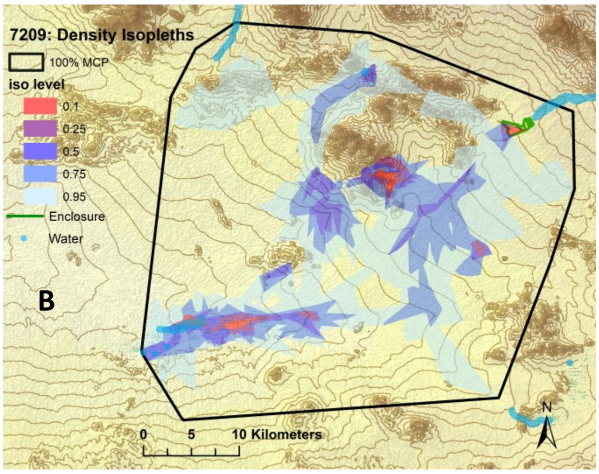
Sizes of 95% UD isopleths ranged between 149 to 628 km² over the entire monitoring period. 95% UDs of the two harems decrease in their second year of monitoring, whereas the UD of *Bachelor West group* increased (Table 3). UD isopleth sizes over the entire monitoring period as well as over the annual periods rapidly decreased from 95% to 10% and values at 50% and 25% suggest that annual core areas are in the range of only a few to several tenths of square kilometres (Table 2).

	7215 (Erkhes)			7209 (Bundan / Bars)			6092 (Bachelor W)		
	all	1st yr	2nd yr	all	1st yr	2nd yr	all	1st yr	2nd yr
100% MCP	761.51	714.1	614.01	1516.27	1481.70	866.6	610.92	367.06	601.08
95% iso	296.46	309.44	189.90	628.10	511.06	404.69	149.12	90.33	131.43
75% iso	93.96	67.06	75.63	222.53	194.56	149.15	40.86	28.01	37.91
50% iso	31.03	17.07	21.66	73.85	46.22	56.63	8.39	7.77	6.00
25% iso	3.72	1.81	3.46	21.84	12.18	22.39	1.31	1.45	0.70
10% iso	0.64	0.49	1.04	6.12	3.02	8.19	0.12	0.66	0.12

Table 3. *Home range defined as the MCP of 100% of locations of each individual for their entire monitoring period and their yearly subsets. Intensities of use (UDs) are raked lowest (95% iso-level) to highest (10% iso-levels).*

Core areas were not continuous, but identified several discrete clusters for all three groups (Fig. 2A-C).





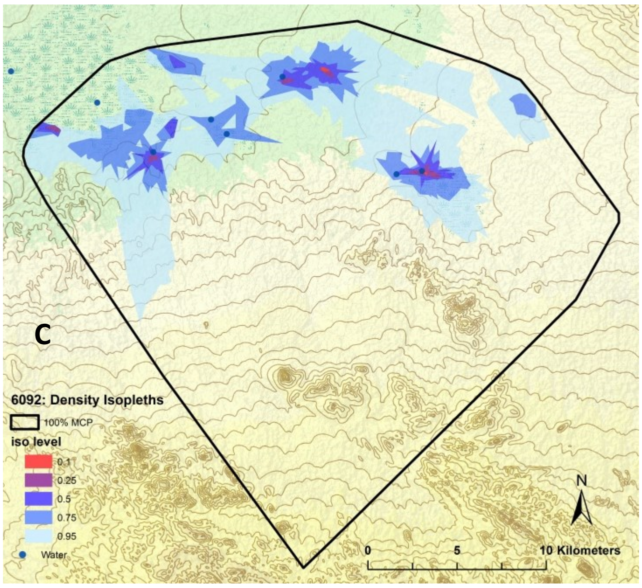


Figure 2. *Density isopleths generated with the 'fixed-k-method' over the whole period of monitoring for (A) the Erkhes harem (7215, k=40,* s=0.0115455*), (B) the Bundan/Bars harem (7209, k=40, s=0.0085370), and the Bachelor group West (6092,k=35, s=0.0068686), sorted by decreasing intensity of use.*

Two areas in the northern portion of 7215's range received high iso-levels of 0.25 (Fig. 10). Both areas also exhibit clusters of high directional movement. No resource (i.e. water or pasture) of known importance occurs at either region. The majority of underlying locations are from October/November 2013 and March 2014, which is similar to 7209's behaviour in a similar region nearby (Fig. 8). Thus, we can only suspect similar behaviour underlying this pattern. The oasis at Chonin Us clearly receives the highest intensity of use being the only area highlighted at iso-level 0.1.

7215 also makes strong use of a hill northeast of Chonin Us (below X-UTM 530000 and UTMY 5030000) throughout the year and only for short periods (see regions plot of 7215's 2nd year) of time (Fig. 2A).

Water points and oasis (i.e. Chonin Us and Takhi Us) generally receive highest intensity of use, which can be well illustrated via density isopleths (Fig. 2A-C). The western portion of 6092's (Bachelor West) range receives reduced intensity of use over the course of monitoring (Fig. 2C).

Confined spatial use at high temporal contiguity within the enclosure rightly caused high iso-levels for both sympatric individuals (Fig. 2A,B). Moreover, coves within high mountain areas seem to be of a certain attraction for both groups in the east. These regions are characterised with high intensity of use, moderate to high duration but minimal revisitation and striking patterns for directional routes (Fig. 8). 7209's (Bundan/Bars harem) density isopleths of year one and two overlap in a cove west of Takhi Tal camp. Date and hour-of-day plots of respective time-use revealed that 7209 spent five consecutive days in this area during April 2015. These areas do not hold any known resources highly selected for (i.e. most productive vegetation communities or water points).

3.2. Time specific differences in range use

3.2.1. Areas used

Sequentially color-coding of locations already indicated seasonal differences in range use in the annual subsets (Fig. 3A-C).

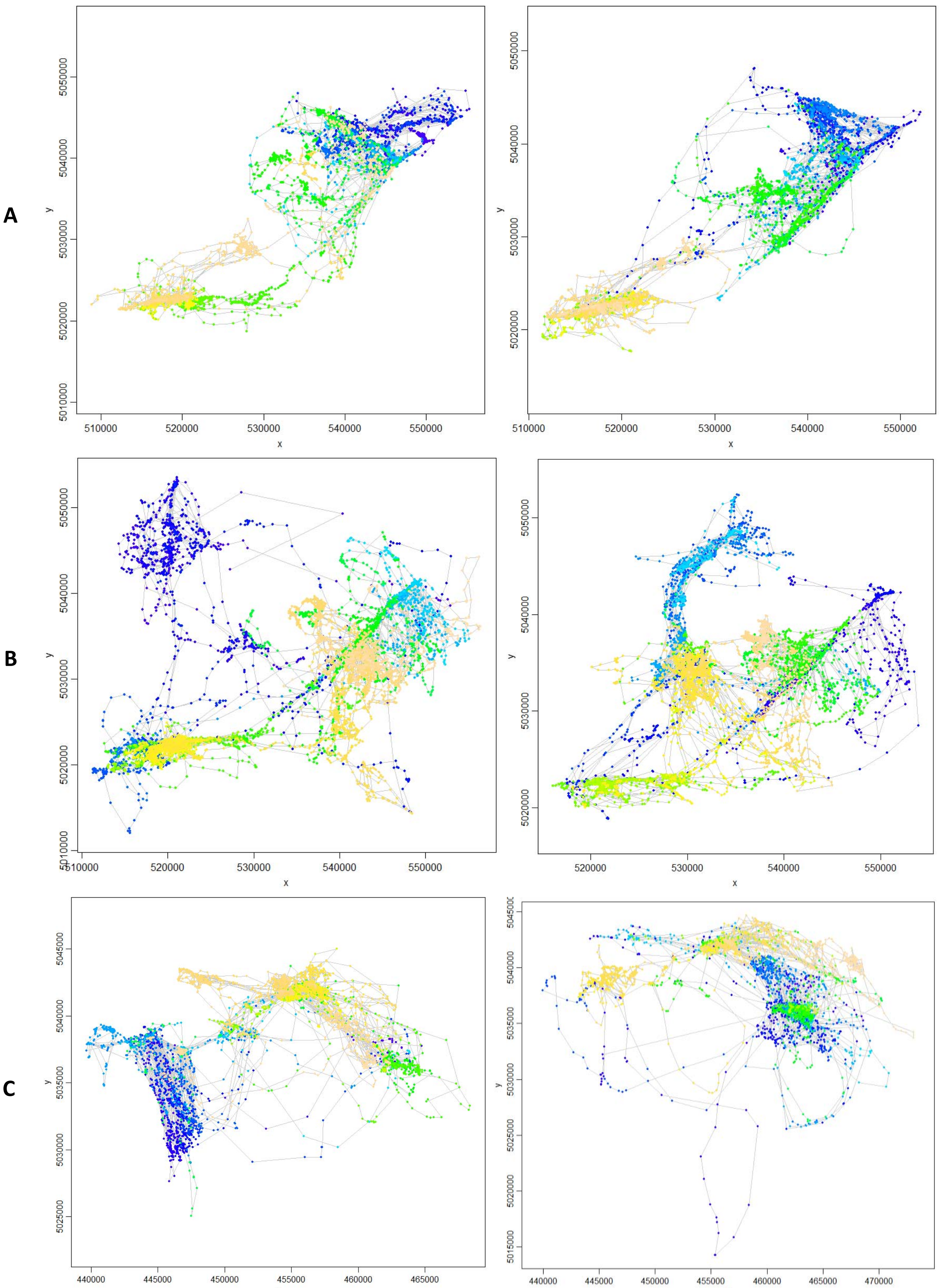


Figure 3. *Colour-coded temporally contiguous locations of all three individuals yearly subsets (see Table 1) with year one of monitoring on then left and year two on the right. (A) Erkhes harem (7215), (B) Bundan/Bars harem (7209), and (C) the Bachelor West group (6092).*

They highlight excursions (e.g. in 6092's 2nd year of monitoring, e.g. Fig. 3C) or areas that have only been visited once (i.e. the NW corner of 7209's range, Fig. 3B). Subsetting this plot generates less convoluted overviews but also potential range shifts or, as in the case of 7215, reveals a more conservative use of the habitat (Fig. 3A). Interestingly, this individual exhibits a more condensed use of space, avoidance of a central portion in its range and no direct travel from the river bed towards Chonin Us in the SW in its second year compared to its first year (turquoise to orange).

3.2.2. Internal space use parameters

Average speed ($m*s^{-1}$) is the time-use metric revealing the most striking patterns over any time axis, even at the 24-hour level. It is constituted from considering the average speed of all (space- and time-selected) enclosed points within a hull and serves as a proxy of velocity. All individuals reduce their average travel speed rather condensed during winter and travel faster during the summer months, with values peaking in June/July (Fig. 4A-C).

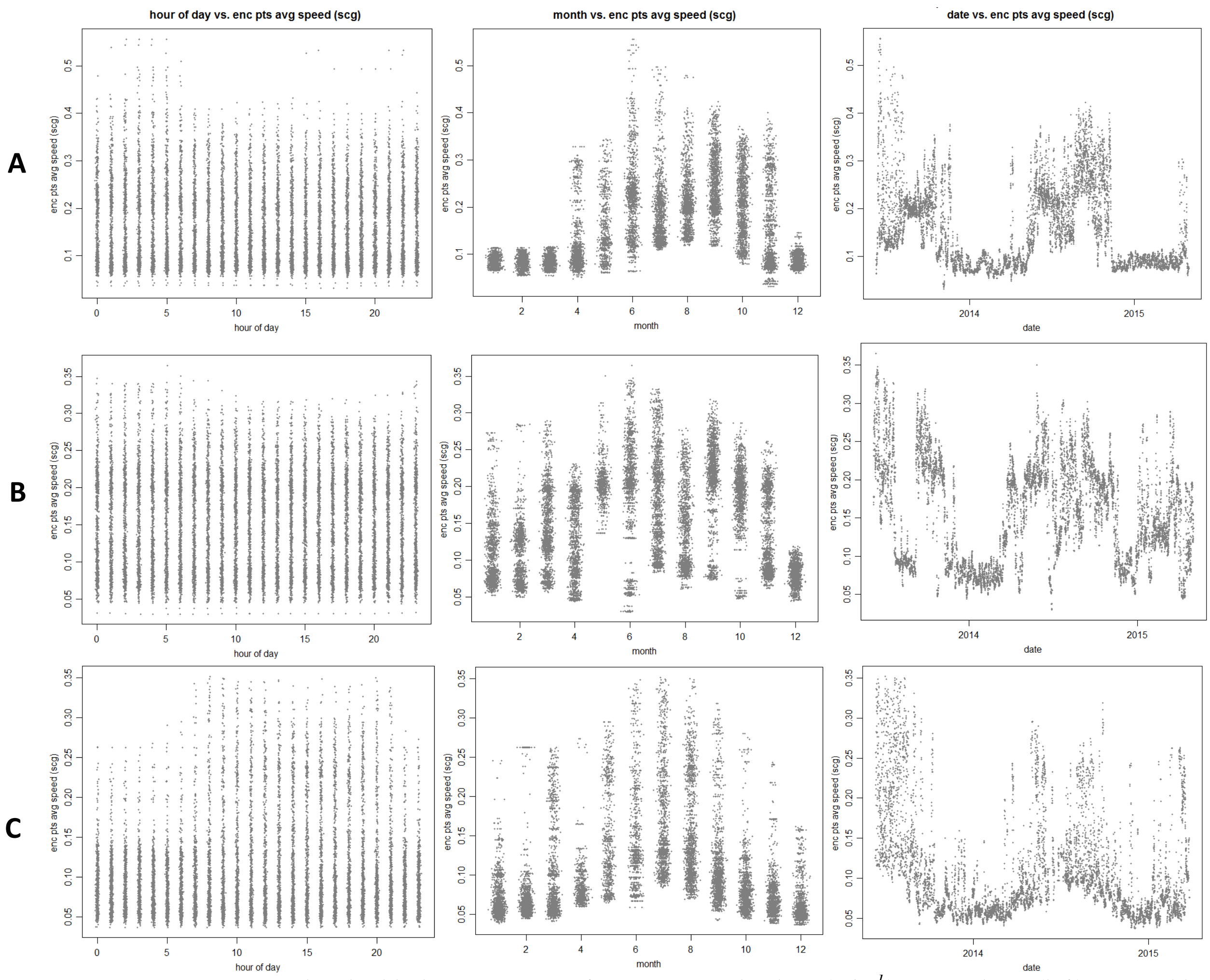
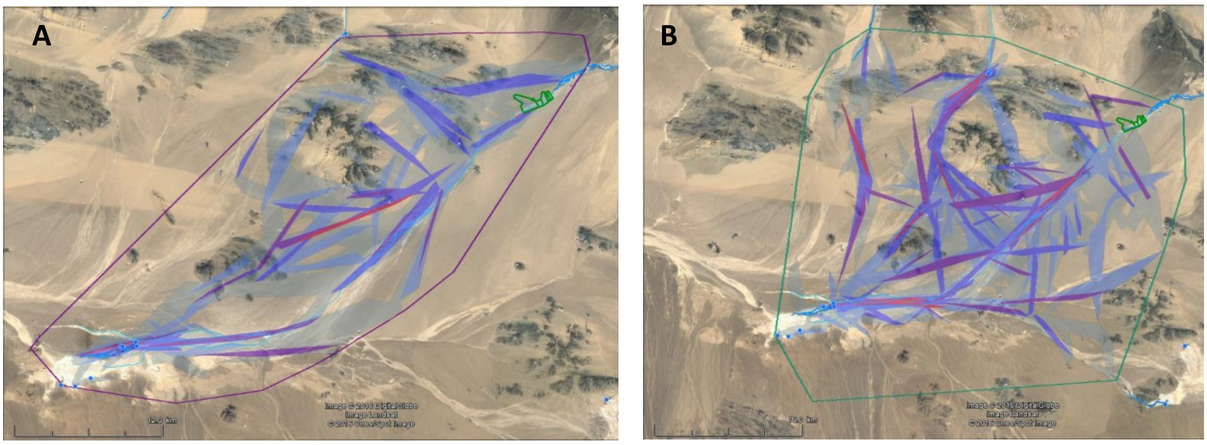


Figure 4. *Auto-scatter-plots highlighting patterns of average speed values ($m*s^{-1}$) at a 24 hour (left), a monthly (middle) and an annual (left) resolution for all three individuals/groups. (A) the Erkhes harem (7215, k=40, s=0.0115455), (B) the Bundan/Bars harem (7209, k=40, s=0.0085370), and the Bachelor group West (6092, k=0.0068686). Each point represents a hull. On the x-axis is date of the parent point. On the y-axis is average 'coming and going speed' (t-1 to t+1) of each point enclosed by the hull.*

No individual exhibits this pattern more clearly than 7215, which appears to drastically cease faster states of travelling between December and March. June clearly marks the month where average speed reaches its peak and also exhibits largest variation. 6092 exhibits elevated average speed during daylight hours (07:00 to 21:00). Contrary, 7215 slightly increases average speed at night, whereas 7209 exhibits this pattern to a lesser extent.

3.3. Directional movements

Main movement direction and important time-space use of corridors can be illustrated well for all three groups. Corridors could be identified between water points, around demanding topographical features as well as on plains and in river valleys (Fig. 5A-C).



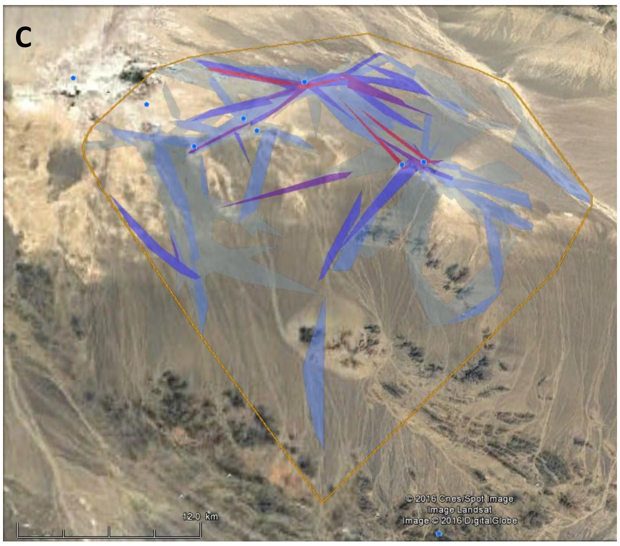


Figure 5. *Elongation distribution map over the whole period of monitoring for all three individuals/groups. Hulls were created using the 'fixed-a-method'. (A) The Erkhes harem (7215, a=30,000, s=0.0115455), (B) the Bundan/Bars harem (7209, a=30,000, s=0.0085370), and (C) the Bachelor West group (6092, a=25,000, s=0.0068686). Isopleths are sorted by descending elongation (ecc) on a Google Earth image.*

Water sources in the northern portion of Bundan/Bars harem's range resulted in and high iso-levels toward those (Fig. 5B). Moreover, the Bij river valley, Chonin Us and extended areas in the southeastern portion of its range received elevated elongation. Dried out river beds, especially the Bij valley for the sympatric groups, generally receive high elongation distribution, which become especially evident when isopleths are exported into Google Earth

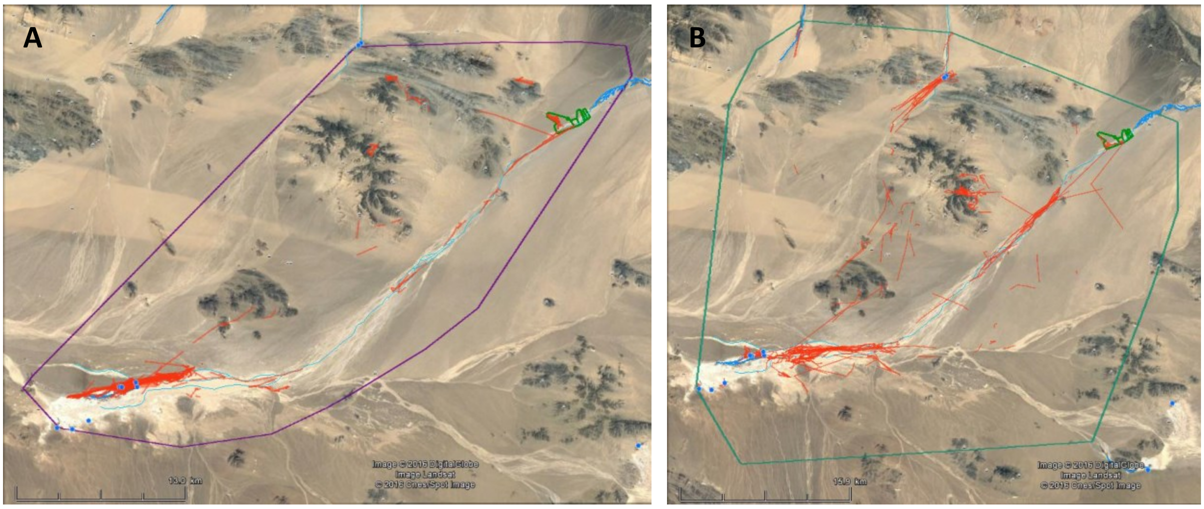
(Fig. 5A,B). The most striking behaviour 7209 exhibits regarding elongation distribution is its directional movement occuring around the central mountainous area. Thus, four main corridors can be identified for 7209: (1) horizontal movement east of Chonin Us, (2) the Bij river valley, (3) the southwestern circumvention of the mountain, and (4) a longitudinal movement from Chonin Us towards northern pastures and water sources.

Similar to 7209, 7215 utilizes the Bij river valley for highly directional movements. Also, horizontal movement at the latitude of Chonin Us and high elongation of hulls around the central high mountains is similar (and evident when hulls of both individuals are overlapped (Fig. 14B)). However, 7215 exhibits highly directional back and forth movement at Chonin Us, especially west of the oasis, which 7209 did not do. The entire mountainous area is encompassed with directional movement. Moreover, a clear shift and condensed use towards a northern traverse to get from Bij to Chonin Us is evident.

3.4. Directional routes

Another behavioural metric turns out to be a valuable tool for the detection of spatially concentrated important resources (such as water points, supplementary feeding sites), structures unrelated to resources (such as corridors or the enclosure), and most directional continuous movement patterns: directional routes, illustrating the top 15% of hull elongation (Fig. 6A-C).

Water sources in the northern portion of 7209's (Bundan/Bars harem) range resulted in directional routes (Fig. 6B). Water points within 6092's (Bachelor West group) range as well as southwest of 7209's (range are highlighted as criss-cross clusters of directional routes (Fig. 6B,C).



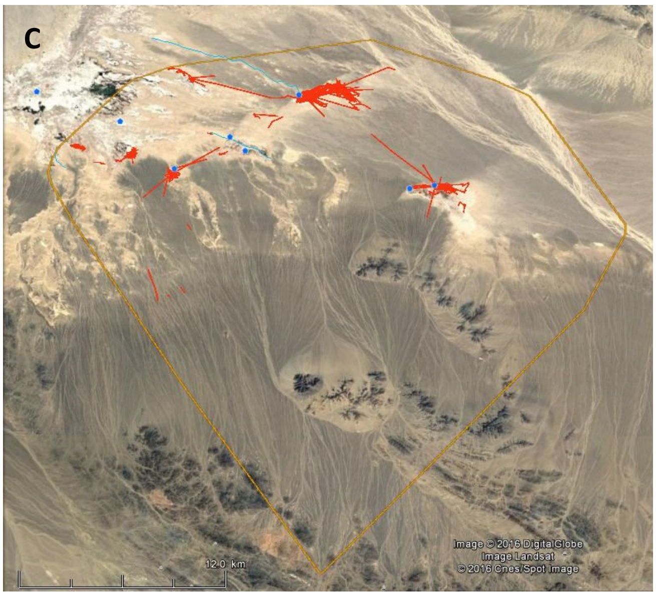


Figure 6. *Directional routes over the whole period of monitoring for all three individuals/groups. Generated from temporally contiguous hull parent points of the top 15% of hull elongation using the 'fixed-a-method'. (A) The Erkhes harem (7215, a=30,000, s=0.0115455), (B) the Bundan/Bars harem (7209, a=30,000, s=0.0085370), and (C) the Bachelor West group (6092, a=25,000, s=0.0068686).*

Moreover, directional routes of 7215's (Erkhes harem) second year of monitoring exactly match known feeding sites northeast of the oasis (Chonin Us) exhibit angles outside the wet area could be successfully identified for 7215 (Fig. 7). The Erkhes harem was the only one targeted with supplementary winter forage.

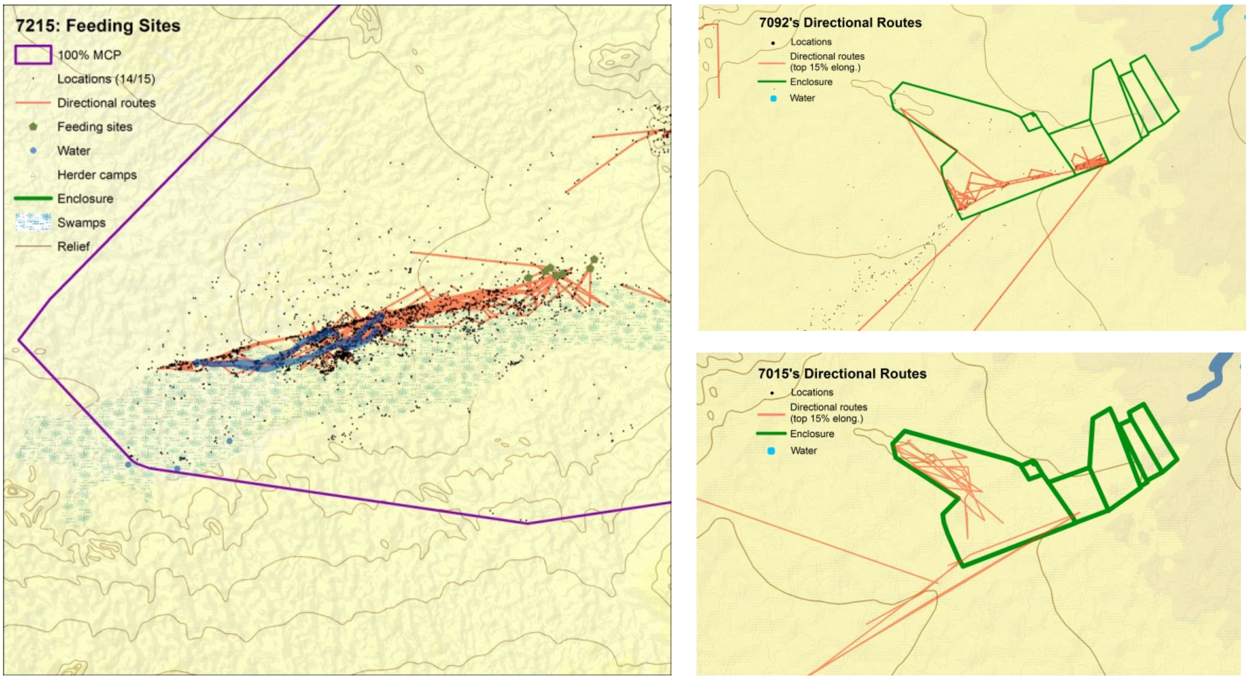


Figure 7. *Left: Detail of Chonin Us including 7215's (Erkhes harem) locations of the second year of monitoring (2014/15), feeding sites (olive points), and directional routes (top 15% of hull elongation, a=30,000) in red. Right: Enclosure (green frame) and directional routes within for sympatric groups (7209 and 7215).*

Additionally, this metric could demark boundaries well and was the tool that elucidated a second (voluntary) visit of this structure by 7215 best after its application to yearly subsets.

Coves within high mountain areas seem to be of a certain attraction for both groups in the east. These regions are characterised with high intensity of use, moderate to high duration but minimal revisitation and striking patterns for directional routes (Fig. 8). 7209 (Bundan/Bars harem) density isopleths of year one and two overlap in a cove west of Takhi Tal camp. Date and hour-of-day plots of respective time-use revealed that 7209 spent five consecutive days in this area during April 2015. These areas do not hold any known resources highly selected for (i.e. most productive vegetation communities or water points).

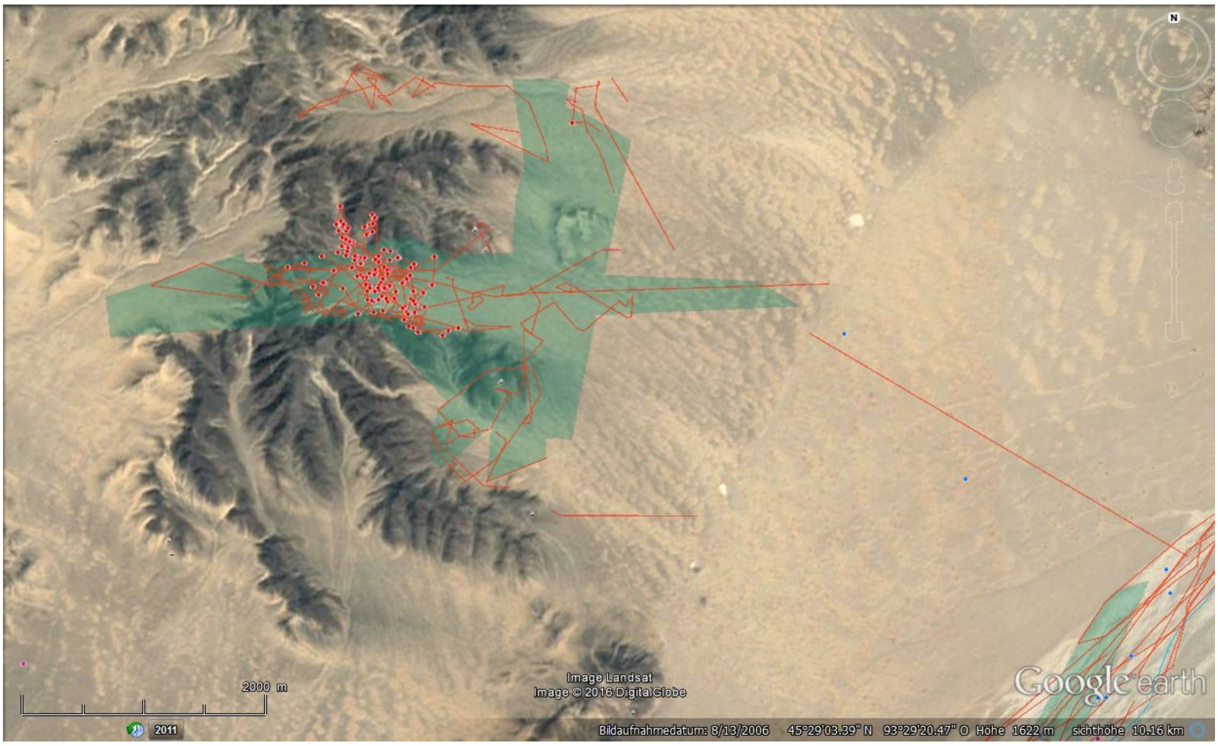


Figure 8. *Overlap of 7209's (Bundan Bars harem) first and second year's density isopleths (at iso-level 0.5 in green, k=40, s=0. 0081996) are overlaid with red lines highlighting confined directional routes (a=30,000) within a high mountain cove west of Takhi Tal camp. Locations (red points) of manually selected regions from the hsp from the second year of monitoring (k=40, s0.0081996), illustrating moderate to high duration at minimal revisitation rate during April 2015.*

3.5. Habitat characteristics of high use intensity areas versus movement corridors

Assigning raster values of vegetation communities to random and actual locations of the entire and subsetted dataset reveals a rather conservative utilization of those. Neither composition of vegetation community nor utilization patterns change much over yearly subsets, even if the individuals experience a range shift (Fig. 9).

Important year-long resources were identified via UD-overlaps of the first and second year of monitoring (Fig. 10) and of overlaps of UD's of sympatric individuals (Fig. 11).

Caragana l. and *Nanophython e.* communities were pooled in the Bachelor group West's range due to negligible availability and utilization trends. Both communities are present and cause utilization trends in the range of sympatric harems in the east. Clipping polygons with underlying vegetation communities revealed that *Haloxylon a.* and *Stipa* grassland constitute the major fractions of vegetation communities within the range (100% MCP) of the Bachelor group, suggesting highest availbability (Fig. 10).

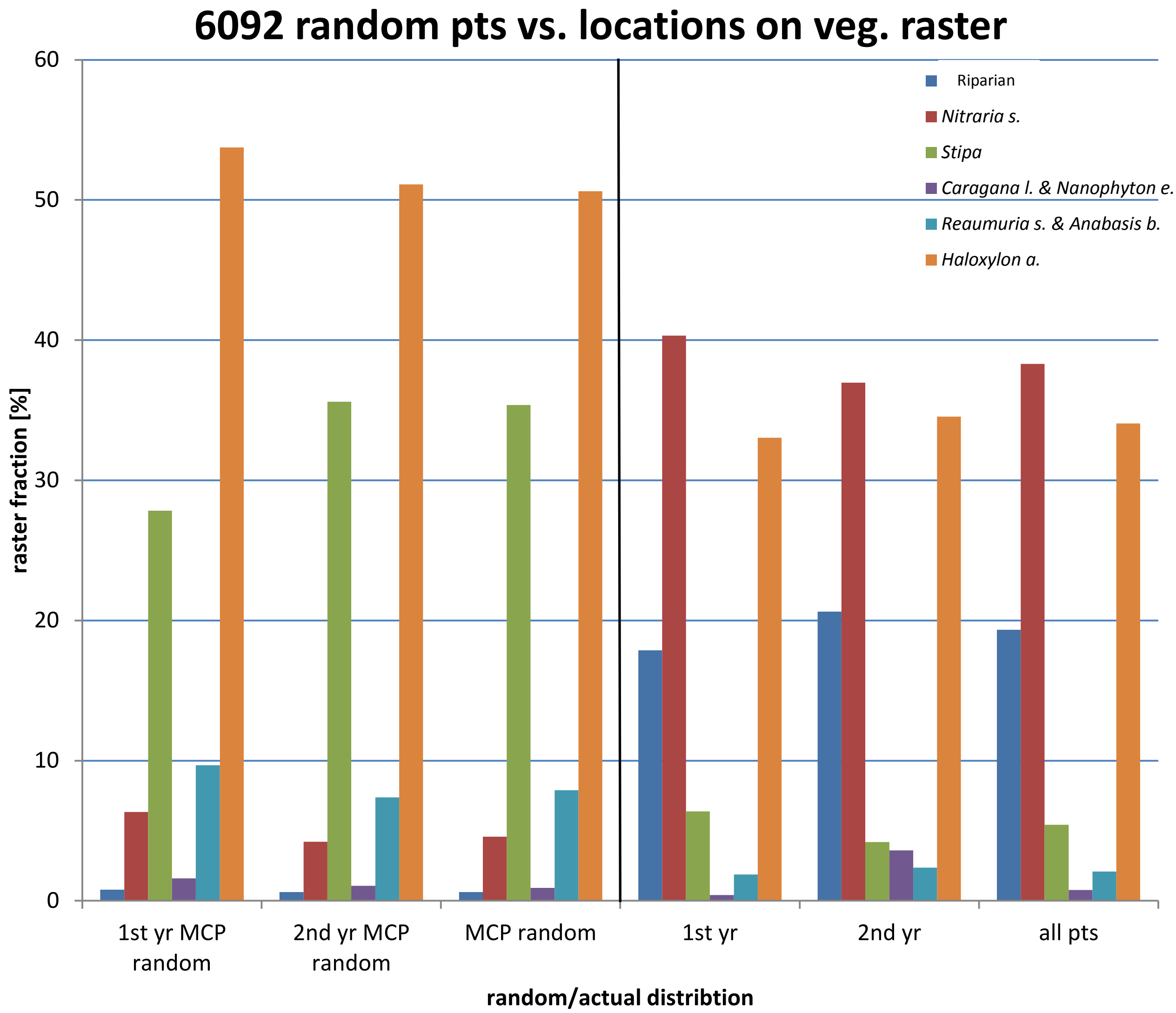


Figure 9. *Random distribution of the number of locations per yearly subset and the entire monitoring period across 6092's range (100% MCP) and its underlying vegetation communities (left). Actual locations in their annual subsets and entire monitoring period (right). Caragna l. and Nanophyton e. were pooled due to their underrepresented portion within 6092's range and lack of obvious utilization trends.*

The higher the intensity of use, the higher the proportion of the two most productive habitat types *Riparian* and *Nitraria*. Quite contrary, the composition of the travel corridors only slightly changes with increasing intensity of use and consists primarily of *Haloxylon* communities.

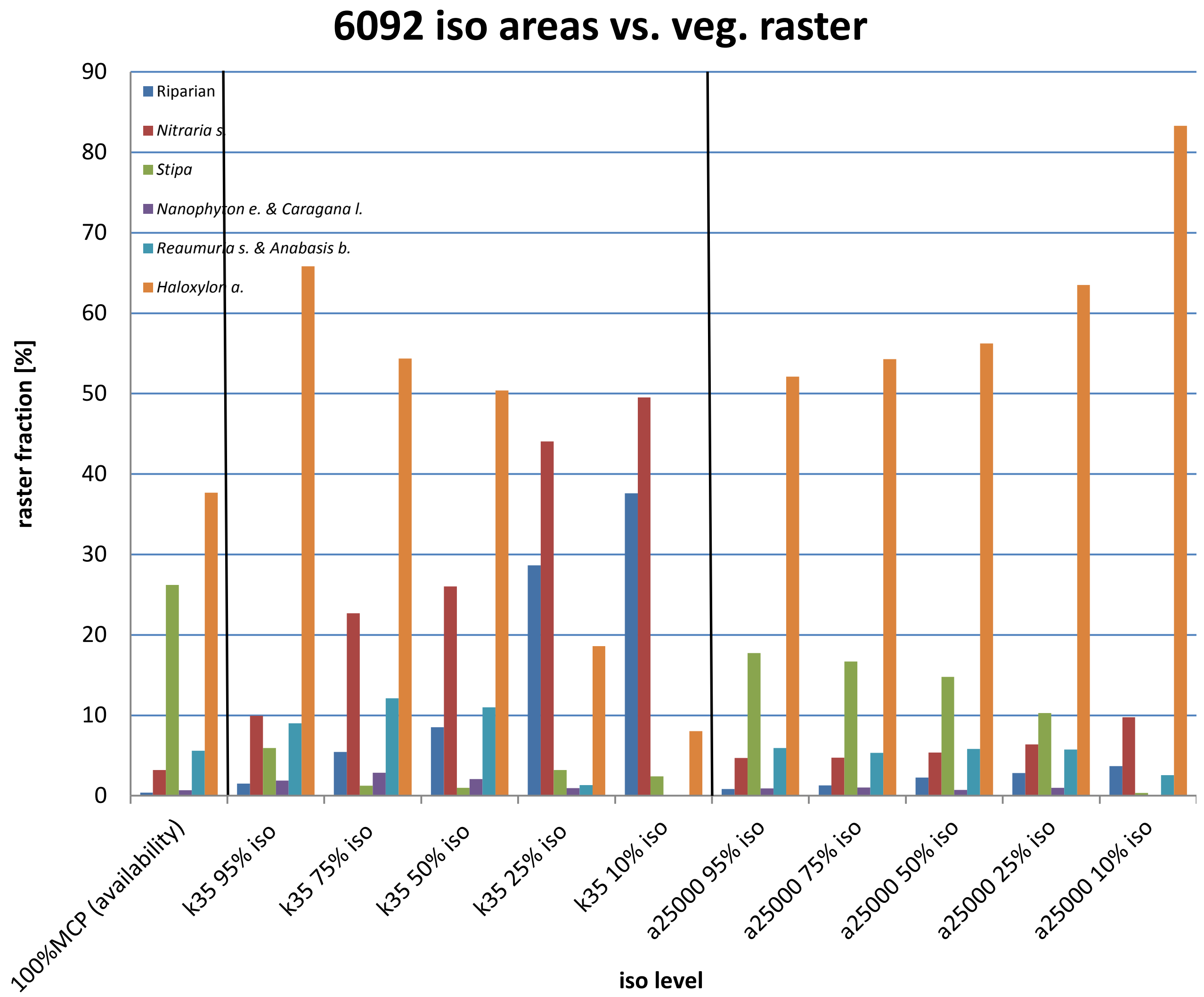


Figure 10. *Overview of 6092's availability of all vegetation communities within its range over the entire monitoring period (100% MCP, far left), followed by its utilization of respective communities with increasing intensity of use at k=40. Right: vegetation communities underlying isopleths with increasing eccentricity-isopleth level at a=30,000 (imperfect measure of directionality of movement).*

The most striking patterns the Bachelor group exhibits regarding the vegetation raster are decreasing fractions of the least productive vegetation community (*Haloxylon a.*) while least available but most productive communities (riparian vegetation and *Nitraria s.*) – associated with water points in this range – constitute major fractions with increasing intensity of use. Contrary, the *Haloxylon a.* community – characterizing desert areas – holds over-proportionally high fractions with increasing directionality of movement. *Stipa* grassland is hardly utilized at any intensity of use (95%-10% iso) and constitutes decreasing portions with increasing levels of elongation for this individual.

Combined ranges (100% MCP) as well as combined utilization and elongation distributions of the sympatric groups in the east exhibit very similar patterns regarding the use of vegetation communities (Fig. 11).

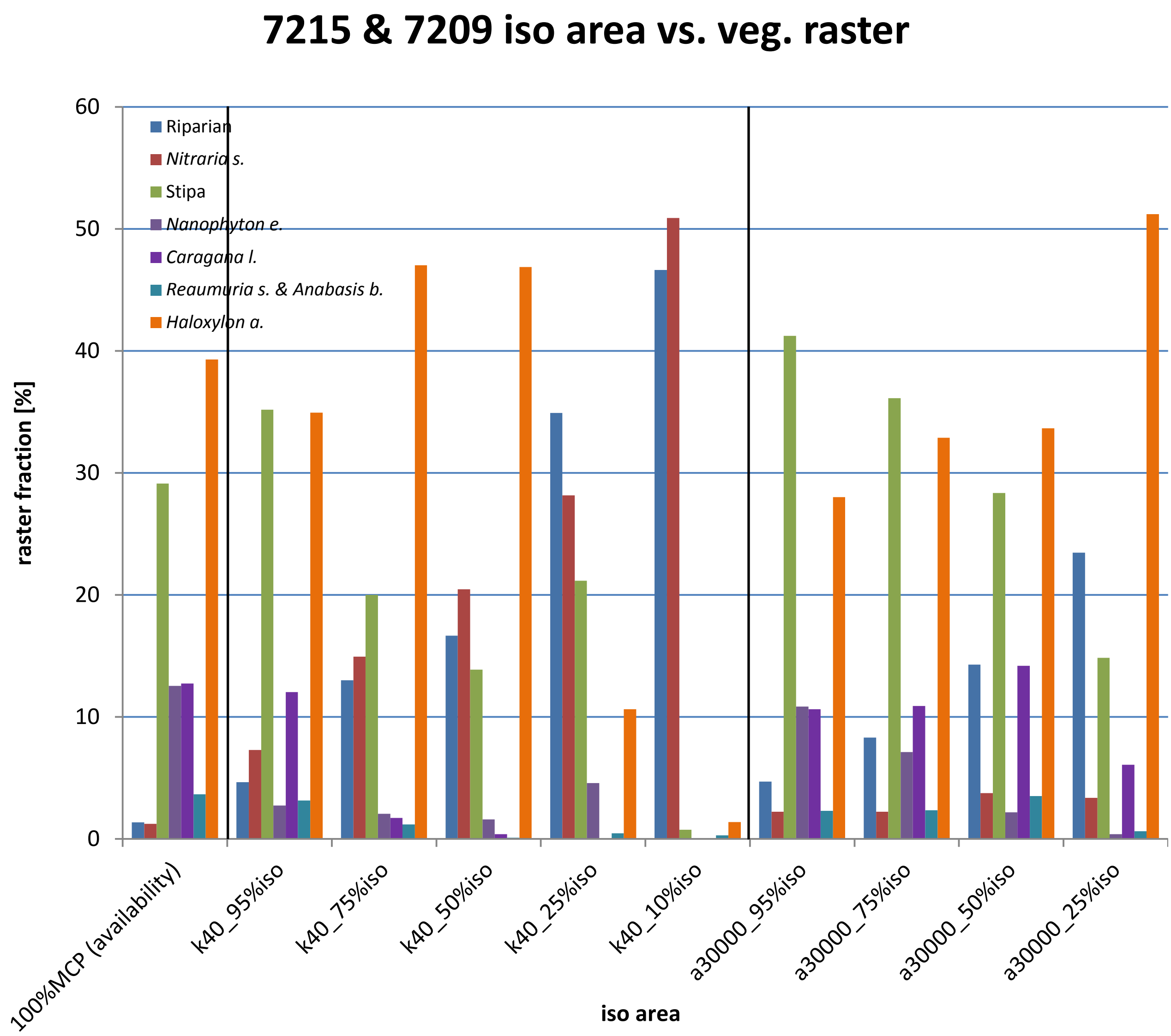


Figure 11. *Overview of 7209's and 7215's availability of all seven vegetation communities (100% MCP, far left) in their combined range, their utilization with increasing intensity of use at k=40, followed by vegetation communities underlying isopleths with increasing eccentricity-isopleth level at a=30,000 (imperfect measure of directionality of movement).*

The least productive plant community (*Haloxylon a.*) is also by far the most dominant in their range, followed by *Stipa* grassland. The most productive communities (riparian vegetation and *Nitraria s.*, constituting 1.36% and 1.23% respectively) are almost equally least available within the 100% MCP of both individuals. *Stipa* grassland receives a deceasing trend of intensity of use overall, whereas riparian vegetation constitutes a major component of the highest iso-levels (for both elongation and intensity of use). However, only with increasing intensity of use (not with increasing directionality of movement) are *Nitraria s.* communities utilized up to over 40-fold their availability within both mare's range. Increasing directionality of movement leads to a decrease in the fraction of *Stipa* grassland and *Nanophyton e.* communities, whereas *Haloxylon a.* communities and riparian vegetation exhibit positive trends at higher levels of elongation.

3.6. Areas frequently revisited or visited for a long duration

Time-use metrics based of revisitation (nsv) and duration (mnlv) could not precisely distinguish important seasonal from year-long resources. Differentiation of resources (i.e. grazing vs. drinking) or behavioural states (e.g. resting vs. moving) could not be determined precisely. Instead, manually defined regions of the most prominent features from the hsp could reveal other interesting time-use behaviour, especially after individual data was subsetted into separate years of monitoring (Fig. A2).

Typically, the hsp of yearly subsets of individuals would constitute a peak of moderate duration at minimal rate of revisitation, one tapering tale of moderate revisitation rates and long durations and a sharp peak of revisitation at minimal duration per visit (Fig. 12). Consequently, regions selected from peak values of nsv and mnlv coincide at oasis, a pattern consistent throughout individuals (e.g. Fig. 12, Fig. A2 and Fig. A3).

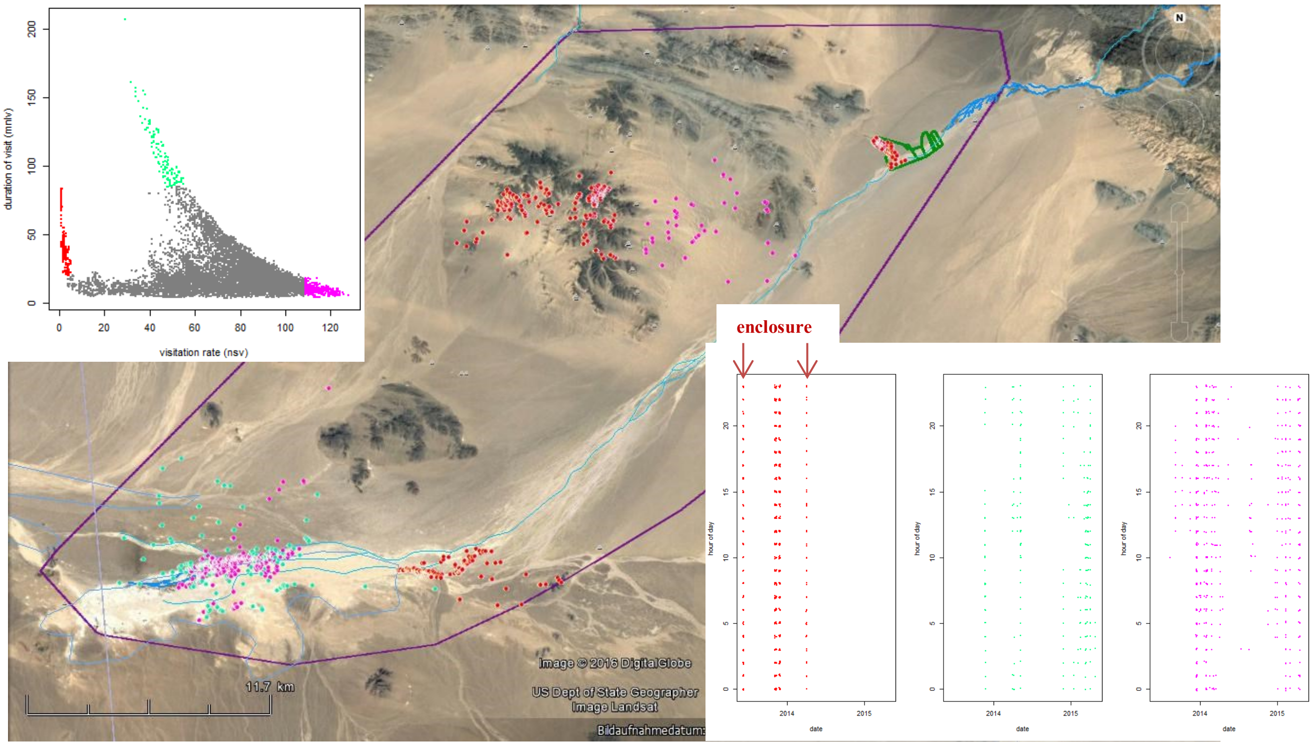


Figure 12. *Colour-coded symbology of manually defined regions from the hsp (nsv vs. mnlv) and respective date and hour-of-day plot drawn from 7215's locations of the entire period of monitoring (k=40*, s=0.01155, *IVG=21). Regions highlighted in red represent areas that are infrequently utilized or search areas. Turquoise regions represent longest duration of stay in areas with intermediate revisitation rate, whereas areas highlighted in purple receive maximal revisitation but a short duration of visit. 100% MCP and the enclosure at Takhi Tal camp are highlighted with purple and green frames, respectively.*

Selecting minimal values of revisitation at moderately high duration of stay never missed to illustrate confined space-time use, e.g. time spent in the enclosure. Regions selected at minimal visitation rate and short duration of visit were typically located in peripheral areas of any groups range. Furthermore, date and hour-of-day plots deriving from manually selected regions of the hsp did not reveal striking 24h patterns for any individual. Even though, no obvious day-night pattern for any selected hsp-region is evident, the oasis at Chonin Us received longest stays as well as highest revisitation from 7215 during the winter (Fig. 12). This behaviour could be best illustrated in the first year's subset of the Erkhes group (Fig. A2). 7215's entire dataset turns out to produce the most comprehensible hull scatter plot, allowing the most accurate definition of regions among all three individuals and their yearly subsets.

3.7. Overlap in high intensity areas between years

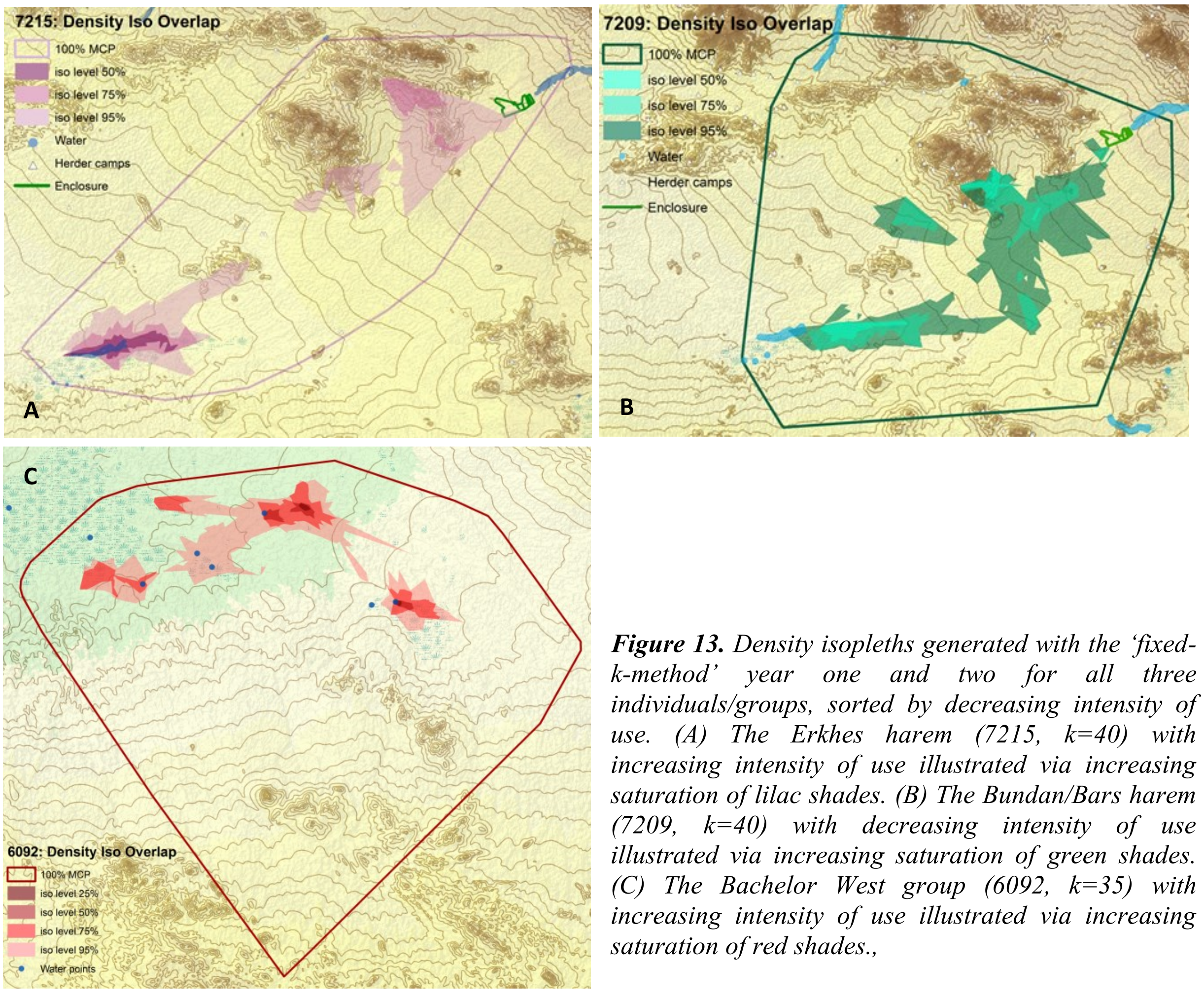


Figure 13. *Density isopleths generated with the 'fixed-k-method' year one and two for all three individuals/groups, sorted by decreasing intensity of use. (A) The Erkhes harem (7215, k=40) with increasing intensity of use illustrated via increasing saturation of lilac shades. (B) The Bundan/Bars harem (7209, k=40) with decreasing intensity of use illustrated via increasing saturation of green shades. (C) The Bachelor West group (6092, k=35) with increasing intensity of use illustrated via increasing saturation of red shades.,*

3.8. Overlap in high intensity areas between the two harem groups

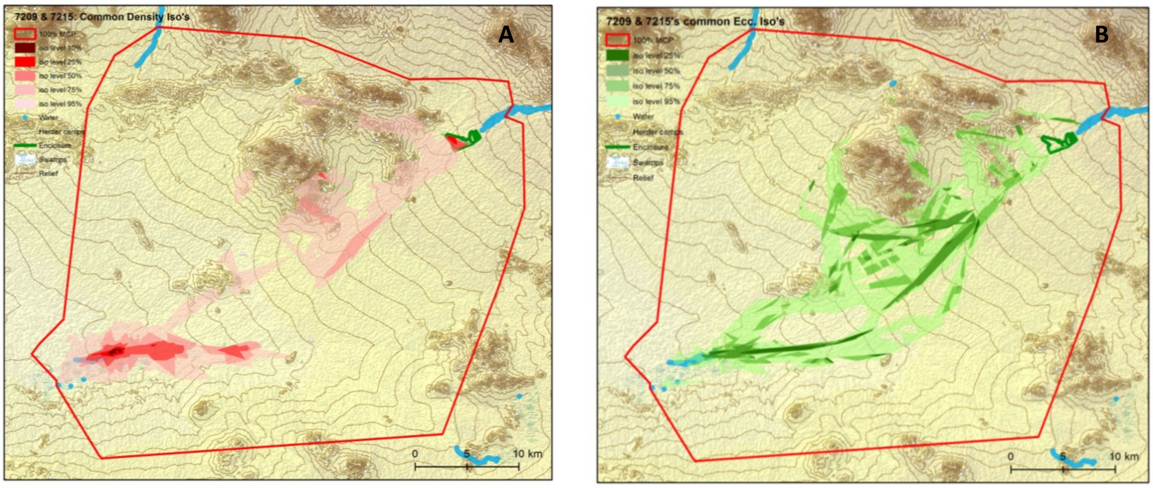


Figure 14 *A) Common density isopleths (k=40) between sympatric harems (7209 and 7215) illustrating intensity of use within their combined range over the entire monitoring period. B) Common eccentricity isopleths (a=30,000) between the groups illustrate directionality of movement.*

Sympatric groups in the northeastern portion of the B SPA both exhibit utilization of enclosure, areas seemingly unrelated to important resources at higher elevations and slopes. The oasis of Chonin Us and Takhi Us are central regarding UDs of all groups as well as least costly corridor utilization between important resources, e.g. the Bij valley and around central mountains. All individuals exhibit sudden and strong reduction of the average speed metric during winter. However, only the two eastern groups exhibit similar reduction of average speed during daytime, whereas the stallion group exhibits a contrary and more clear pattern of decreased speed values during nighttime. Except for outputs of the average speed value, no striking day/night patterns were observed in either social group.

Chonin Us was by far the most intensely used area (dark red 10% density isopleth, Fig. 14A) of both harems over the entire study period. The central mountainous area seems to be of secondarily high importance followed by the river bed between Bij/Takhi Tal camp and Chonin Us.

The Erkhes harem, represented by 7215 was released from the enclosure at the beginning of monitoring, whereas 7209 was pushed into this structure after changing groups to reunite with its foal (22.06.2014, 18:00 until 30.06.2014, 08:00). This is already evident regarding locations only but highlighted especially well when density isopleths the entire 2-year datasets of sympatric individuals (7215 and 7209) were overlapped (Fig. 14A). However, producing manually defined regions of lowest revisitation and moderate duration of visit of the hsp from the entire period of monitoring revealed that 7215 (Erkhes harem) somehow got into the enclosure multiple times also during the time 7209 (Bundan/Bars harem) was in there (Fig. 12). This was confirmed by transferring respective regions onto the date and hour-of-day plot (Fig. 12) and further investigation in 7215's Attribute Table in ArcMap. These "visits" occurred only at nighttime between 20:00 and 03:00 and never exceeded more than 2 fixes. Moreover, another behavioural metric - directional routes - of 7215's second year's subset could confirm the second visit by 7215. This strange phenomenon seems to be unrelated to social interaction, since 7215 already visited the enclosure five nights ahead of 7209's presence.

Even though other individual's hsp-plots seem to lack distinct patterns, all animals exhibited regionally defined behaviour throughout the 24h-cycle.

Haloxylon a. and *Stipa* grassland are the communities with highest availabilities within all individual's ranges (100% MCP). Moreover, the fraction of *Haloxylon a.* is usually decreasing with intensity of use but increasing at iso-levels that represent highly directional movement, whereas fractions of *Stipa* grassland decrease with increased elongation. Even though Stipa grassland is generally well available within all individual's ranges (100% MCP), it constitutes minor fractions within UDs illustrated via density isopleths. However, increasing intensity of use constitutes major fractions of water associated vegetation communities of highest productivity, even though they constitute minor fractions within the horses range. The least productive plant community (*Haloxylon a.*) is by far the most common one in all individual's ranges, followed by *Stipa* grassland.

3 DISCUSSION

The Erkhes group seems to just establish to the SPA, since their space-time use – both in terms of utilization and elongation distribution – obviously becomes less random or more conservative during the second year of monitoring. This behaviour might indicate increased spatial familiarity (Wolf et al., 2009) and a certain degree of site fidelity in terms of resource optimization to certain areas. The stallion group was also naïve to the area upon the start of monitoring and shows a similar trend regarding UD's at higher iso-levels.

The circumvention of demanding topographical features and highly directional movement on desert step plains (e.g. in the southern portion of sympatric harems) certainly offer less attractive forage and rather allow the horses to travel with least effort, which highlights the importance these areas constitute as corridors.

Manually selected regions from the hsp and subsequent computation of date and hour-of-day plots proof to be valuable tools to identify structures that cause confinement of any kind.

Utilization of coves within high mountain areas, exhibited by both sympatric groups seems unrelated to known resources horses would select for. Moreover, other behaviour such as foaling or breeding can be ruled out during that time. However, site fidelity can be attributed to some of these areas, since high density isopleths of year one and two of monitoring (for 7209, Bundan/Bars harem) overlap locally. Since 7209 did not leave the area for 5 consecutive days during April, water of some form (also snow) must be available, since they have to drink daily. The hill northeast of Chonin Us – used primarily by the Erkhes harem – may also be an important lookout or stop-over site (Sawyer et al., 2009) for individuals traversing to and from the oasis at Chonin Us. Beneficial topographic features may allow the animals to bask in the sun or avoid insect harassment. They might also get a better view of the Bij valley (e.g. on predator activity) or seek resources of mineral origin.

The identification of the enclosure via the application of multiple metrics (hsp, density isopleths, and directional routes) confirm the successful implementation of T-LoCoH as an explorative tool that would reveal such a structure even if the observer was not aware of its existence.

A clear summer-winter pattern of velocity can be observed in all individuals. This may be attributed to reducing energy expenditure during the harsh Mongolian winter, where high snow pack will slow down travel speed additionally. Finding 6092's (Bachelor West) average speed values to be elevated during the day is a behaviour that was unexpected, since these hours are hottest – its cause remains unknown. Increasing travel speed during the night, however, would appear less costly regarding decreased energy demands during chillier nighttime. Furthermore, it has to be considered that average speed of all seasons is taken into account regarding its hourly patterns. If cool hours in summer are utilized for faster travelling to safe energy demands then warm daylight hours could be the preferred for the same reasons during the winter months.

The very obvious decrease of nsv's (revisitation rate) in the summer, detected in 6092's dataset, was unexpected. Water sources were assumed to cause elevated revisitation rates during drier periods (i.e. summer, when snow could neither be utilized as a water source) since maximum daily travel distance from water sources during summer is more restrict than during winter (Kaczensky et al. 2008), limiting the capacity for explorative behaviour.

Important resources central to analysed Przewalski's horses' UDs, i.e. highly productive vegetation communities (Kaczensky, et al. 2008) and water, are often times associated in the B SPA, which is likely why their spatiotemporal differentiation is hampered. Oasis could, nevertheless, be highlighted as central habitat components regarding multiple behavioural states. They did not only receive highest intensity of use but also substantial back and forth movement (e.g. at Chonin Us). Overlaps of subsetted years of monitoring as well as overlaps of sympatric individual's datasets, highlights the central role of oasis and certain corridors to utilization (and elongation) distributions for all analysed groups (Fig. 13 and Fig. 14).

The fact that 6092's utilization of the least productive (*Haloxylon a.*) community decreases with intensity of use but does not do so with increasing directionality of movement is a clear indicator for the different behavioural traits illustrated by density isopleths (intensity of use, i.e. important resources) and by elongation isopleths (directionality of movement; i.e. corridors). This is confirmed by over-proportionally increased use of the most productive vegetation types with increasing density-iso level. These communities also receive a slight increase at the highest levels of elongation, which can be explained by criss-cross short distance directional movement around water points where those vegetation types are most common and likely utilized within this individual's range (Fig. 5, Fig. 6, Fig. 7A, Fig. 15B).

While fractions of *Nitraria s.* communities (typically associated with oasis) remain rather constant with increasing levels of directional movement, riparian vegetation receives increased use within the combined mare's ranges. This is due to the fact the the Bij river valley is holding major fractions of riparian vegetation and is simultaneously heavily utilized as a corridor (but not necessarily as forage) by both groups. Nonetheless, does it exemplify the importance of most productive vegetation communities in Przewalski's horse habitat, since they constitute 97.5% of the shared isopleths of highest use (iso-level 10%, Fig. 10 and Fig. 13C) while they constitute only 2.6% within their available range (100% MCP). The shared 10%-isopleth is located at the center of Chonin Us only, and thus emphasises this oasis as the most intensely used area of the sympatric groups over the whole period of monitoring. Generally, less clear patterns of utilization of plant communities were detected for sympatric individuals compared to the stallion. This might be due to additional utilization of the river bed and topographical features as well as the extensive oasis at Chonin Us and skewed confined utilization within the enclosure (which both mares experienced); features that 6092 lacks within its range. Not least has 7209 changed harem (from Bundan to Bars) and was pushed into the enclosure, which clearly inflated its range and may be the reason for even less clear utilization patterns compared to the more conservative range utilized by the Erkhes harem. The fact that the most productive communities (riparian vegetation and *Nitraria s.*) are increasingly utilized with intensity of use (density isopleths) and beyond availability by all three individuals is confirmed by their geographical reference around water sources and had already been emphasised by Kaczensky et al. (2008).

4 CONCLUSION

Rigorous discussions of researchers over superior home range estimators are pushing efforts to improve the accuracy of methods (Lyons et al., 2013). Their selection, however, is certainly question-dependent (Fieberg and Börger, 2012) and likely requires an array of statistical constructs (Kie et al., 2010) to achieve satisfying results. T-LoCoH certainly proofs a valuable tool to identify important corridors and other highly directional movement as well as areas central to foraging and unknown behaviour. However, it turned out a less suitable tool to distinguish resources (e.g. water from pastures), which may be a consequence of spatial overlap of these behavioural states. Very large ranges lead to a substantial spectrum between small and large hulls, which may lead to less conclusive results provided by time-use metrics (i.e. revisitation and duration) for non-territorial animals, such as equids (Wakefield et al., 2002). Moreover, being non-ruminating bulk feeders allows or requires them to be constantly on the move, which makes differentiation of behavioural states especially difficult (no real day-night pattern, no "hanging out"). Long periods of monitoring at high sampling frequency allows a great input of data into UD estimation but at the same time increases the probability of the animal to alter its 'cognitive map' since the beginning of its monitoring (Powell and Mitchell, 2012). Large multi-year datasets in combination with range shifts made the illustration provided by the hsp rather convoluted and selection of meaningful regions almost impossible (Fig. A3). Yearly subsets allowed a more meaningful selection and illustration of regions for the hsp. Additionally, subsetting of the dataset allowed inferring trends of space-time use, e.g. by creating isopleth overlaps to detect areas of spatiotemporal importance of both years of monitoring. At a different resolution (smaller amounts of data by further subsetting) day/night/crepuscular behaviour might become more evident. However, further analysis of additional subsets would have gone beyond the scope of this thesis.

Space-time characterization of Przewalski's horses via T-LoCoH's toolbox approach lead to deeper and sufficient insights about the underlying drivers of both space and time use (Lyons et al., 2013). Nonetheless, will a suite of spatial analysis methods along with T-LoCoH benefit a species of such large ranges and datasets along with similar physiological traits in similarly stable environments best.

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6 APPENDIX

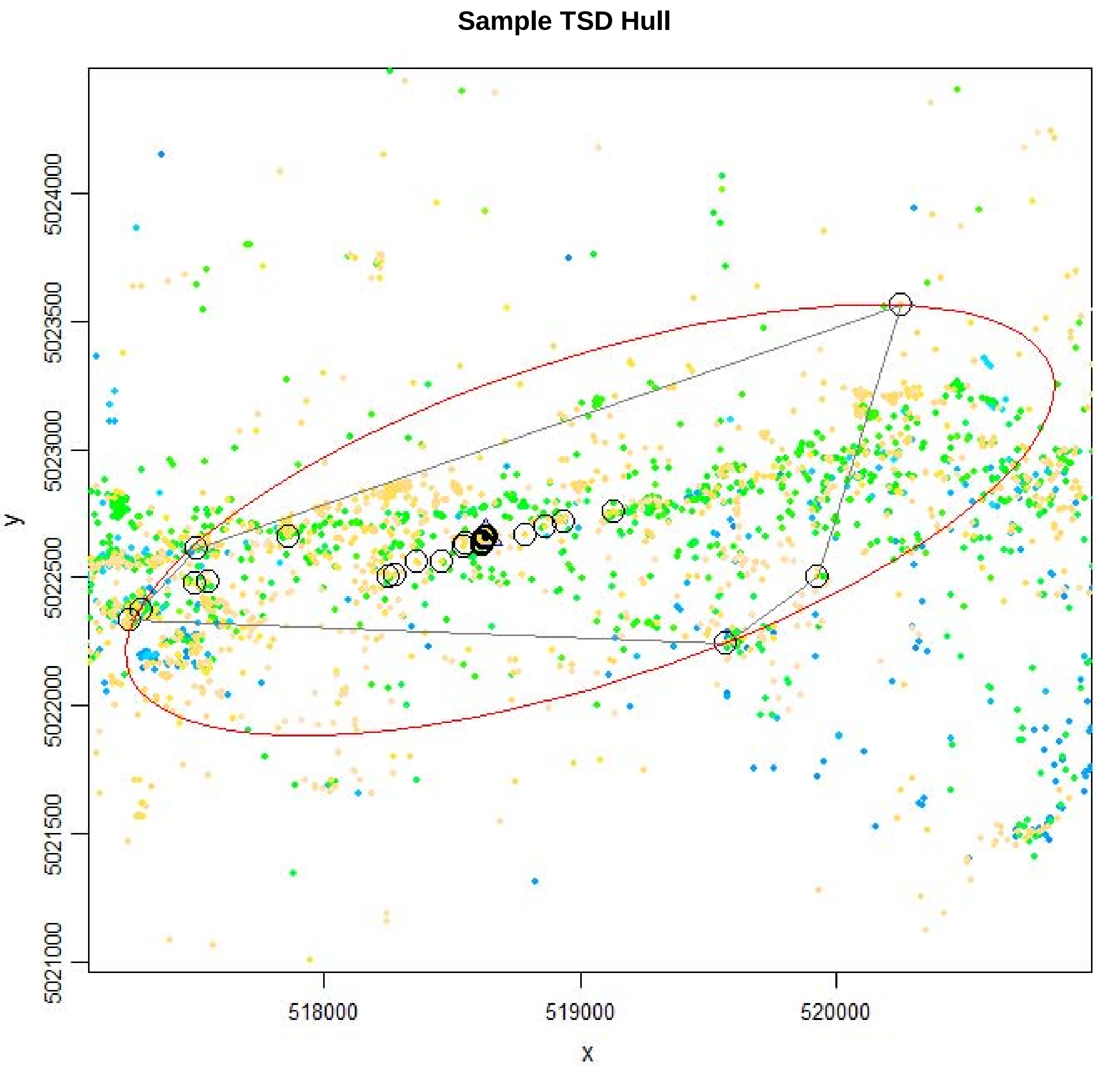

Figure A1. *Sample hull for a single point from a 7215's GPS dataset (N=16535). Similarly coloured points represent continuity in time. The parent-point (ptid=12936) is shown by a triangle; nearest neighbours (circled) are identified using the fixed-a-method at a=30,000 and a TSD with s=0.0115455. Non-circled points within the hull are closer to the parent point but were bypassed as nearest neighbours due to their distance in time. The ellipse outlined in red is the bounding ellipse whose eccentricity is one of the metrics of hull elongation.*

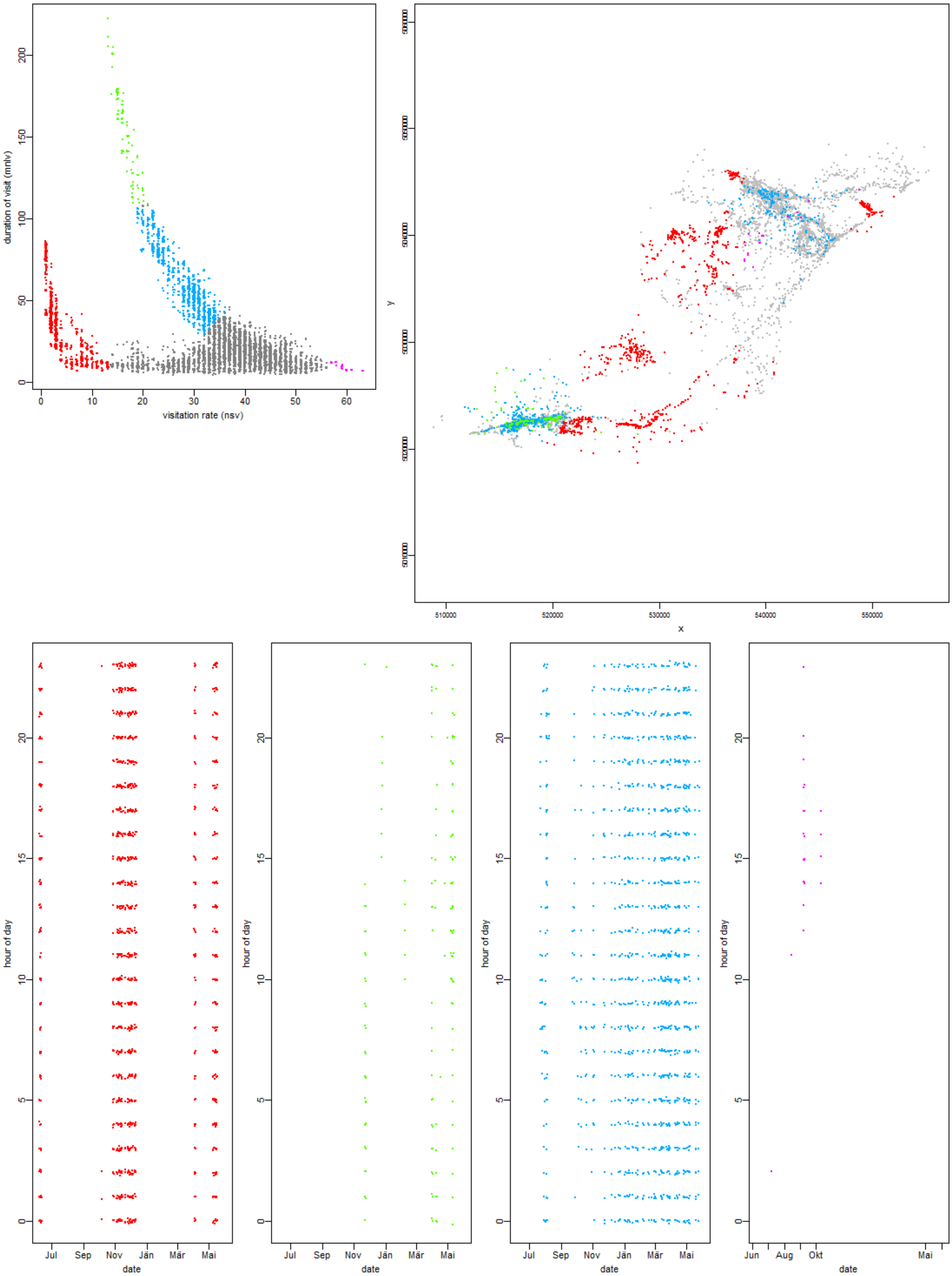

Figure A2. *Manually selected regions and respective date and hour-of-day plot of regions. of 7215's hsp of revisitation and duration computed from its first year of monitoring.*

A

B

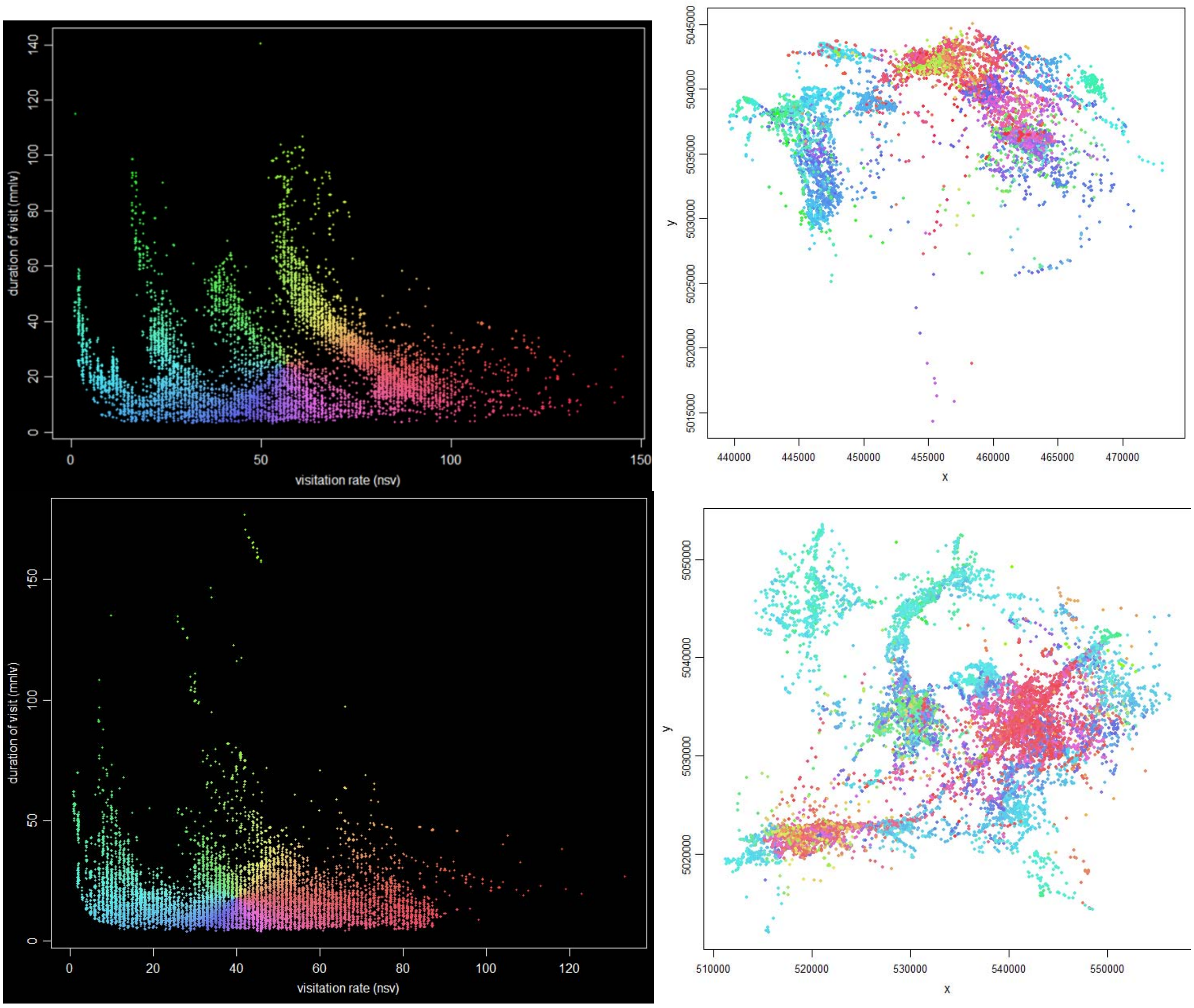

Figure A3. *(A) 6092's (Bachelor West group) and (B) 7209's (Bundan/Bars harem) hsp of revisitation and duration of its entire dataset. Each point represents a hull (n=15021 and n=16850 respectively). Left: On the x-axis is visiation rate and on the y-axis is duration of visit. Separate visits are defined by an IVG >= 21hs. Hulls were created using the fixed-k-method. Right: Parent points coloured by their location in nsv-mnlv space.*