

MASTERARBEIT / MASTER'S THESIS

Titel der Masterarbeit / Title of the Masters's Thesis

„Effects of Transfer and Acclimatisation on Spatial and
Temporal Patterns in European Wolves (*Canis lupus*
lupus)“

verfasst von / submitted by

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angestrebter akademischer Grad / in partial fulfilment of the requirements for the degree of
Master of Science (MSc)

Wien, 2019 / Vienna, 2019

Studienkennzahl lt. Studienblatt /
degree programme code as it appears on
the student record sheet:

A 066 831

Studienrichtung lt. Studienblatt /
degree programme as it appears on
the student record sheet:

Masterstudium Zoologie UG2002

Betreut von / Supervisor:

Univ.-Prof. i. R. Dr. Kurt Kotrschal

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ABSTRACT

In this study, a pack of European wolves (*Canis lupus lupus*) was monitored in early spring 2018 before and after their transfer into a larger enclosure. The results showed an increased synchronisation between the animals and a higher rate of resting behaviour after the transfer. As well as a higher rate of stereotypical behaviour in reaction to visitors and staff. The animals also showed less location preferences for specific behaviours in the new enclosure, unlike the significant preferences in the old one. Acclimatisation of the pack to the new environment seemed not to be achieved within the observation period and with further observations of the pack at a later date, those results could be added for a more in-depth analysis.

ZUSAMMENFASSUNG

In dieser Studie wurde ein Rudel europäischer Wölfe (*Canis lupus lupus*) im Frühjahr 2018 beobachtet, vor und nach ihrem Umzug in ein größeres Gehege. Die Resultate nach dem Umzug zeigen ein erhöhtes Maß an Synchronisation des Verhaltens zwischen den Tieren, sowie verstärktes Ruheverhalten. In Bezug auf Besucher und Pfleger zeigten die Wölfe vermehrt stereotypisches Verhalten. Im neuen Gehege war es nicht möglich Präferenzen für bestimmte Gehegeabschnitte, in denen natürliches Verhalten gezeigt wurde, zu erkennen. Anders war dies im alten Gehege, wo signifikante Präferenzen für bestimmte Gehegeabschnitte beobachtbar waren. Innerhalb des Beobachtungszeitraums, konnte noch keine Gewöhnung des Rudels an das neue Gehege beobachtet werden. Ein möglicher Anknüpfungspunkt an diese Studie wäre es, zu einem späteren Zeitpunkt weitere Beobachtungen durchzuführen, um neue Erkenntnisse über die Gewöhnung des Rudels an das neue Gehege zu erlangen.

ACKNOWLEDGEMENTS

I want to thank the scientists at the Wolf Science Center in Ernstbrunn, Austria, for giving me access to their ethograms and for the possibility to test it on their wolves first. Thanks to all the employees of the Cumberland Wildpark Grünau for their help, and the scientists at the Konrad-Lorenz-Forschungsstelle for moral support, a place to sleep and their friendship. Special thanks to Verena Pühringer-Sturmayer, Phd and Mario Gallego-Abenza, Phd, who both helped figuring out the statistics for this thesis. And of course Univ.Prof. Dr. Kurt Kotrschal for the opportunity to work on this project, his counsel and his support.

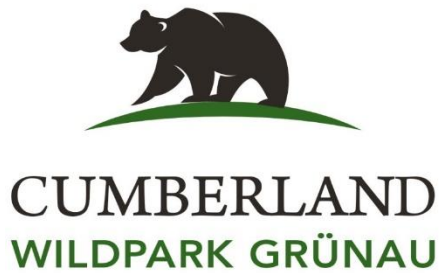


Photo made by Felix Steinmaurer. All other photographs made by Sabrina Jungheim.

1 INTRODUCTION

Transferring zoo animals into a new enclosure can be a highly stressful event. It should therefore only be undertaken when the positive effects of the new enclosure outweigh the negative impact of the transfer (Ogden et al. 1990; Price 1992; Ross et al. 2011). To study these effects, the pack of three European wolves (*Canis lupus lupus*) at the Cumberland Wildpark in Grünau im Almtal was monitored in early spring 2018 before and after their transfer into a larger enclosure, which they now share with two brown bears (*Ursus arctos*). The new enclosure with its approximately 8.000 m² is much larger than the approximately 1.000 m² of the old enclosure. The new enclosure will be divided into three large areas after the construction on the final area is completed in the early spring of 2019. Two of these areas will be accessible by both bear and wolf, while a smaller area of 1600 m² is only accessible to the wolves. To monitor the effect of the transfer on the behaviour of the wolves related to the time of the day and their habitat use, also referred to as behavioural temporal and spatial patterns, and the stereotypical behaviour of the wolves, they were observed four weeks before their move to establish a behavioural baseline.

The new enclosure is much larger than the old one, even when considering only the part the wolves have access to. The temporal composition of the wolves' daytime routine should therefore change, as a larger enclosure should lessen the amount of time the wolves spent with stereotypical behaviour, such as stereotypical route tracing or pacing, since these behaviours are significantly negative correlated to the animals' natural ranging behaviour (Mech & Boitani 2006; Clubb & Mason 2007). The more naturalistic environment provided by the new enclosure, with forest-like areas and lots of hiding places, makes it more likely to be a suitable natural-like environment for the wolves (Fàbregas et al. 2012). These conditions might also positively influence the amount of time spent performing species-specific behaviours (Brummer et al. 2010; Frézard & Le Pape 2003) and decrease the time spent performing stereotypical behaviours. Actually, this study focused on pacing as an indicator of stereotypical behaviour since this is the most prevalent among carnivores (97% of reported stereotypes) (Rushen & Mason 2006) and as it is easily recognised.

In general, the temporal patterns were hypothesised to be highly influenced by the movements of visitors and staff, both before and after the transfer. This influence, described as the "zoo visitor effect" (Davey 2005), seems to have a largely negative impact on the animals' behaviour, shown through an increase in vigilance and socio-negative behaviours, like dominant and submissive behaviours, as well as an increased rate of stereotypical behaviours and time spent hiding when visitor numbers rise (Chamove et al. 1988; Mallapur et al. 2005; Sellinger & Ha 2005; Davey 2006; Quadros et al. 2014). The effect of humans on wolves can also be found in wild wolves, as they decrease their movements and activity during daytime when sharing their territory with humans, either as a direct effect of human presence (Ciucci et al. 1997; Hebblewhite & Merrill 2008; Kojola et al. 2016; Mancinelli et al. 2018), or due to the affected behaviour of prey species (Theuerkauf & Rouys 2008; Bonnot et al. 2013). Taking these findings into account, it was hypothesised that the presence of visitors and staff would negatively influence the wolves, resulting in them showing more stereotypical behaviour when people are around, thus showing less species-specific behaviours. This is seen as a negative effect, since pacing is related to high arousal and stress hormones (Clubb 2001; Clubb & Vickery 2006; Mason 2010) and inactivity has proven to take up a large proportion of the daytime routine in canids in the wild (Kolenosky & Johnston 1967; Theuerkauf et al. 2003; Packard 2006; Gunning n.d.). Inactivity thus provides a sound example of an observable species-typical behaviour, defined as a general behaviour that is expected to occur in a similar fashion in all members of a species (Greenberg & Haraway 1998). The larger size, and the more natural-like environment of the new enclosure are hypothesised to lessen the negative impact of the zoo visitor effect in relation to the old enclosure, due to the increased hiding possibilities for the wolves. However, a higher rate of inactivity could also be caused by the wolves' retreat due to their new enclosure.

Lastly, while the animals will probably use the entire enclosure after the move to investigate and claim their new territory, studies found that wolves in zoos, generally use only parts of their enclosure for species-specific behaviours, but spend most of their time resting when in a large, comfortable enclosure (Mallapur 1999; Frézard & Le Pape 2003; Gunning n.d.), just like they only use parts of their territory continuously in the wild (Vilà 1995; Ciucci et al. 1997). The time it takes to reach a new equilibrium in time budgets and activities will indicate the time it takes the wolves to acclimatise after their move into the new enclosure.

This analysis will show if the move of the Cumberland Wildpark pack of wolves will dampen the impact of the zoo visitor effect on the wolves' activity and decrease stress related behaviours, like e.g. stereotypical route tracing. Analysing the location preferences and habitat use of the animals will also show the duration of the acclimatisation of the wolves in the new enclosure.



Siska standing on top of the den in grid 4E in the new enclosure.

2 ANIMALS AND METHODS

2.1 EXPERIMENTAL SUBJECTS

For this study a pack of three wolves was observed at the Cumberland Wildpark in Grünau im Almtal, Austria. The pack consisted of two males and one female, all spayed and neutered. The oldest male, Rován, was born in 2007 in the Alpine Zoo in Innsbruck, Austria. The younger female and male, Siska and Sky, were both born in 2009, from the same dominant pair as Rován. The three siblings lived at the Cumberland Wildpark since 2010.

For moving into their new enclosure, the wolves were anaesthetised with a stunning gun early in the morning before opening hours of the Cumberland Wildpark. All three were checked by a vet and got an anthelmintic therapy while still asleep. They were put into the middle of their new enclosure after been given the antidote for the anaesthetics.

Two weeks after the wolves moved into the new enclosure, the two brown bears, which lived next to the wolves in the old enclosure, moved into the second part of the new enclosure. Two weeks later the doors between the wolf and bear enclosure were opened, giving the wolves the possibility to move into the bear enclosure, but keeping the bears out of the wolf enclosure. Construction started on the third part of the enclosure after the bears moved.

2.1.1 INTERACTION WITH STAFF MEMBERS

The wolves were fed pieces of meat at 8 am each day at the old enclosure by students from the Konrad-Lorenz-Forschungsstelle observing the ravens (*Corvus corax*) that participated in the feedings. Feedings were changed to the afternoon in the new enclosure and the meat was placed into an enclosed area by staff members to monitor the amount of meat the wolves truly needed since the ravens theoretically could not reach the meat. Unlike the old enclosure, the feeding was not done at a set time. Whole animal carcasses were fed to the wolves irregularly and left in the enclosure for a couple of days.

Since the bears were the wolves' only neighbours in both the old and the new enclosure, the only other times staff members were regularly near the wolves was during the bears cleaning and feeding routines. This happened at 7 am each morning in the old as well as in the new enclosure.



All three wolves vigilant in front of the den in the new enclosure, shortly after transfer.

2.1.2 MEET THE WOLVES

ROVAN



Rovan is the largest of the three wolves. Born in 2007 in the Alpenzoo in Innsbruck, Austria. He is the oldest of the three.

He used to be the leader of the pack, until a vicious fight with Sky in 2017 which resulted in his scarred nose.

Now he is more of a loner and afraid of confrontations with the other two wolves, although he accompanies Siska on some of her walks.

He is more relaxed than the other two wolves in relation to visitors and staff and is more likely to sleep through a staff visit than to get agitated.

SISKA

Siska is the only female of the pack and the smallest of the whole bunch.

She and Sky are from the same litter and were born in the Alpenzoo in Innsbruck, Austria, in 2009.

Being the most nervous wolf in the pack, she is running around the most during the day. Every sound has to be investigated.

She is also most of the time the initiator of a fight or a play session.



SKY



Sky is the dominant wolf of the Cumberland Wildpark pack since 2017. He and his littermate Siska often terrorize the older Rovan.

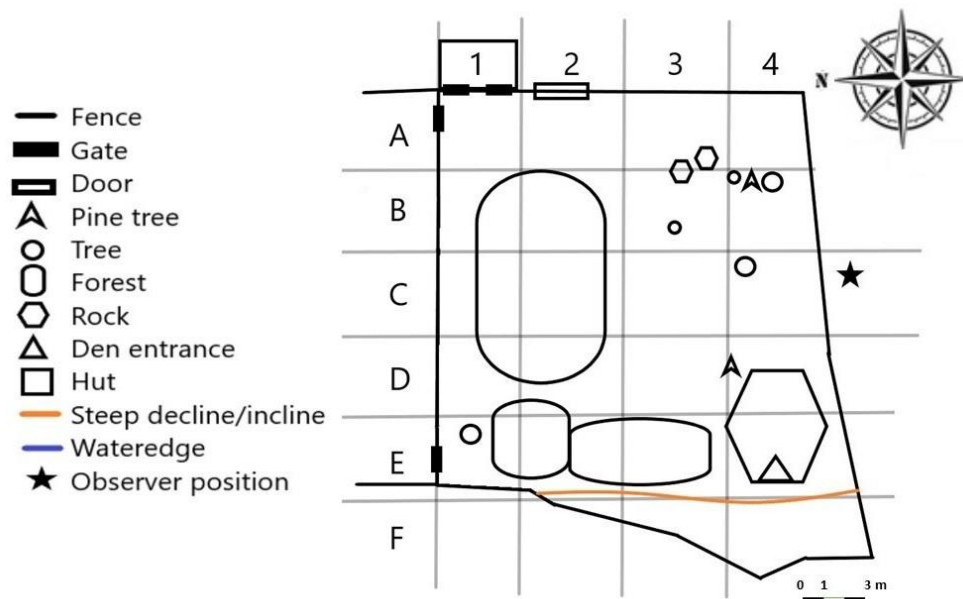
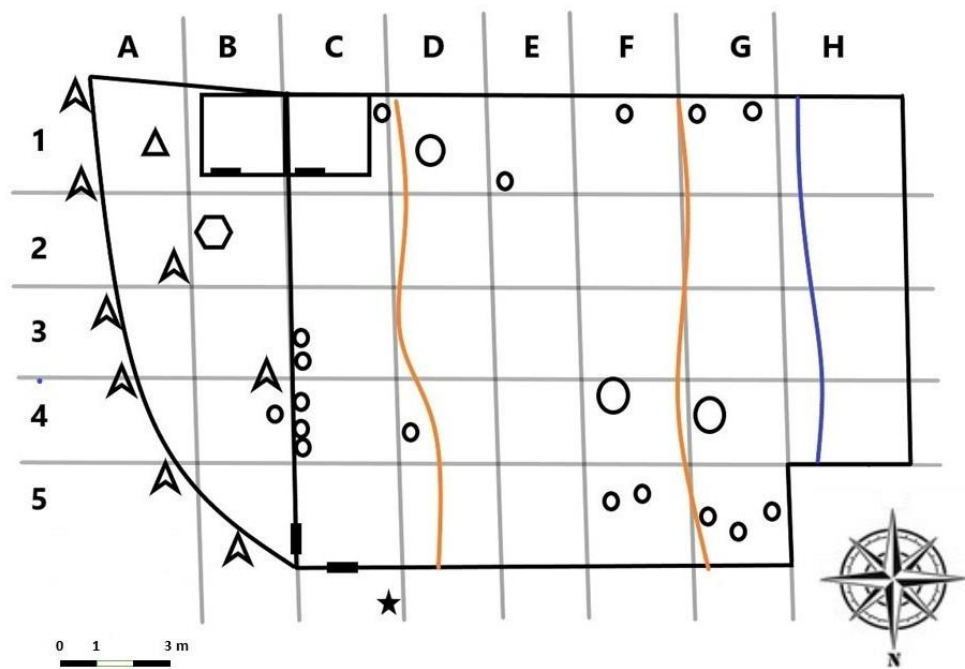
Sky is very nervous around staff and is mostly found running around in circles during cleaning and feeding times.

Visitors don't bother him that much and like Rovan he sleeps through a large part of the day.

stream. The fence along A1 to H1 divided the wolf and bear enclosure, visual contact was only possible through a chain-link fence along grids A1 and B1 (Fig. 2).

The wolf-only part of the new enclosure is approximately 1600 m² large and visitors can only move along the bottom part of the enclosure along the fence in grids 1F to 4F. Along the fence is a trench, which enables the visitors to be eye to eye with the wolves when they walk along the forest edge or stand in the entrance to their den. Large parts of the enclosure are covered in trees, shrubs and grassland, providing coverage for the wolves. Feedings take place in grid 1A and in the small cage situated next to it. Water is also provided here. The chain-link fence from 1A to 1E divides the wolf-only part of the enclosure from the shared bear enclosure. Doors to the shared bear enclosure are situated in 1A and 1E (Fig. 2).

Figure 2 Grid placed over the old enclosure (upper) and the wolf-only part of the new enclosure (lower), used to determine the wolves' whereabouts during the noted behaviour.





Pictures from top to bottom: Sky vigilant in grid C2 in front of the hut in grid C1 in the old enclosure.
A view from the stream in grids H1 to H4 up the hill in the old enclosure. The den in grid 4E in the new enclosure.

2.3 ETHOGRAM

The observed behavioural elements were grouped into 16 categories which show a differentiation between active and inactive behaviours as well as positive and negative social interactions (Table 1). Short bursts of activity or inactivity between the scans were incorporated as well and simply noted as active or inactive without a detailed distinction.

<i>Categories</i>	<i>Description</i>
<i>Resting</i>	Sleeping, and lying or sitting in different positions
<i>Standing</i>	Standing motionless
<i>Vigilant</i>	Standing or sitting motionless while staring intensely at something
<i>Locomotion</i>	Walking, trotting, running, carrying something, chasing objects
<i>Stereotyped behaviour</i>	pacing or walking/running in circles
<i>Self-directed behaviour</i>	Rubbing on objects, licking paws, stretching, auto-grooming
<i>Sniffing</i>	Smelling the ground or objects
<i>Eating</i>	Eating, taking or carrying food
<i>Drinking</i>	Drinking from a water source or licking dew from leaves
<i>Urination</i>	Peeing or marking
<i>Defecate</i>	
<i>Digging</i>	Breaking up the ground or caching food
<i>Social positive</i>	Grooming, greeting, body rubbing, sniffing
<i>Play</i>	Ambush, bow, hide and seek, tug of war
<i>Social negative</i>	Submissive and agonistic behaviour, biting, growling
<i>Vocalization</i>	Howling, growling, jipping
<i>Invisible</i>	The wolf is not visible from the observers' position

Table 1 Description of the used behavioural categories. Behaviours as described by Goodmann, et al. (Goodmann et al. 2002)

All behaviours except resting and stereotyped behaviour were grouped together under the name “overall activity” for the detailed data analysis.

2.4 VISITORS, STAFF AND DISTURBANCES

2.4.1 VISITORS

To analyse the reaction of the animals towards visitors, the number of visitors was divided into three levels. These levels were written down in combination with the location and the behaviour for each observation point.

Level 1 means that no visitors were at the enclosure of the wolves or the neighbouring bear enclosure. When one family or one person was at the enclosures they were noted as level 2. Multiple families, school classes and multiple single persons or pairs were noted as level 3.

2.4.2 STAFF

Just like the visitors, the movements of staff members were noted at each 2-minute scan. Level 1 means that no staff members were near the wolf or the bear enclosure. During level 2 staff members were driving or walking by or working at the bear enclosure. Staff members working in or at the wolf enclosure were noted as level 3.

2.4.3 OUTSIDE INFLUENCES AND DISTURBANCES

During the observations several disturbances occurred. These were only marked down as being present. Not their duration or intensity.

When no disturbances occurred during the observation this was marked down as 0. Interactions with ravens, like chasing, play or food stealing, were noted as 1. Overflying planes and helicopters were noted as 2. Construction work at the wolf or bear enclosure or within hearing distance was noted as 3. Disturbances in category 4 were cars driving by the enclosure. And lastly, category 5 were occurrences where the wolves were fed with an animal carcass.

2.5 DATA ANALYSIS

	<i>stand</i>	<i>vigilant</i>	<i>move</i>	<i>self-dir</i>	<i>sniff</i>	<i>eat</i>	<i>drink</i>	<i>urinate</i>	<i>defecate</i>	<i>dig</i>	<i>sozio.pos</i>	<i>play</i>	<i>sozio.neg</i>	<i>vocal</i>
<i>Old enclosure</i>														
<i>Total Rován</i>	256	22	239	33	28	26	10	0	0	3	5	0	36	0
<i>Total Siska</i>	172	94	278	12	35	46	2	3	3	0	7	3	1	1
<i>Total Sky</i>	131	83	154	3	19	23	5	3	1	1	2	4	3	1
<i>New enclosure</i>														
<i>Total Rován</i>	33	149	239	5	25	6	22	0	0	0	6	1	0	4
<i>Total Siska</i>	20	264	208	11	32	8	19	1	0	2	8	1	0	4
<i>Total Sky</i>	12	258	217	6	18	13	4	1	2	1	4	0	2	6

Table 2 Overview of the number of observations of each behaviour except resting and pacing in the old and in the new enclosure. These behaviours were grouped together as overall activity for the detailed analyses.

All statistics were calculated with the use of R-Studio, v. 3.2.2. (R Core Team 2018). All the analyses are based on 2335 observations per wolf in the old enclosure and 2223 observations per wolf in the new enclosure. Each observation being one notation of behaviour and location of the instantaneous sampling during the observation period.

The degree of synchronisation between the wolves was calculated by testing the differences between wolves for different behaviours.

To determine if visitors, staff or disturbances had an influence on the resting and pacing behaviour of the wolves, the number of observations per level was compared with the number of observations for the category 0, where no visitors, staff or disturbances were present.

Location preferences for certain behaviours were determined by comparing the observations per grid of each behaviour with the expected numbers as if the wolves would not have a preference.

The potential effect of acclimatisation on resting, pacing and activity was tested by comparing the average behaviour per week with the other weeks.

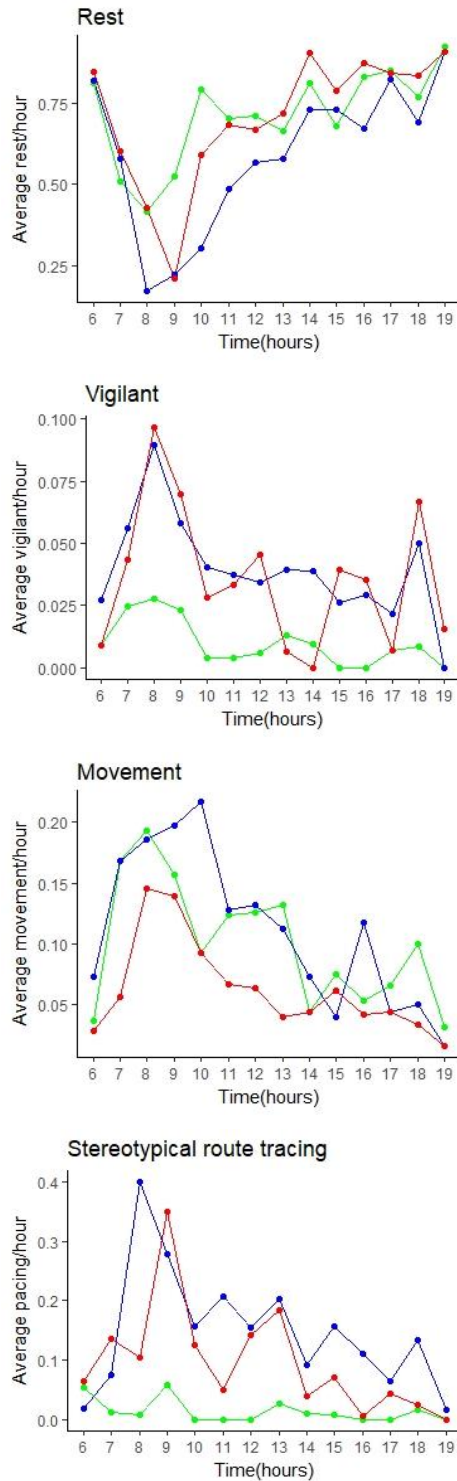
The graphs were made with ggplot in R package ggplot2 (Wickham 2009), the function bwplot in R package lattice (Sarkar 2008) and the function ggdotchart in R package ggpvr (Kassambara 2017). The maps were created using Paint 3D.

3 RESULTS

3.1 BEHAVIOURAL AND TEMPORAL PATTERNS

3.1.1 DAYTIME ROUTINE

Old enclosure



New enclosure

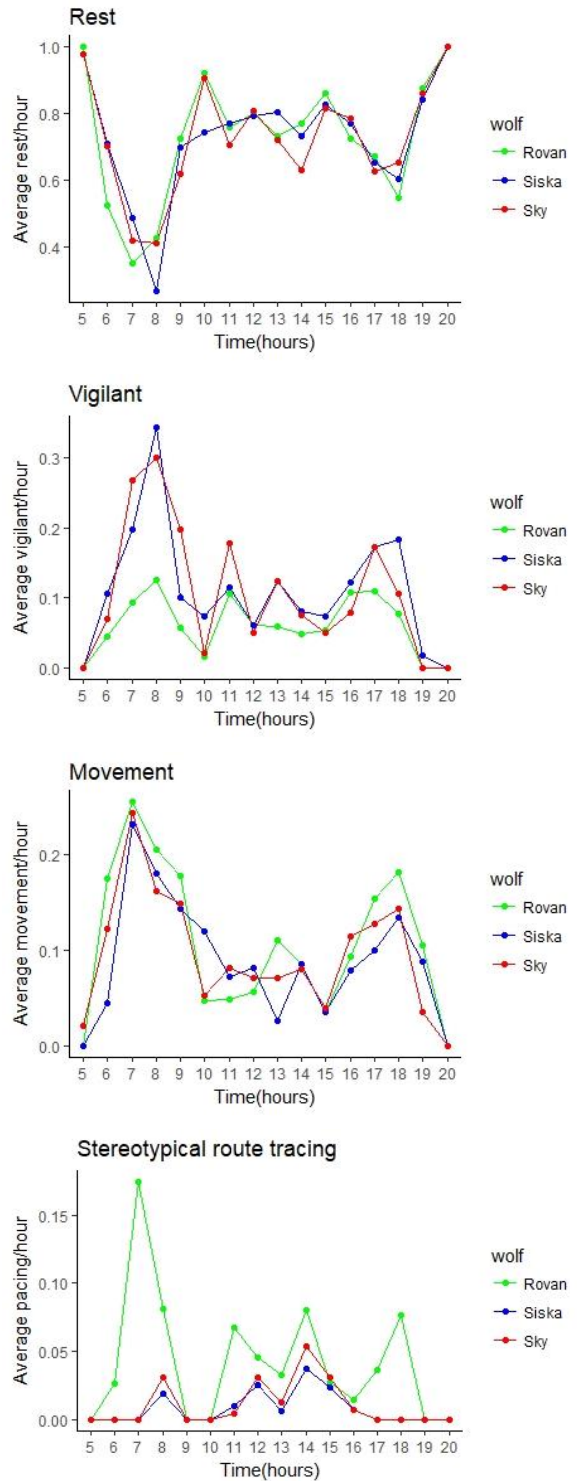


Figure 3 Average behaviour per hour over the whole observation period for every wolf in both old and new enclosure. A higher peak indicates a higher recorded average presence of this behaviour during the respective hour. The mean of the number of observations of each behaviour per hour was used to minimise the number of dots in the graphs and get a clearer image.

Both in the old and in the new enclosure the wolves showed a steep incline in activity shortly after sunrise (Fig. 3), this tapered off after a few hours and resting was again the more dominant behaviour in the afternoon. This incline in activity in the old enclosure seemed to concur with the presence of staff in or nearby the enclosure (Fig. 4). The high peak in stereotypical route tracing in Siskas behaviour before feeding time in the old enclosure (9 am) indicated expectation on her part, while Skys peak in pacing during the feeding seemed to be more anxiety fuelled.

Old enclosure



New enclosure

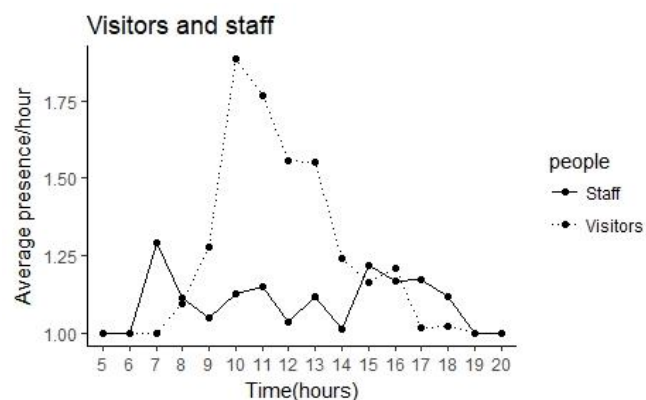
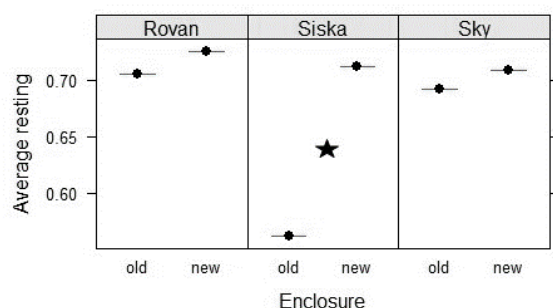


Figure 4 Presence level of visitors and staff during the day at both old and new enclosure. Staff presence levels: 1= no staff, 2= staff nearby, 3= staff in or at enclosure. Visitor presence levels: 1= no visitors, 2= one group of visitors, 3= multiple groups of visitors. Cleaning bear enclosure and feeding bears (7 am) and feeding wolves (9 am) in the old enclosure. Feeding bears (7 am) and feeding wolves in the afternoon in the new enclosure.

3.1.2 OLD VS. NEW ENCLOSURE

Resting



Pacing

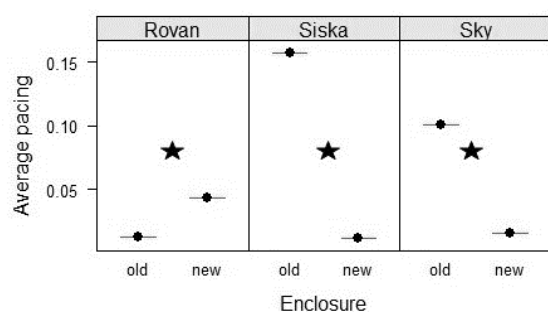


Figure 5 Graph showing a comparison of the average resting and pacing behaviour of each wolf between the old and new enclosures. Significantly different values between old and new enclosure are marked with a star ($p < 0.05$). (Results of the statistical analysis in Table A.1)

The average resting behaviour of both Rovan and Sky was not significantly different between the old and new enclosure. Only Siska showed a significant increase of time spent resting in the new enclosure. Both Siska and Sky showed a significant decrease in pacing behaviour in the new enclosure, compared to the old one. Rovan showed a significant increase in pacing behaviour in the new enclosure within the ten weeks after the transfer (Fig. 5).

3.1.3 SYNCHRONISATION BETWEEN THE THREE WOLVES

The graphs in Fig. 3 showed a more synchronised behaviour between the three wolves after their transfer into the new enclosure. The statistical analyses of the data showed that the differences in resting behaviour between the wolves in the old enclosure were significantly different, indicating less synchronised behaviour in the old enclosure, unlike the non-significant values in the new enclosure (Table 3). The same holds true for the non-significant differences between wolves with regards to movement. There were no indicators for synchronisation between the three wolves in relation to vigilance and pacing.

<i>Resting</i>							
<i>Old enclosure</i>				<i>New enclosure</i>			
<i>contrast</i>	<i>estimate</i>	<i>SE</i>	<i>p-value</i>	<i>contrast</i>	<i>estimate</i>	<i>SE</i>	<i>p-value</i>
<i>Rovan - Siska</i>	0.1430	0.0135	<.0001	<i>Rovan - Siska</i>	0.0130	0.0139	N.S.
<i>Rovan - Sky</i>	0.0128	0.0135	N.S.	<i>Rovan - Sky</i>	0.0171	0.0139	N.S.
<i>Siska - Sky</i>	-0.130	0.0135	<.0001	<i>Siska - Sky</i>	0.0040	0.0139	N.S.
<i>Vigilance</i>							
<i>Old enclosure</i>				<i>New enclosure</i>			
<i>contrast</i>	<i>estimate</i>	<i>SE</i>	<i>p-value</i>	<i>contrast</i>	<i>estimate</i>	<i>SE</i>	<i>p-value</i>
<i>Rovan - Siska</i>	-0.0308	0.0070	<.0001	<i>Rovan - Siska</i>	-0.0517	0.0072	<.0001
<i>Rovan - Sky</i>	-0.0261	0.0070	0.0006	<i>Rovan - Sky</i>	-0.0490	0.0072	<.0001
<i>Siska - Sky</i>	0.0047	0.0070	N.S.	<i>Siska - Sky</i>	0.0027	0.0072	N.S.
<i>Movement</i>							
<i>Old enclosure</i>				<i>New enclosure</i>			
<i>contrast</i>	<i>estimate</i>	<i>SE</i>	<i>p-value</i>	<i>contrast</i>	<i>estimate</i>	<i>SE</i>	<i>p-value</i>
<i>Rovan - Siska</i>	-0.0167	0.0087	N.S.	<i>Rovan - Siska</i>	0.0139	0.0089	N.S.
<i>Rovan - Sky</i>	0.0364	0.0087	0.0001	<i>Rovan - Sky</i>	0.0099	0.0089	N.S.
<i>Siska - Sky</i>	0.0531	0.0087	<.0001	<i>Siska - Sky</i>	-0.0040	0.0089	N.S.
<i>Pacing</i>							
<i>Old enclosure</i>				<i>New enclosure</i>			
<i>contrast</i>	<i>estimate</i>	<i>SE</i>	<i>p-value</i>	<i>contrast</i>	<i>estimate</i>	<i>SE</i>	<i>p-value</i>
<i>Rovan - Siska</i>	-0.1448	0.0066	<.0001	<i>Rovan - Siska</i>	0.0315	0.0068	<.0001
<i>Rovan - Sky</i>	-0.0878	0.0066	<.0001	<i>Rovan - Sky</i>	0.0279	0.0068	0.0001
<i>Siska - Sky</i>	0.0570	0.0066	<.0001	<i>Siska - Sky</i>	-0.0036	0.0068	N.S.

Table 3 Results of a pairwise model testing the differences between wolves in each behaviour in the old and the new enclosure. Non-significant results indicate that the wolves were more synchronised in their behaviour, significant results therefore indicate different behaviour patterns between the two wolves.

3.1.4 ACCLIMATISATION

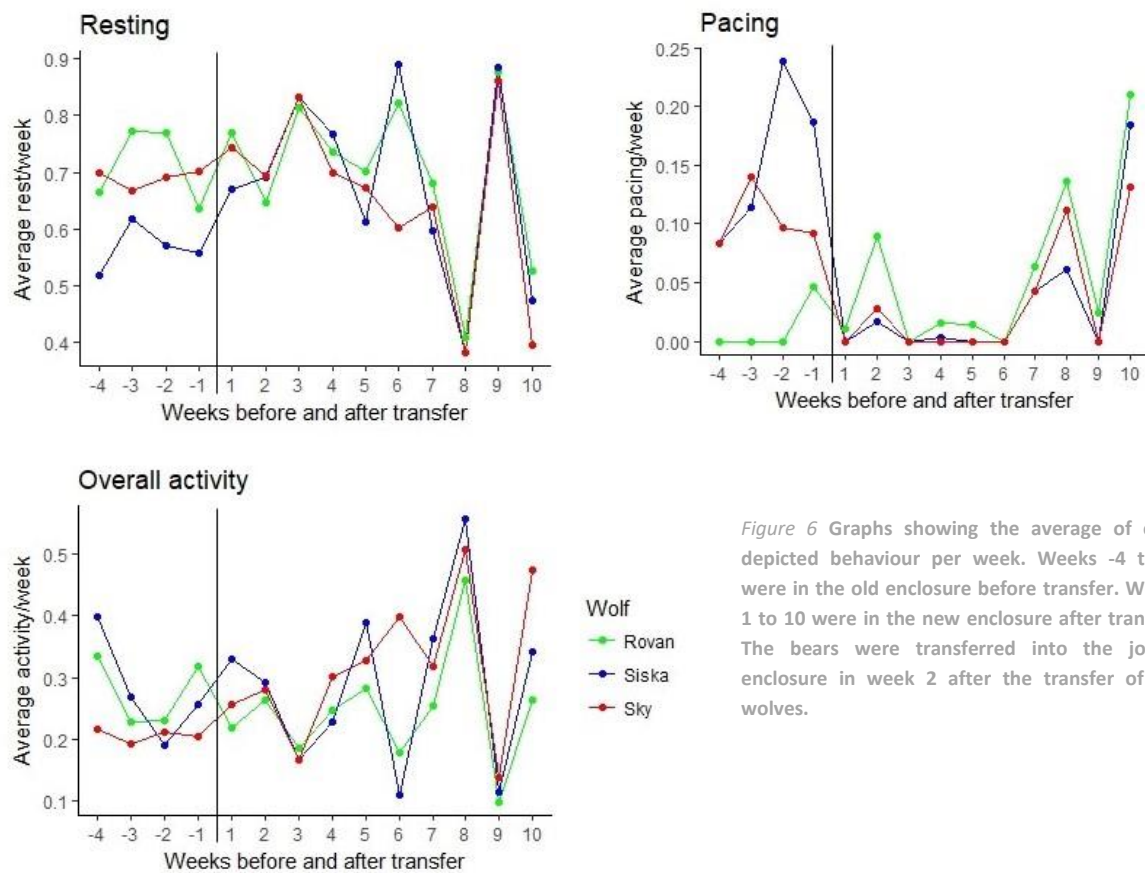


Figure 6 Graphs showing the average of each depicted behaviour per week. Weeks -4 to -1 were in the old enclosure before transfer. Weeks 1 to 10 were in the new enclosure after transfer. The bears were transferred into the joined enclosure in week 2 after the transfer of the wolves.

The three graphs in Fig. 6 show that the wolves synchronised their behaviour in week 7 to 10 after the transfer, while they operated individually before the transfer and shortly after. Shortly after the transfer there was a decline in time spent pacing in both Siska and Sky in relation to before the transfer, while Rovan seemed to spend more time pacing. In the ninth week after the transfer all three wolves showed an abrupt decline in the time spent pacing and overall activity, as well as a steep incline in time spent resting. According to the data of the weeks before week 9 and those of week 10, the data of week 9 seemed to be an outlier.

Shortly after the transfer into the new enclosure in week 2 the average amount of time spent pacing in comparison to week -3 before the transfer was significantly higher in Rovan and lower in both Siska and Sky ($p < 0.0001$). On average Rovan spent a significantly less amount of time resting in week -3 ($p = 0.0007$), while Siska and Sky showed no significant difference to week -3. The overall activity did not differ between week -3 and week 2 in any of the wolves.

The average amount of time spent resting in week 8 after the transfer was significantly lower than in week 2 after transfer for all three wolves (Rovan $p = 0.0008$, Siska $p < 0.0001$, Sky $p = 0.0001$). The incline of the time spent pacing between weeks 2 and 8 after the transfer was not significant in any of the wolves, while the incline of the overall activity between week 2 and week 8 after the transfer was significant for all three wolves (Rovan $p = 0.0127$, Siska $p < 0.0001$, Sky $p = 0.0008$).

When comparing week -3 before and week 8 after the transfer, the average amount of time spent resting declined significantly for all three wolves (Rovan $p < 0.0001$, Siska $p = 0.0015$, Sky $p < 0.001$). The data showed no significant difference in time spent pacing, but the average amount of time spend on overall activity showed a significant incline in all three wolves (Rovan $p = 0.0010$, Siska $p < 0.0001$, Sky $p = 0.0008$). (Results of the statistical analysis in Table A.2).

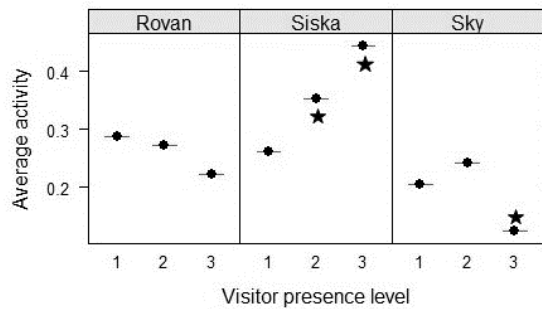
3.2 ZOO VISITOR EFFECT

3.2.1 VISITORS

3.2.1.1 OVERALL ACTIVITY

Old enclosure

1: n=1923, 2: n=331, 3: n=81



New enclosure

1: n=1636, 2: n=457, 3: n=130

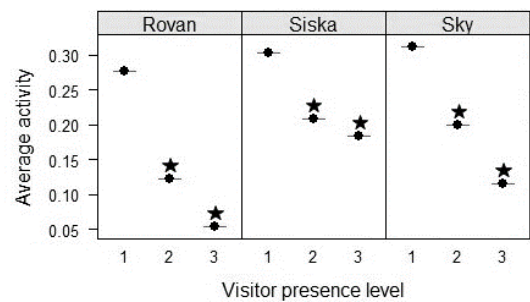
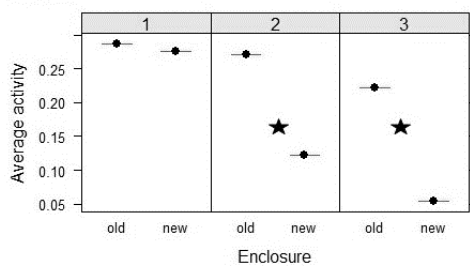


Figure 7 Average amount of activity (every recorded behaviour except resting and pacing) per visitor presence level over the course of the entire observation period. 1= no visitors, 2= one group of visitors, 3= multiple groups of visitors. An average amount of activity of 1 means always active with this visitor presence level, an average amount of activity of 0 means never active with this visitor presence level. Visitor presence levels where the average amount of activity within a wolf is significantly different to level 1 are marked with a star ($p < 0.05$). (Results of the statistical analysis in Table A.3)

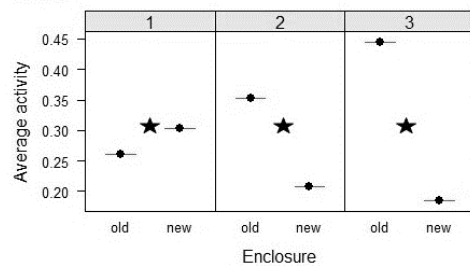
Both Siska and Sky were more active when multiple groups of visitors were at the old enclosure. Siska was also more active when one group of visitors was present. Rovans level of activity didn't depend on the number of visitors. All three wolves showed decreasing levels of activity with an increasing visitor frequency at the new enclosure (Fig. 7).

3.2.1.2 OVERALL ACTIVITY OLD VS. NEW ENCLOSURE

Rovan



Siska



Sky

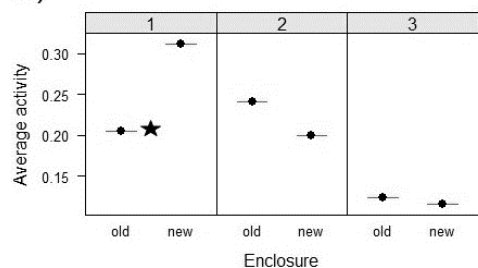


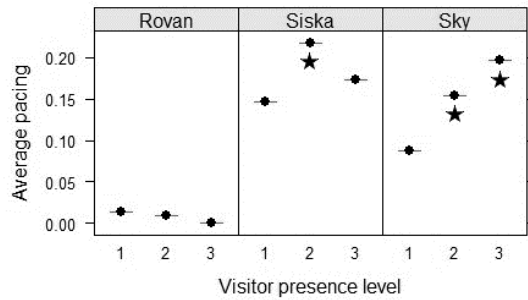
Figure 8 Comparisons between the average amount of activity (every recorded behaviour except resting and pacing) of each wolf in the old and in the new enclosure per visitor presence level. 1= no visitors, 2= one group of visitors, 3= multiple groups of visitors. An average amount of activity of 1 means always active with this visitor presence level, an average amount of activity of 0 means never active with this visitor presence level. Visitor presence levels where the average amount of activity between the old and the new enclosure was significantly different are marked with a star ($p < 0.05$). (Results of the statistical analysis in Table A.4)

Rovan and Siska were significantly more active in the old enclosure when visitors were present. Siska was less active in the old enclosure when no visitors were at the enclosure, as was Sky. Sky showed no significant difference in activity with visitors around (Fig. 8).

3.2.1.3 PACING

Old enclosure

1: n=1923, 2: n=331, 3: n=81



New enclosure

1: n=1636, 2: n=457, 3: n=130

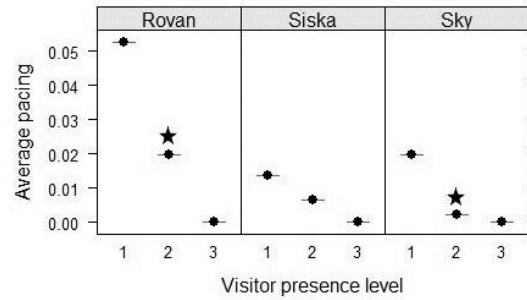
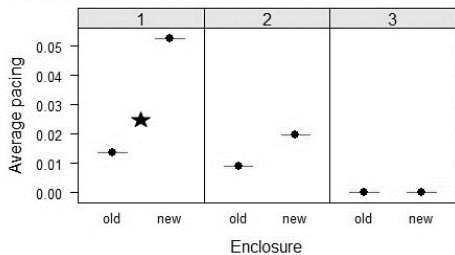


Figure 9 Average amount of pacing behaviour per visitor presence level over the course of the entire observation period. 1= no visitors, 2= one group of visitors, 3= multiple groups of visitors. An average amount of pacing of 1 means always pacing with this visitor presence level, an average amount of pacing of 0 means never pacing with this visitor presence level. Visitor presence levels where the average amount of pacing behaviour within a wolf is significantly different to level 1 are marked with a star ($p < 0.05$). (Results of the statistical analysis in Table A.6)

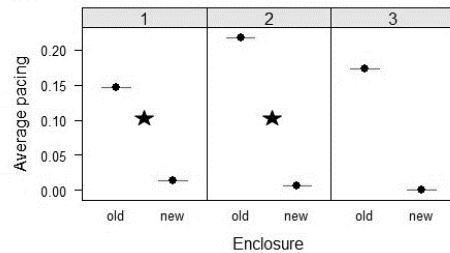
Rován showed no significant effect on pacing when faced with visitors in the old enclosure, while Sky particularly showed significantly more pacing with an increasing visitor frequency. Both Rován and Sky showed decreasing levels of pacing with an increasing visitor frequency in the new enclosure (Fig. 9).

3.2.1.4 PACING OLD VS. NEW ENCLOSURE

Rován



Siska



Sky

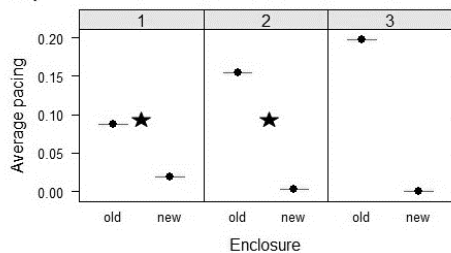


Figure 10 Comparisons between the average amount of pacing behaviour of each wolf in the old and in the new enclosure per visitor presence level. 1= no visitors, 2= one group of visitors, 3= multiple groups of visitors. An average amount of pacing of 1 means always pacing with this visitor presence level, an average amount of pacing of 0 means never pacing with this visitor presence level. Visitor presence levels where the average amount of pacing behaviour between the old and the new enclosure was significantly different are marked with a star ($p < 0.05$). (Results of the statistical analysis in Table A.5)

Rován paced significantly more when no visitors were near the new enclosure, but showed no difference in pacing with varying visitor levels. Siska and Sky both paced significantly less when no or only one group of visitors was at the new enclosure (Fig.10).

3.2.2 STAFF PRESENCE

3.2.2.1 OVERALL ACTIVITY

Old enclosure

1: n=2179, 2: n=143, 3: n=13

New enclosure

1: n=2035, 2: n=131, 3: n=57

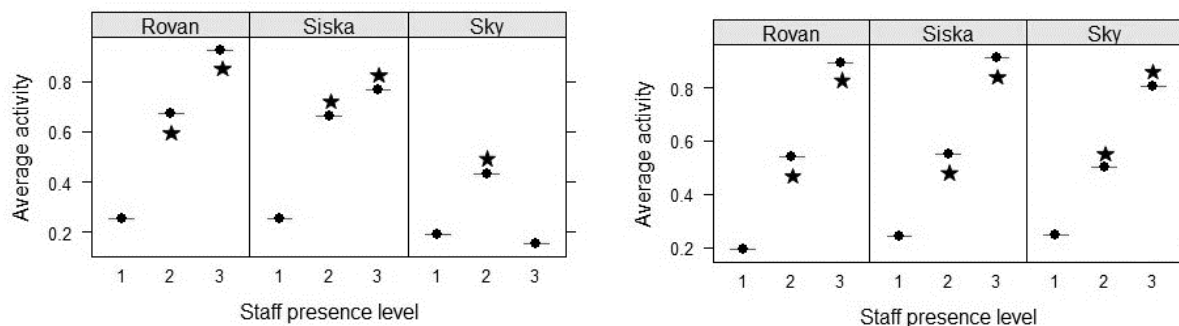
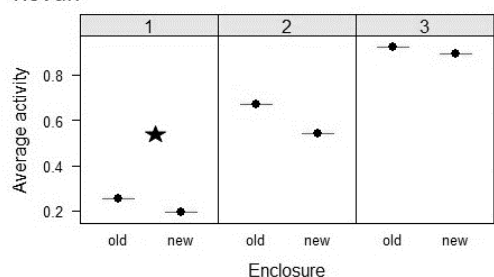


Figure 11 Average activity (every recorded behaviour except resting) per staff presence level over the course of the entire observation period. 1= no staff around, 2= staff nearby, 3= staff in or at enclosure. An average activity of 1 means always active with this staff presence level, an average activity of 0 means never active with this staff presence level. Staff presence levels where the average amount of activity within a wolf is significantly different to level 1 are marked with a star ($p < 0.05$). (Results of the statistical analysis in Table A.3)

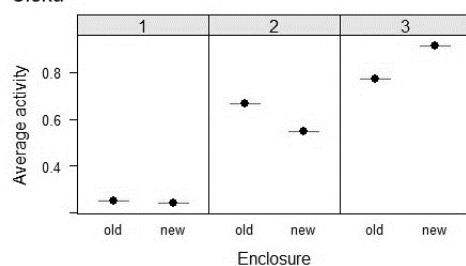
All three wolves showed increased levels of activity with staff members near the old or the new enclosure. In both the old and the new enclosure Rovan and Siska also exhibited an increased level of activity when staff was in the enclosure, Sky only showed an increase in overall activity when staff was in the new enclosure (Fig. 11).

3.2.2.2 OVERALL ACTIVITY OLD VS. NEW ENCLOSURE

Rovan



Siska



Sky

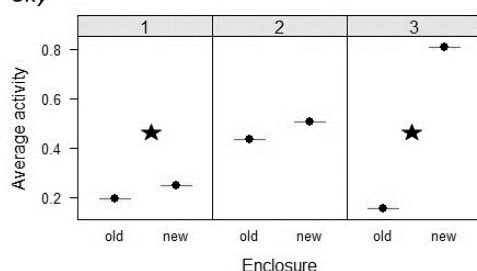


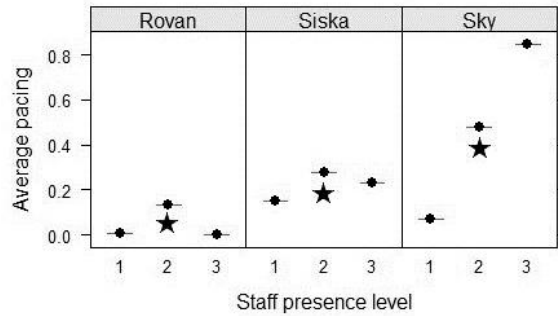
Figure 12 Comparisons between the average amount of activity (every recorded behaviour except resting and pacing) of each wolf in the old and in the new enclosure per staff presence level. 1= no staff around, 2= staff nearby, 3= staff in or at enclosure. An average amount of activity of 1 means always active with this staff presence level, an average amount of activity of 0 means never active with this staff presence level. Staff presence levels where the average amount of activity between the old and the new enclosure was significantly different are marked with a star ($p < 0.05$). (Results of the statistical analysis in Table A.4)

Rovan was significantly less active when no staff was nearby the new enclosure, but showed no significant difference in activity when staff was nearby. Sky was significantly more active when no staff was nearby and when staff was in the new enclosure, while Siska showed no difference in activity in relation to staff presence between the old and the new enclosure (Fig. 12).

3.2.2.3 PACING

Old enclosure

1: n=2179, 2: n=143, 3: n=13



New enclosure

1: n=2035, 2: n=131, 3: n=57

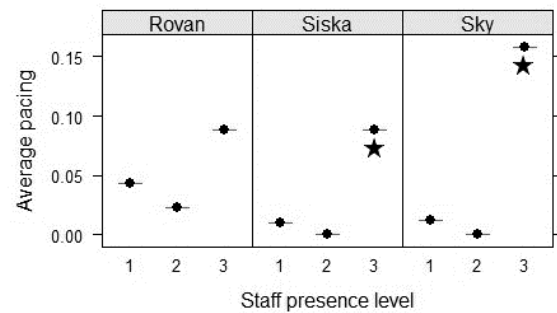
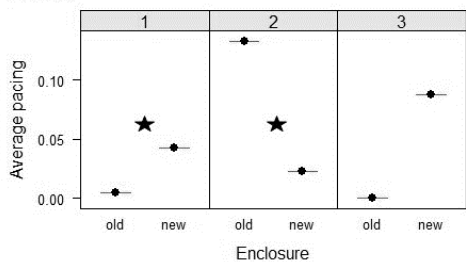


Figure 13 Average amount of pacing behaviour per staff presence level over the course of the entire observation period. 1= no staff around, 2= staff nearby, 3= staff in or at enclosure. An average amount of pacing of 1 means always pacing with this staff presence level, an average amount of pacing of 0 means never pacing with this staff presence level. Staff presence levels where the average amount of pacing behaviour within a wolf is significantly different to level 1 are marked with a star ($p < 0.05$). (Results of the statistical analysis in Table A.6)

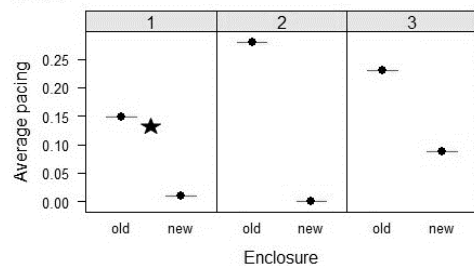
All three wolves only exhibited significantly higher levels of pacing in the old enclosure with staff nearby. Rován showed no significant difference in pacing in the new enclosure with changing staff presence. Both Sky and Siska showed a significant increase in pacing when staff was in or at the enclosure (Fig. 13).

3.2.2.4 PACING OLD VS. NEW ENCLOSURE

Rován



Siska



Sky

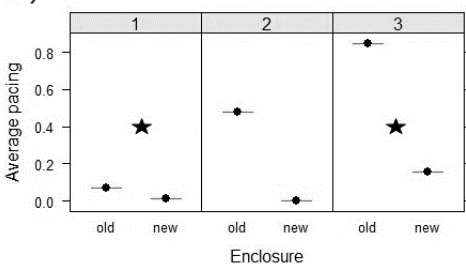


Figure 14 Comparisons between the average amount of pacing behaviour of each wolf in the old and in the new enclosure per staff presence level. 1= no staff around, 2= staff nearby, 3= staff in or at enclosure. An average amount of pacing of 1 means always pacing with this staff presence level, an average amount of pacing of 0 means never pacing with this staff presence level. Staff presence levels where the average amount of pacing behaviour between the old and the new enclosure was significantly different are marked with a star ($p < 0.05$). (Results of the statistical analysis in Table A.5)

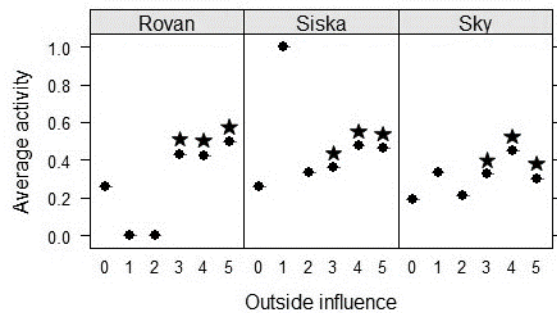
Rován showed significantly more pacing while no staff was nearby the new enclosure, while he paced less when staff was nearby. Siska and Sky both paced less in the new enclosure when no staff was nearby, but Sky also paced less in the new enclosure when staff was in or at the enclosure (Fig. 14).

3.2.3 OUTSIDE INFLUENCES, DISTURBANCES

3.2.3.1 OVERALL ACTIVITY

Old enclosure

0: n=1722, 1: n=3, 2: n=33, 3: n=358, 4: n=71, 5: n=164



New enclosure

0: n=1685, 1: n=4, 2: n=9, 3: n=150, 4: n=111, 5: n=280

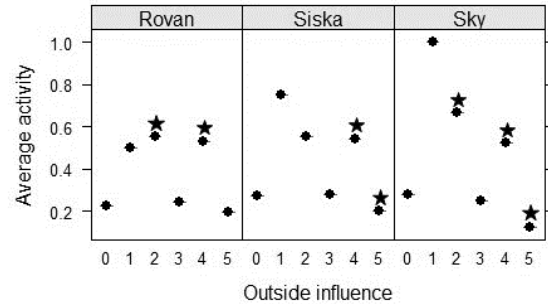
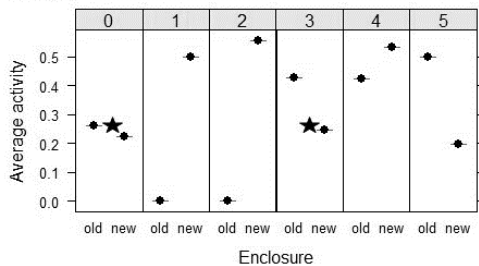


Figure 15 Average amount of activity (every recorded behaviour except resting) per outside influence over the course of the entire observation period. 0= no disturbances, 1= raven interactions, 2= plane/helicopter, 3= construction work, 4= car, 5= animal carcass. An average amount of activity of 1 means always active with this outside influence, an average activity of 0 means never active with this outside influence. Outside influences where the average amount of activity within a wolf is significantly different to level 1 are marked with a star ($p < 0.05$). (Results of the statistical analysis in Table A.7)

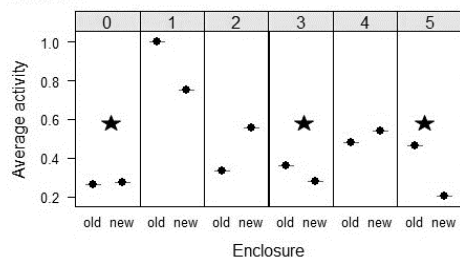
All three wolves were significantly more active in the old enclosure when disturbed by construction noises, cars and during animal carcass feedings. The low number of occurrences of raven interactions was the only reason this was not significant in both Siska and Sky, as was the case with the raven interactions in the new enclosure. In the new enclosure both Siska and Sky reacted significantly less to an animal carcass feeding, while the significantly increased reaction to planes in Rován and Sky was a new occurrence in the new enclosure (Fig. 15).

3.2.3.2 OVERALL ACTIVITY OLD VS. NEW ENCLOSURE

Rován



Siska



Sky

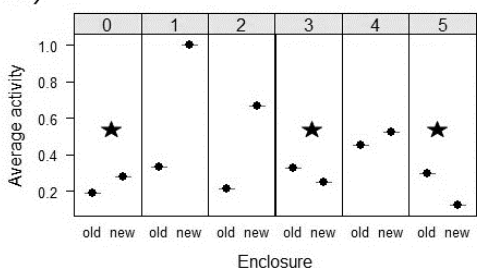


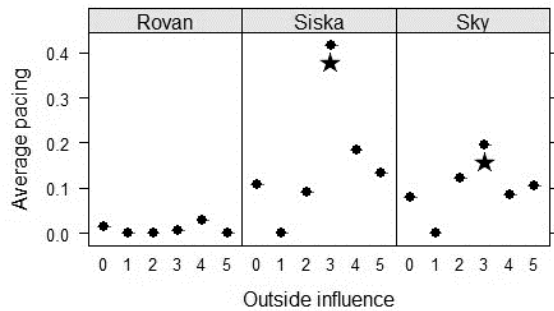
Figure 16 Comparisons between the average amount of activity (every recorded behaviour except resting) of each wolf in the old and in the new enclosure per outside influence. 0= no disturbances, 1= raven interactions, 2= plane/helicopter, 3= construction work, 4= car, 5= animal carcass. An average amount of activity of 1 means always active with this outside influence, an average activity of 0 means never active with this outside influence. Outside influences where the average amount of activity between the old and the new enclosure was significantly different are marked with a star ($p < 0.05$). (Results of the statistical analysis in Table A.9)

Both Siska and Sky were significantly more active with no influences in the new enclosure, while Rován was significantly less active. All three wolves were less active during construction noise in the new enclosure. Siska and Sky both showed significantly less activity during carcass feedings in the new enclosure (Fig. 16).

3.2.3.3 PACING

Old enclosure

0: n=1722, 1: n=3, 2: n=33, 3: n=358, 4: n=71, 5: n=164



New enclosure

0: n=1685, 1: n=4, 2: n=9, 3: n=150, 4: n=111, 5: n=280

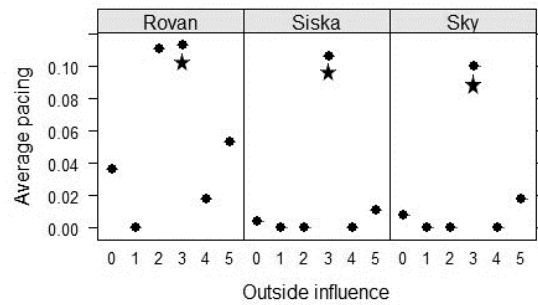
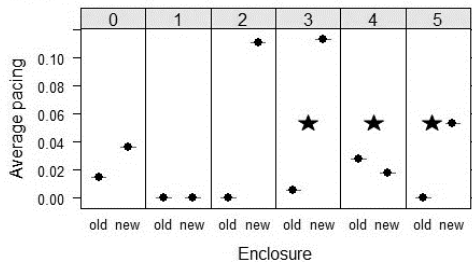


Figure 17 Average amount of pacing behaviour per outside influence over the course of the entire observation period. 0= no disturbances, 1= raven interactions, 2= plane/helicopter, 3= construction work, 4= car, 5= animal carcass. An average amount of pacing of 1 means always pacing with this outside influence, an average amount of pacing of 0 means never pacing with this outside influence. Outside influences where the average amount of pacing behaviour within a wolf is significantly different to level 1 are marked with a star ($p < 0.05$). (Results of the statistical analysis in Table A.8)

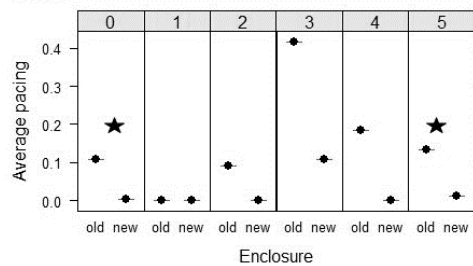
Rován showed no significant effect on pacing when faced with different outside influences in the old enclosure, while both Siska and Sky showed significantly more pacing when confronted with construction noise. All three wolves reacted to construction noise in the new enclosure with a significant increase in pacing. Rován's reaction to planes was not significant due to the small sample size (Fig. 17).

3.2.3.4 PACING OLD VS. NEW ENCLOSURE

Rován



Siska



Sky

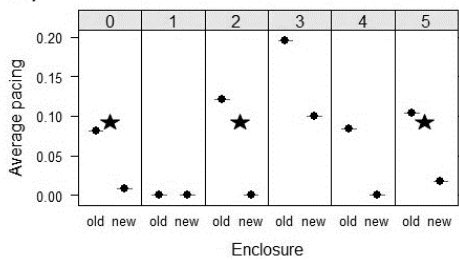
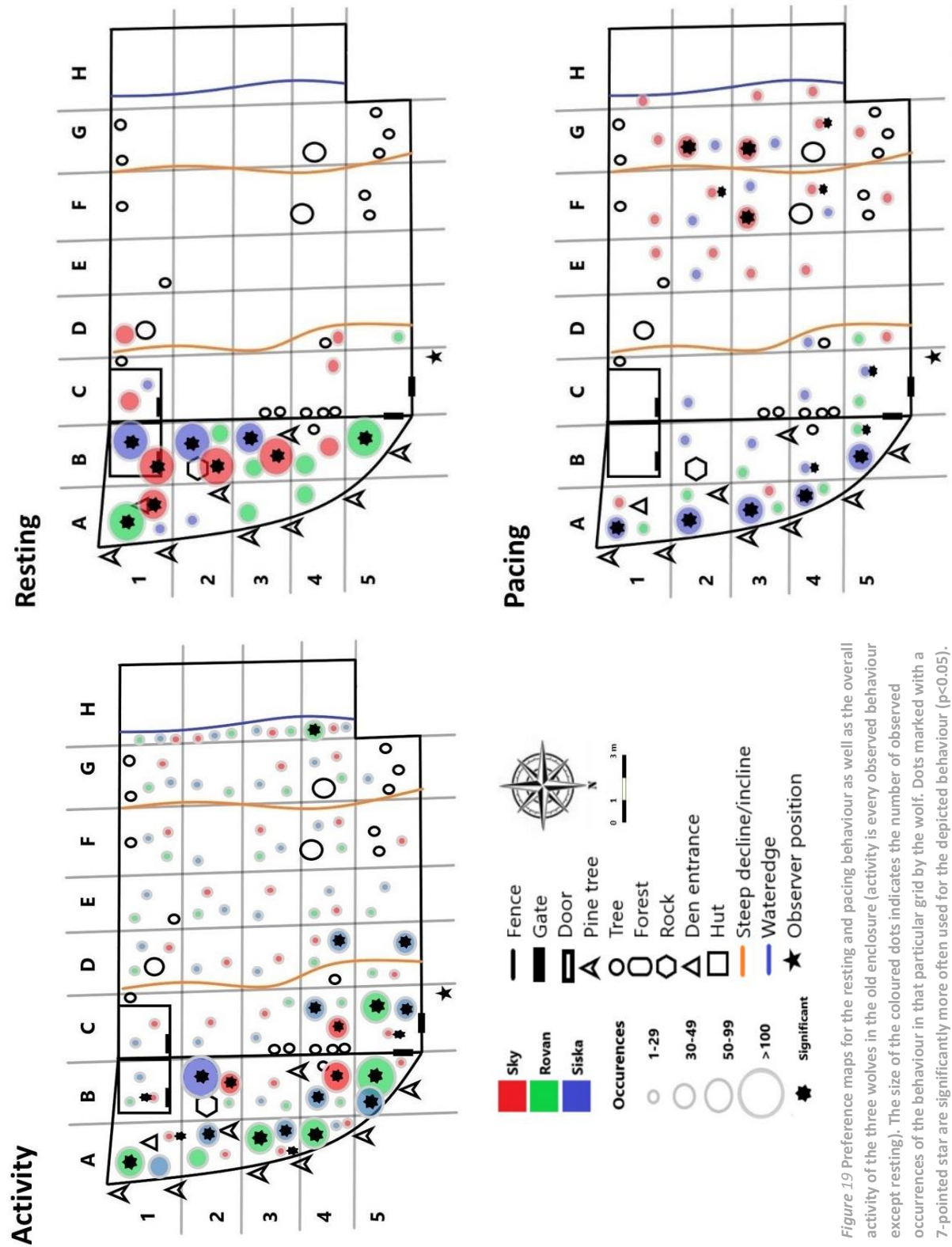


Figure 18 Comparisons between the average amount of pacing behaviour of each wolf in the old and in the new enclosure per outside influence. 0= no disturbances, 1= raven interactions, 2= plane/helicopter, 3= construction work, 4= car, 5= animal carcass. An average amount of pacing of 1 means always pacing with this outside influence, an average pacing of 0 means never pacing with this outside influence. Outside influences where the average amount of pacing between the old and the new enclosure was significantly different are marked with a star ($p < 0.05$). (Results of the statistical analysis in Table A.9)

Rován paced significantly more in the new enclosure during construction noise and carcass feedings, but less with cars driving by the new enclosure. Both Siska and Sky paced less while there were no disturbances in the new enclosure and during carcass feeding. Sky also reacted significantly less to overflying planes and helicopters (Fig. 18).

3.3 BEHAVIOURAL SPATIAL PATTERNS

Old enclosure location maps



3.3.1 OLD ENCLOSURE

The significantly higher frequencies of observed resting behaviour in A1 and B5 showed Rovans preference for resting in these grids. While Siska and Sky both showed a significant preference for the grids B1, B2 and B3. Sky also showed a preference for the grid A1 (Fig. 19).

Rovan was overall only a few times observed pacing in the old enclosure (n=29), but those observations were made significantly more often in grid B5. Siska paced significantly more often in grids A1 - A4, B4, B5 and C5. Her route followed the fence in the higher part of the enclosure, while Skys route was along the edge of the water in the lower part of the enclosure, shown by the significantly higher frequencies in the grids F1 - F4 and G1 - G4.

Rovan showed a significant preference for grids A1, A3, A4, B5 and C5 for all activity related behaviour. Siska also preferred the higher part of the enclosure and showed a significant preference for grids A1 - A3, B2, B5 and C5. While Sky also showed a significant amount of activity in the higher parts of the enclosure in grids A1, B2, B4, B5, C4, C5, he also showed a significant preference for F2 - F4 and G1 - G4 in the lower part of the enclosure.

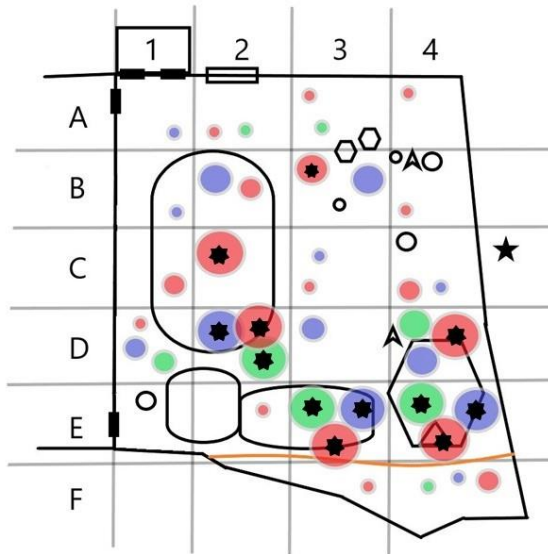
3.3.2 NEW ENCLOSURE

In the new enclosure all three wolves showed a significant preference for resting in the grids 2D, 3E and 4E. Sky also rested significantly more in the grids 2C, 3B and 4D (Fig. 20).

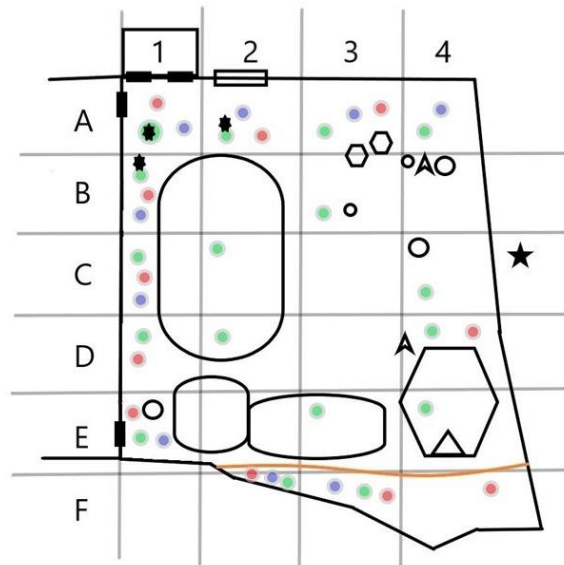
Pacing frequencies of the three wolves in the new enclosure seemed opposite to the old enclosure. Both Siska and Sky were only observed pacing a few times (n=25 and n=33) in the new enclosure, this was not enough to see a significant pattern for the two. Rovan showed a significant preference for passing through grids 1A, 1B and 2A while pacing.

Activity seemed not to be isolated to a few grids, the whole enclosure was used quite evenly by all three wolves, although there was a slight preference to grid 4E for all three wolves. Siska was also observed significantly more often in grid 4D and Rovan in 1A.

Resting



Pacing



Activity

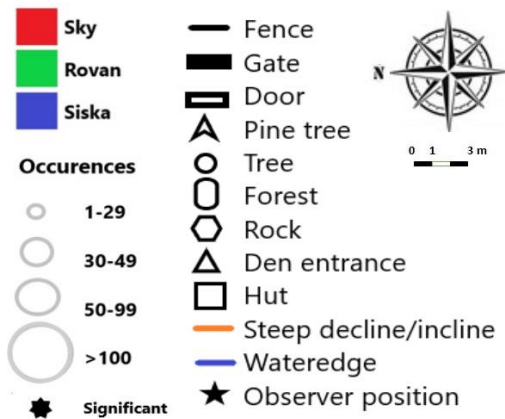
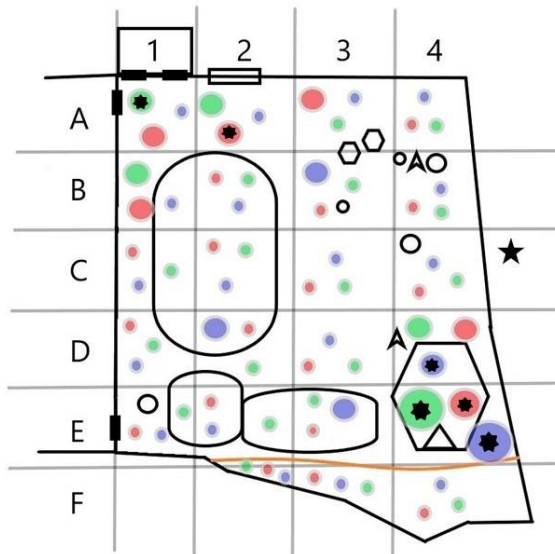


Figure 20 Location maps for the resting and pacing behaviour as well as the overall activity of the three wolves in the new enclosure (activity is every observed behaviour except resting). The size of the coloured dots indicates the number of observed occurrences of the behaviour in that particular grid by the wolf. Dots marked with a 7-pointed star are significantly more often used for the depicted behaviour ($p < 0.05$).

4 DISCUSSION

4.1 OLD ENCLOSURE (BEHAVIOURAL AND TEMPORAL BASELINE)

Observing the wolves in the old enclosure showed that they indeed had a preference for certain parts of the enclosure for species-specific behaviour, as was described in other wild and captive carnivores (Vilà 1995; Ciucci et al. 1997; Mallapur 1999; Frézard & Le Pape 2003; Gunning n.d.). The maps in figure 19 show a clear concentration of species-specific behaviour, like resting and activity, for all three wolves in the higher elevated part of the enclosure. Stereotypical behaviour was concentrated along the fence in the upper part of the enclosure for Siska and along the water in the lower part for Sky.

Resting was the most prevalent behaviour during the day for all three wolves. They were most active shortly after sunrise until after feeding time in the morning. The strict feeding routine for the wolves led to peaks in movement, stereotypical behaviour and vigilance before and during the feeding. The increase in pacing and vigilance shortly before feeding time indicates anticipation in Siska (Carlstead 1998; Weller & Bennett 2001), while Skys peek in pacing during the feeding seemed to indicate anxiety.

The hypothesised increase in stereotypical behaviours with rising visitor numbers was found in both Siska and Sky, but only Sky showed a significant decrease in activity related behaviour, thus an increase in resting, with rising visitor numbers when not pacing just as found in previous studies (Chamove et al. 1988; Mallapur et al. 2005; Sellinger & Ha 2005; Davey 2006; Quadros et al. 2014). Rovans pacing and other activity related behaviours were not significantly influenced but showed a slight decrease with rising visitor numbers. As previously predicted, the three wolves reacted with higher levels of stereotypic and activity related behaviour when staff was near the enclosure. This was likely due to the fact that staff was only near the wolves' enclosure shortly before or during feeding time. Only Sky reacted with an increase in pacing when staff was at the enclosure. The wolves also reacted with an increase in overall activity related behaviours to construction noise, passing cars and carcass feedings. Only Siska and Sky showed an increase in pacing when faced with construction noise, compared to times without any other disturbances.

Overall Siska and Sky reacted with significantly higher levels of pacing and activity related behaviours to any disturbances at the old enclosure, while Rovans was much more laid back and spent overall significantly less time pacing as the other two wolves.

4.2 NEW ENCLOSURE

Unlike the old enclosure, the maps in Fig. 20 show no definite location preference for species-specific behaviour indicating that the pack has not yet acclimatised, since studies found that wolves in zoos, generally use only parts of their enclosure for species-specific behaviours (Mallapur 1999; Frézard & Le Pape 2003; Gunning n.d.). Resting seemed to be mostly done in wooded areas or around the den, although mostly only Rovans seemed to use the den itself during the day. Pacing again occurred predominantly along the boundary of the fence, but was less evident than in the old enclosure.

Resting was the most dominant behaviour during the day just like in the old enclosure. However, both Siska and Sky showed a significant decrease in pacing in the new enclosure, while Rovans time spent pacing increased. This decrease in pacing in both Siska and Sky could be seen as a positive reaction to the new enclosure, due to more space and more hiding places. The presence of a synchronisation in resting behaviour, however, seemed to indicate that the decrease in stereotypical behaviour was more related to stress (Sulser et al. 2008; Meagher et al. 2013). The wolves still showed a decrease in resting shortly after sunrise, but the increase in activity and pacing was only caused by the presence of staff members at the neighbouring bear enclosure, since the wolves were fed during changing times in the afternoon.

All three wolves were less active with rising visitor numbers, which was originally expected, since other studies showed that animals spent more time hiding when visitor numbers rise (Chamove et al. 1988; Mallapur et al. 2005; Sellinger & Ha 2005; Davey 2006; Quadros et al. 2014). But, unlike those studies, all three wolves paced less with rising visitor numbers, Rován and Sky significantly so. Comparing the reaction to visitors in the old and in the new enclosure, both Rován and Siska reacted significantly less with active behaviour when more visitors were at the new enclosure. Sky did not show a difference in activity when visitors were at the enclosure, but, like Siska, was significantly more active in the new enclosure when no visitors were around. Siska and Sky both showed a decrease in pacing when visitors were around, while Rován showed an increase in pacing when no visitors were around.

Like in the old enclosure, the wolves reacted with an increase in activity when staff members were near or at the enclosure, but pacing was only significantly increased in Siska and Sky when staff was in the enclosure. Also, when comparing the data from the new enclosure with the old enclosure Sky showed an increase in activity and a decrease in pacing when no staff was around or when staff was in the enclosure. Siska only showed a decrease in pacing when no staff was around, while Rován was less active when no staff was around but paced significantly more during those instances.

Unlike the old enclosure, construction noise only caused an increase in pacing, not in overall activity. All three still reacted with an increase in activity to cars driving by and during the event of a carcass feeding, but both Rován and Sky now also reacted to overflying planes and helicopters with an increase in overall activity. Both Siska and Sky were more active and paced less in the new enclosure when no disturbances took place but were less active during construction noise and carcass feedings. Both also paced less during those feedings. Rován was less active when no disturbances took place and just like the other two was also less active during construction noise. However, he showed an increase in pacing during times with construction noise and during carcass feedings.

While the time spent pacing was overall less in the new enclosure, Rován showed an increase in pacing, in relation to the old enclosure. The synchronisation of resting and resting location indicates a higher level of stress in the new enclosure. This could be caused by the transfer itself, the new environment or the increase in construction noise after the transfer.

4.3 ACCLIMATISATION

The first few weeks after the transfer into the new enclosure both Siska and Sky spent much less time pacing than before, while Rován showed a sudden incline in pacing. After a few weeks all three wolves started pacing more again, unlike the old enclosure, where Rován paced significantly less than the other two wolves.

The sudden decline in resting and pacing and the incline in activity in week 9 seemed to be a random event, since there were no changes in visitor and staff movement and weather that could explain the sudden differences between weeks 8 and 10 and week 9. But the steeper inclines and declines in the graphs in Fig. 6 after the transfer seem to indicate that 10 weeks were not enough for the wolves to acclimatise in the new enclosure. Especially since synchronisation of the wolves' behaviour was only visible from week 7 after the transfer onwards, this could be a result of the relatively short-term process of adaptation and acclimatisation to the environment (Ross et al. 2011). Other studies used much longer periods to observe the acclimatisation period (6 months (Ogden et al. 1990) or 1 year (Ross et al. 2011)), new observations of the wolves a year after transfer could paint a finalised picture of the behaviour in the new enclosure.

5 CONCLUSION

While the transfer definitely had an impact on the behaviour of the wolves, the 10-week observation period was not long enough to see if the new enclosure had a positive effect on the stereotypical behaviour and promoted species-specific behaviour. The data indicated a decline in stereotypical route tracing and an increase in species-specific behaviours, like resting during the day, but it is safe to say that those behavioural changes also could be an indicator of stress due to the new environment. The overall decrease in activity and pacing during disturbances like rising visitor numbers, could indicate an appropriate new enclosure with hiding places to feel safer during busy daytime hours.

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7.1 BEHAVIOURAL AND TEMPORAL PATTERNS

7.1.1 RESULTS OTHER OBSERVED BEHAVIOURS

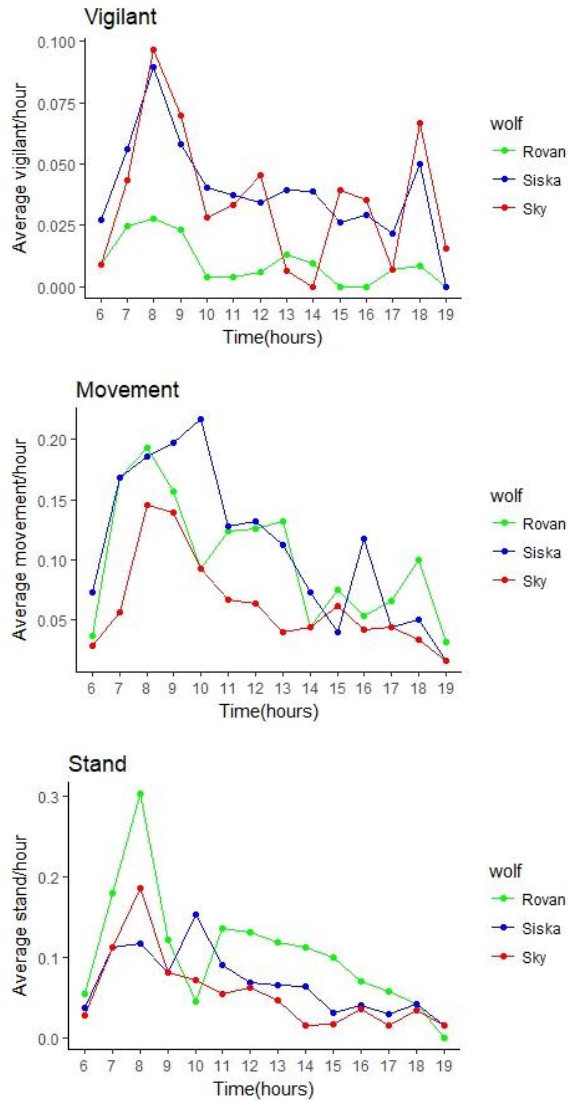
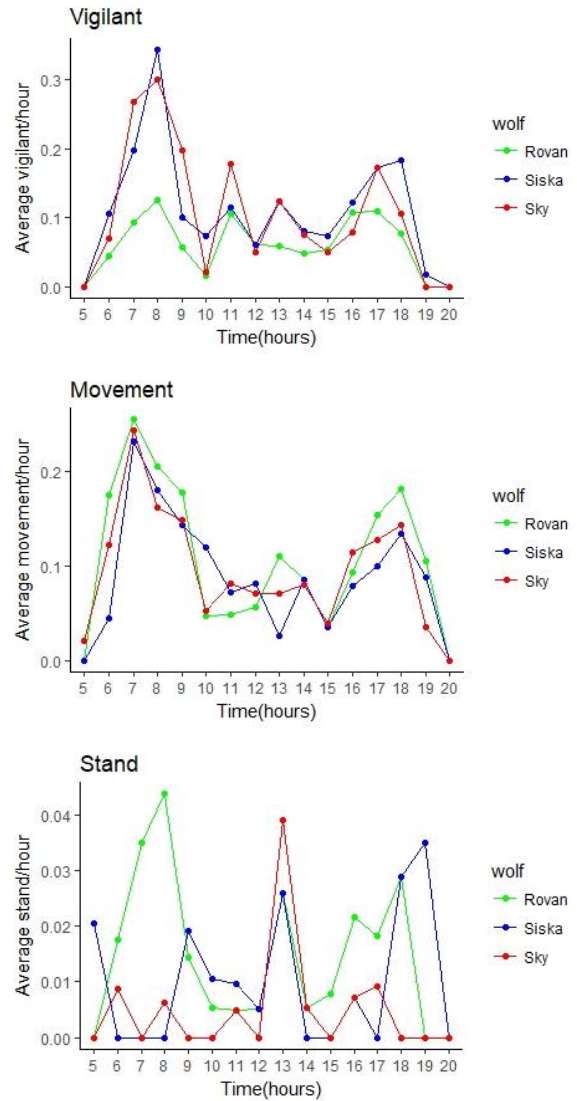
Old enclosure*New enclosure*

Figure A.1 Average behaviour per hour for every wolf in both old and new enclosure. A higher peak indicates a higher recorded average presence of this behaviour during the respective hour. These behaviours were not tested because the number of observations per wolf was <280 for all wolves. This was deemed a too small number to get accurate results. Other observed behaviours had an even lower number of observations (see table A.1 and table A.2).

7.1.1.2 OLD VS. NEW ENCLOSURE

<i>Resting</i>				<i>Pacing</i>			
<i>Rovan</i>				<i>Rovan</i>			
	<i>estimate</i>	<i>SE</i>	<i>p-value</i>		<i>estimate</i>	<i>SE</i>	<i>p-value</i>
<i>new vs old</i>	0.0202	0.0137	N.S.	<i>new vs old</i>	0.0303	0.0067	<.0001
<i>Siska</i>				<i>Siska</i>			
	<i>estimate</i>	<i>SE</i>	<i>p-value</i>		<i>estimate</i>	<i>SE</i>	<i>p-value</i>
<i>new vs old</i>	0.1502	0.0137	<.0001	<i>new vs old</i>	-0.1459	0.0067	<.0001
<i>Sky</i>				<i>Sky</i>			
	<i>estimate</i>	<i>SE</i>	<i>p-value</i>		<i>estimate</i>	<i>SE</i>	<i>p-value</i>
<i>new vs old</i>	0.0160	0.0137	N.S.	<i>new vs old</i>	-0.0854	0.0067	<.0001

Table A.1 Table showing the results of the analysis comparing the average resting and pacing behaviour of each wolf between the old and the new enclosure. Significant values mean that there is a difference in behaviour in this wolf between the old and the new enclosure.

7.1.3 ACCLIMATISATION

<i>Resting</i>				<i>Pacing</i>			
<i>Rovan</i>				<i>Rovan</i>			
<i>contrast</i>	<i>estimate</i>	<i>SE</i>	<i>p-value</i>	<i>contrast week</i>	<i>estimate</i>	<i>SE</i>	<i>p-value</i>
-3 – 2	0.1257	0.0281	0.0007	-3 – 2	-0.0889	0.0138	<.0001
-3 – 8	0.3645	0.0550	<.0001	-3 – 8	-0.1358	0.0269	<.0001
2 – 8	0.2388	0.0539	0.0008	2 – 8	-0.0469	0.0264	N.S.
<i>Siska</i>				<i>Siska</i>			
<i>contrast week</i>	<i>estimate</i>	<i>SE</i>	<i>p-value</i>	<i>contrast week</i>	<i>estimate</i>	<i>SE</i>	<i>p-value</i>
-3 – 2	-0.0730	0.0281	N.S.	-3 – 2	0.0979	0.0138	<.0001
-3 – 8	0.2357	0.0550	0.0015	-3 – 8	0.0523	0.0269	N.S.
2 – 8	0.3087	0.0539	<.0001	2 – 8	-0.0456	0.0264	N.S.
<i>Sky</i>				<i>Sky</i>			
<i>contrast week</i>	<i>estimate</i>	<i>SE</i>	<i>p-value</i>	<i>contrast week</i>	<i>estimate</i>	<i>SE</i>	<i>p-value</i>
-3 – 2	-0.0264	0.0281	N.S.	-3 – 2	0.1129	0.0138	<.0001
-3 – 8	0.2840	0.0550	<.0001	-3 – 8	0.0292	0.0269	N.S.
2 – 8	0.3103	0.0539	<.0001	2 – 8	-0.0836	0.0264	0.0857
<i>Activity</i>							
<i>Rovan</i>							
<i>contrast week</i>	<i>estimate</i>	<i>SE</i>	<i>p-value</i>				
-3 – 2	-0.0369	0.02669	N.S.				
-3 – 8	-0.2287	0.05214	0.0010				
2 – 8	-0.1918	0.05110	0.0127				
<i>Siska</i>							
<i>contrast week</i>	<i>estimate</i>	<i>SE</i>	<i>p-value</i>				
-3 – 2	-0.0249	0.02669	N.S.				
-3 – 8	-0.2880	0.05214	<.0001				
2 – 8	-0.2631	0.05110	<.0001				
<i>Sky</i>							
<i>contrast week</i>	<i>estimate</i>	<i>SE</i>	<i>p-value</i>				
-3 – 2	-0.0865	0.02669	0.0705				
-3 – 8	-0.3132	0.05214	<.0001				
2 – 8	-0.2267	0.05110	0.0008				

Table A.2 Table with the results of a pairwise model testing the difference in each depicted behaviour between the old and the new enclosure. Significant values indicate a difference in behaviour between before and after the transfer.

7.2 ZOO VISITOR EFFECT

7.2.1 VISITORS AND STAFF

7.2.1.1 ACTIVITY

<i>Visitors</i>							
<i>Old enclosure</i>				<i>New enclosure</i>			
<i>Rovan</i>				<i>Rovan</i>			
	<i>estimate</i>	<i>SE</i>	<i>p-value</i>		<i>estimate</i>	<i>SE</i>	<i>p-value</i>
<i>Intercept</i>	-0.9098	0.0504	<.0001	<i>Intercept</i>	-0.9599	0.0553	<.0001
<i>Level 2</i>	-0.0752	0.1334	N.S.	<i>Level 2</i>	-1.0087	0.1530	<.0001
<i>Level 3</i>	-0.3430	0.2719	N.S.	<i>Level 3</i>	-1.9064	0.3925	<.0001
<i>Siska</i>				<i>Siska</i>			
	<i>estimate</i>	<i>SE</i>	<i>p-value</i>		<i>estimate</i>	<i>SE</i>	<i>p-value</i>
<i>Intercept</i>	-1.0378	0.0519	<.0001	<i>Intercept</i>	-0.8322	0.0538	<.0001
<i>Level 2</i>	0.4340	0.1261	0.0006	<i>Level 2</i>	-0.5056	0.1272	<.0001
<i>Level 3</i>	0.8147	0.2296	0.0004	<i>Level 3</i>	-0.6532	0.2324	0.0050
<i>Sky</i>				<i>Sky</i>			
	<i>estimate</i>	<i>SE</i>	<i>p-value</i>		<i>estimate</i>	<i>SE</i>	<i>p-value</i>
<i>Intercept</i>	-1.3528	0.0565	<.0001	<i>Intercept</i>	-0.7920	0.0534	<.0001
<i>Level 2</i>	0.2094	0.1403	N.S.	<i>Level 2</i>	-0.5998	0.1287	<.0001
<i>Level 3</i>	-0.6073	0.3425	0.0762	<i>Level 3</i>	-1.2449	0.2797	<.0001
<i>Staff</i>							
<i>Old enclosure</i>				<i>New enclosure</i>			
<i>Rovan</i>				<i>Rovan</i>			
	<i>estimate</i>	<i>SE</i>	<i>p-value</i>		<i>estimate</i>	<i>SE</i>	<i>p-value</i>
<i>Intercept</i>	-1.0810	0.0493	<.0001	<i>Intercept</i>	-1.4267	0.0561	<.0001
<i>Level 2</i>	1.7952	0.1847	<.0001	<i>Level 2</i>	1.5951	0.1841	<.0001
<i>Level 3</i>	3.5659	1.0412	0.0006	<i>Level 3</i>	3.5668	0.4352	<.0001
<i>Siska</i>				<i>Siska</i>			
	<i>estimate</i>	<i>SE</i>	<i>p-value</i>		<i>estimate</i>	<i>SE</i>	<i>p-value</i>
<i>Intercept</i>	-1.0834	0.0493	<.0001	<i>Intercept</i>	-1.1457	0.0518	<.0001
<i>Level 2</i>	1.7661	0.1838	<.0001	<i>Level 2</i>	1.3448	0.1831	<.0001
<i>Level 3</i>	2.2874	0.6601	0.0005	<i>Level 3</i>	3.4875	0.4710	<.0001
<i>Sky</i>				<i>Sky</i>			
	<i>estimate</i>	<i>SE</i>	<i>p-value</i>		<i>estimate</i>	<i>SE</i>	<i>p-value</i>
<i>Intercept</i>	-1.4293	0.0543	<.0001	<i>Intercept</i>	-1.1111	0.0514	<.0001
<i>Level 2</i>	1.1620	0.1773	<.0001	<i>Level 2</i>	1.1264	0.1821	<.0001
<i>Level 3</i>	-0.2755	0.7706	N.S.	<i>Level 3</i>	2.5419	0.3395	<.0001

Table A.3 Table with the results of the analysis on differences in average amount of activity per visitor and per staff presence level. 1= no visitors, 2= one group of visitors, 3= multiple groups of visitors. 1= no staff around, 2= staff nearby, 3= staff in or at enclosure. Significant p-values for level 2 and 3 indicate a significant difference in activity between the level and the intercept (level 1 = no visitors or staff).

7.2.1.2 ACTIVITY OLD VS NEW

Visitors				Staff			
Rovan				Rovan			
	estimate	SE	p-value		estimate	SE	p-value
Level 1	0.0502	0.0748	N.S.	Level 1	0.3458	0.0747	<.0001
Level 2	0.9836	0.1887	<.0001	Level 2	0.5459	0.2499	N.S.
Level 3	1.6135	0.4716	0.0006	Level 3	0.3448	1.1268	N.S.
Siska				Siska			
	estimate	SE	p-value		estimate	SE	p-value
Level 1	-0.2056	0.0747	0.0059	Level 1	0.0623	0.0715	N.S.
Level 2	0.7340	0.1628	<.0001	Level 2	0.4835	0.2494	N.S.
Level 3	1.2622	0.3180	<.0001	Level 3	-1.1378	0.8078	N.S.
Sky				Sky			
	estimate	SE	p-value		estimate	SE	p-value
Level 1	-0.5608	0.0777	<.0001	Level 1	-0.3182	0.0747	<.0001
Level 2	0.2483	0.1738	N.S.	Level 2	-0.2826	0.2429	N.S.
Level 3	0.0768	0.4353	N.S.	Level 3	-3.1355	0.8388	0.0002

Table A.4 Results of the analysis comparing the average activity for each visitor and staff level between the old and the new enclosure. 1= no visitors, 2= one group of visitors, 3= multiple groups of visitors. 1= no staff around, 2= staff nearby, 3= staff in or at enclosure. Significant p-values indicate a significant difference in behaviour between the old and the new enclosure for the same level of visitor or staff presence.

7.2.1.3 PACING OLD VS NEW

Visitors				Staff			
Rovan				Rovan			
	estimate	SE	p-value		estimate	SE	p-value
Level 1	-1.3983	0.2264	<.0001	Level 1	-2.2708	0.3354	<.0001
Level 2	-0.7868	0.6706	N.S.	Level 2	1.8776	0.6339	0.0031
Level 3	-4.539e ⁻¹⁴	5.041e ⁰⁴	N.S.	Level 3	-17.2243	2982.627	N.S.
Siska				Siska			
	estimate	SE	p-value		estimate	SE	p-value
Level 1	2.5301	0.2241	<.0001	Level 1	2.8677	0.2326	<.0001
Level 2	3.7393	0.5943	<.0001	Level 2	18.62	939.58	N.S.
Level 3	19.00	1555.06	N.S.	Level 3	1.1378	0.8078	N.S.
Sky				Sky			
	estimate	SE	p-value		estimate	SE	p-value
Level 1	1.5617	0.1960	<.0001	Level 1	1.8589	0.2216	<.0001
Level 2	4.420	1.012	<.0001	Level 2	19.47	939.58	N.S.
Level 3	19.16	1555.06	N.S.	Level 3	3.3787	0.8502	<.0001

Table A.5 Results of the analysis comparing the average pacing for each visitor and staff level between the old and the new enclosure. 1= no visitors, 2= one group of visitors, 3= multiple groups of visitors. 1= no staff around, 2= staff nearby, 3= staff in or at enclosure. Significant p-values indicate a significant difference in behaviour between the old and the new enclosure for the same level of visitor or staff presence.

7.2.1.4 PACING

<i>Visitors</i>							
<i>Old enclosure</i>				<i>New enclosure</i>			
<i>Rovan</i>				<i>Rovan</i>			
	<i>estimate</i>	<i>SE</i>	<i>p-value</i>		<i>estimate</i>	<i>SE</i>	<i>p-value</i>
<i>Intercept</i>	-4.2899	0.1975	<.0001	<i>Intercept</i>	-2.8917	0.1108	<.0001
<i>Level 2</i>	-0.4045	0.6127	N.S.	<i>Level 2</i>	-1.0159	0.3544	0.0042
<i>Level 3</i>	-14.2761	724.7376	N.S.	<i>Level 3</i>	-15.6744	572.0733	N.S.
<i>Siska</i>				<i>Siska</i>			
	<i>estimate</i>	<i>SE</i>	<i>p-value</i>		<i>estimate</i>	<i>SE</i>	<i>p-value</i>
<i>Intercept</i>	-1.7653	0.0646	<.0001	<i>Intercept</i>	-4.2954	0.2146	<.0001
<i>Level 2</i>	0.4852	0.1481	0.0001	<i>Level 2</i>	-0.7241	0.6177	N.S.
<i>Level 3</i>	0.1997	0.3009	N.S.	<i>Level 3</i>	-15.2706	943.1894	N.S.
<i>Sky</i>				<i>Sky</i>			
	<i>estimate</i>	<i>SE</i>	<i>p-value</i>		<i>estimate</i>	<i>SE</i>	<i>p-value</i>
<i>Intercept</i>	-2.3528	0.0810	<.0001	<i>Intercept</i>	-3.9145	0.1785	<.0001
<i>Level 2</i>	0.6498	0.1724	<.0001	<i>Level 2</i>	-2.2080	1.0169	0.0300
<i>Level 3</i>	0.9510	0.2906	0.0001	<i>Level 3</i>	-15.6515	943.1893	N.S.
<i>Staff</i>							
<i>Old enclosure</i>				<i>New enclosure</i>			
<i>Rovan</i>				<i>Rovan</i>			
	<i>estimate</i>	<i>SE</i>	<i>p-value</i>		<i>estimate</i>	<i>SE</i>	<i>p-value</i>
<i>Intercept</i>	-5.3794	0.3170	<.0001	<i>Intercept</i>	-3.1087	0.1096	<.0001
<i>Level 2</i>	3.5036	0.4014	<.0001	<i>Level 2</i>	-0.6448	0.5943	N.S.
<i>Level 3</i>	-12.1866	1097.2470	N.S.	<i>Level 3</i>	0.7668	0.4809	N.S.
<i>Siska</i>				<i>Siska</i>			
	<i>estimate</i>	<i>SE</i>	<i>p-value</i>		<i>estimate</i>	<i>SE</i>	<i>p-value</i>
<i>Intercept</i>	-1.7449	0.0602	<.0001	<i>Intercept</i>	-4.6126	0.2247	<.0001
<i>Level 2</i>	0.7991	0.1958	<.0001	<i>Level 2</i>	-14.9534	939.5825	N.S.
<i>Level 3</i>	0.5409	0.6610	N.S.	<i>Level 3</i>	2.2708	0.5194	<.0001
<i>Sky</i>				<i>Sky</i>			
	<i>estimate</i>	<i>SE</i>	<i>p-value</i>		<i>estimate</i>	<i>SE</i>	<i>p-value</i>
<i>Intercept</i>	-1.4293	0.0543	<.0001	<i>Intercept</i>	-4.4283	0.2053	<.0001
<i>Level 2</i>	1.1620	0.1773	<.0001	<i>Level 2</i>	-15.1377	939.5825	N.S.
<i>Level 3</i>	-0.2755	0.7706	N.S.	<i>Level 3</i>	2.7544	0.4173	<.0001

Table A.6 Table with the results of the analysis on differences in average amount of pacing per visitor and per staff presence level. 1= no visitors, 2= one group of visitors, 3= multiple groups of visitors. 1= no staff around, 2= staff nearby, 3= staff in or at enclosure. Significant p-values for level 2 and 3 indicate a significant difference in pacing between the level and the intercept (level 1 = no visitors or staff).

7.2.2 OUTSIDE INFLUENCES, DISTURBANCES

7.2.2.1 ACTIVITY

Activity							
Old enclosure				New enclosure			
Rovan				Rovan			
	estimate	SE	p-value		estimate	SE	p-value
Intercept	-1.1663	0.05663	<.0001	Intercept	-1.2960	0.0593	<.0001
Ravens	-14.3997	840.2742	N.S	Ravens	1.2960	1.0018	N.S
Helicopter/plane	-14.3997	253.3522	N.S	Helicopter/plane	1.5192	0.6734	0.0241
Construction	0.8738	0.1209	<.0001	Construction	0.1795	0.1985	N.S
Car seen/heard	0.4943	0.2572	0.0546	Car seen/heard	1.4223	0.1992	<.0001
Animal carcass	1.1664	0.1661	<.0001	Animal carcass	-0.1128	0.1617	N.S
Siska				Siska			
	estimate	SE	p-value		estimate	SE	p-value
Intercept	-1.1696	0.0567	<.0001	Intercept	-1.0126	0.0551	<.0001
Ravens	14.7356	309.1198	N.S.	Ravens	2.1112	1.1560	0.0678
Helicopter/plane	0.47642	0.3736	N.S.	Helicopter/plane	1.2358	0.6731	0.0664
Construction	0.6078	0.1237	<.0001.	Construction	0.0682	0.1900	N.S.
Car seen/heard	1.0850	0.2442	<.0001.	Car seen/heard	1.1751	0.1983	<.0001
Animal carcass	1.0230	0.1665	<.0001	Animal carcass	-0.3515	0.1583	0.0264
Sky				Sky			
	estimate	SE	p-value		estimate	SE	p-value
Intercept	-1.6263	0.0650	<.0001	Intercept	-0.9263	0.0540	<.0001
Ravens	0.9331	1.2265	N.S.	Ravens	14.4924	267.7056	N.S.
Helicopter/plane	0.3141	0.4308	N.S.	Helicopter/plane	1.6194	0.7092	0.0224
Construction	0.9163	0.1299	<.0001	Construction	-0.1546	0.1954	N.S:
Car seen/heard	1.4284	0.2472	<.0001	Car seen/heard	1.0164	0.1976	<.0001
Animal carcass	0.7731	0.1826	<.0001	Animal carcass	-1.0196	0.1886	<.0001

Table A.7 Table with the results of the analysis on differences in average amount of activity per outside influence. 0= no disturbances, 1= raven interactions, 2= plane/helicopter, 3= construction work, 4= car, 5= animal carcass. Significant p-values for level 2 and 3 indicate a significant difference in activity between the influence and the intercept (0 = no disturbances).

7.2.2.2 PACING

<i>Pacing</i>							
<i>Old enclosure</i>				<i>New enclosure</i>			
<i>Rovan</i>				<i>Rovan</i>			
	<i>estimate</i>	<i>SE</i>	<i>p-value</i>		<i>estimate</i>	<i>SE</i>	<i>p-value</i>
<i>Intercept</i>	-4.2177	0.2015	<.0001	<i>Intercept</i>	-3.2818	0.1304	<.0001
<i>Ravens</i>	-15.3483	6208.8323	N.S.	<i>Ravens</i>	-11.2843	441.3717	N.S.
<i>Helicopter/plane</i>	-15.3483	1872.0334	N.S.	<i>Helicopter/plane</i>	1.2023	1.0686	N.S.
<i>Construction</i>	-0.9640	0.7372	N.S.	<i>Construction</i>	1.2246	0.2887	<.0001
<i>Car seen/heard</i>	0.6768	0.7450	N.S.	<i>Car seen/heard</i>	-0.7164	0.7254	N.S.
<i>Animal carcass</i>	-15.3483	839.7474	N.S.	<i>Animal carcass</i>	0.4101	0.2957	N.S.
<i>Siska</i>				<i>Siska</i>			
	<i>Estimate</i>	<i>SE</i>	<i>p-value</i>		<i>estimate</i>	<i>SE</i>	<i>p-value</i>
<i>Intercept</i>	-2.1112	0.0776	<.0001	<i>Intercept</i>	-5.6342	0.4090	<.0001
<i>Ravens</i>	-11.4549	309.1198	N.S.	<i>Ravens</i>	-13.9319	5377.0065	N.S.
<i>Helicopter/plane</i>	-0.1914	0.6105	N.S.	<i>Helicopter/plane</i>	-13.9319	3584.6710	N.S.
<i>Construction</i>	1.7728	0.1324	<.0001	<i>Construction</i>	3.5089	0.4871	<.0001
<i>Car seen/heard</i>	0.6157	0.3165	0.0518	<i>Car seen/heard</i>	-13.9319	1020.7258	N.S.
<i>Animal carcass</i>	0.2464	0.2419	N.S.	<i>Animal carcass</i>	1.1088	0.7101	N.S.
<i>Sky</i>				<i>Sky</i>			
	<i>estimate</i>	<i>SE</i>	<i>p-value</i>		<i>estimate</i>	<i>SE</i>	<i>p-value</i>
<i>Intercept</i>	-2.4326	0.0885	<.0001	<i>Intercept</i>	-4.8568	0.2784	<.0001
<i>Ravens</i>	-11.1335	309.1198	N.S.	<i>Ravens</i>	-14.7092	5377.0065	N.S.
<i>Helicopter/plane</i>	0.4516	0.5407	N.S.	<i>Helicopter/plane</i>	-14.7092	3584.6710	N.S.
<i>Construction</i>	1.0181	0.1600	<.0001	<i>Construction</i>	2.6596	0.3894	<.0001
<i>Car seen/heard</i>	0.0500	0.4358	N.S.	<i>Car seen/heard</i>	-14.7092	1020.7258	N.S.
<i>Animal carcass</i>	0.2754	0.2710	N.S.	<i>Animal carcass</i>	0.8495	0.5302	N.S.

Table A.8 Table with the results of the analysis on differences in average amount of pacing per outside influence. 0= no disturbances, 1= raven interactions, 2= plane/helicopter, 3= construction work, 4= car, 5= animal carcass. Significant p-values for level 2 and 3 indicate a significant difference in pacing between the influence and the intercept (0 = no disturbances).

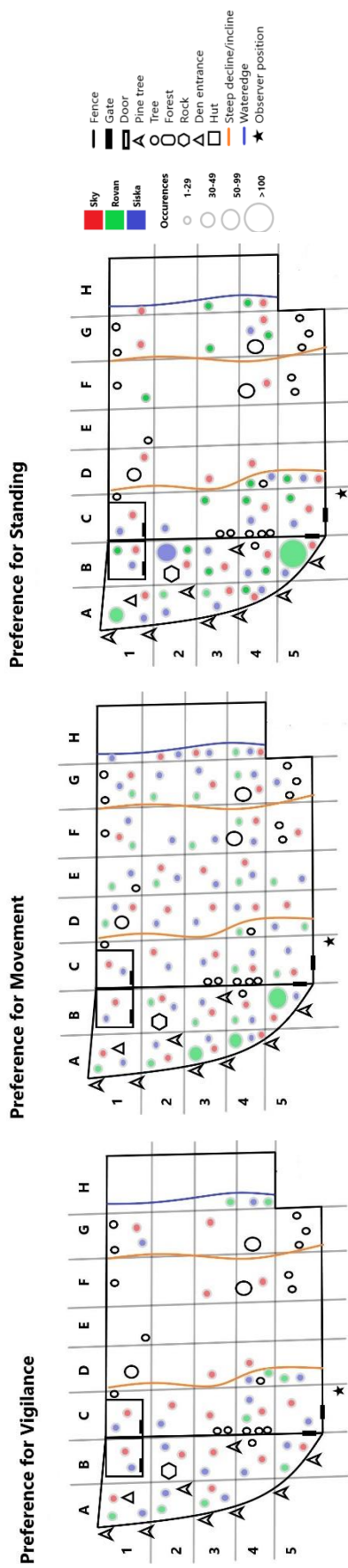
7.2.2.3 OLD VS NEW

<i>Activity</i>				<i>Pacing</i>			
<i>Rovan</i>				<i>Rovan</i>			
	<i>estimate</i>	<i>SE</i>	<i>p-value</i>		<i>estimate</i>	<i>SE</i>	<i>p-value</i>
<i>0</i>	-0.9360	0.2400	<.0001	<i>0</i>	0.12966	0.0820	N.S.
<i>Ravens</i>	1.799e-14	1.001e+05	N.S.	<i>Ravens</i>	-1.957e+01	6.209e+03	N.S.
<i>Helicopter/plane</i>	-19.487	5088.714	N.S.	<i>Helicopter/plane</i>	-21.7892	5088.7143	N.S.
<i>Construction</i>	-3.1246	0.7544	<.0001	<i>Construction</i>	0.8239	0.2175	0.0002
<i>Car seen/heard</i>	0.4572	1.0117	N.S.	<i>Car seen/heard</i>	-0.7984	0.3148	0.0112
<i>Animal carcass</i>	-17.6944	1384.5093	N.S.	<i>Animal carcass</i>	1.4088	0.2168	<.0001
<i>Siska</i>				<i>Siska</i>			
	<i>estimate</i>	<i>SE</i>	<i>p-value</i>		<i>estimate</i>	<i>SE</i>	<i>p-value</i>
<i>0</i>	3.5230	0.4163	<.0001	<i>0</i>	-0.15695	0.07905	0.0471
<i>Ravens</i>	1.799e-14	1.001e+05	N.S.	<i>Ravens</i>	18.467	6208.832	N.S.
<i>Helicopter/plane</i>	17.26	3584.67	N.S.	<i>Helicopter/plane</i>	-0.9163	0.7657	N.S.
<i>Construction</i>	1.7869	0.2854	<.0001	<i>Construction</i>	0.3827	0.2125	0.0717
<i>Car seen/heard</i>	19.07	1682.89	N.S.	<i>Car seen/heard</i>	-0.2471	0.3045	N.S.
<i>Animal carcass</i>	2.6606	0.6240	<.0001	<i>Animal carcass</i>	1.2175	0.2158	<.0001
<i>Sky</i>				<i>Sky</i>			
	<i>estimate</i>	<i>SE</i>	<i>p-value</i>		<i>estimate</i>	<i>SE</i>	<i>p-value</i>
<i>0</i>	2.4242	0.2921	<.0001	<i>0</i>	-0.69997	0.08455	<.0001
<i>Ravens</i>	1.799e-14	1.001e+05	N.S.	<i>Ravens</i>	-21.26	8865.19	N.S.
<i>Helicopter/plane</i>	17.59	3584.67	N.S.	<i>Helicopter/plane</i>	-2.0053	0.8254	0.0151
<i>Construction</i>	0.7828	0.3030	0.0098	<i>Construction</i>	0.3710	0.2188	0.0900
<i>Car seen/heard</i>	19.18	2774.62	N.S.	<i>Car seen/heard</i>	-0.28798	0.30496	N.S.
<i>Animal carcass</i>	1.8501	0.5189	0.0004	<i>Animal carcass</i>	1.0928	0.2485	<.0001

Table A.9 Results of the analysis comparing the average activity and pacing behaviour per outside influence between the old and the new enclosure. 0= no disturbances, 1= raven interactions, 2= plane/helicopter, 3= construction work, 4= car, 5= animal carcass. Significant p-values indicate a significant difference in behaviour between the old and the new enclosure for the individual influence.

7.3 BEHAVIORAL SPATIAL PATTERNS

Old enclosure preference maps



New enclosure preference maps

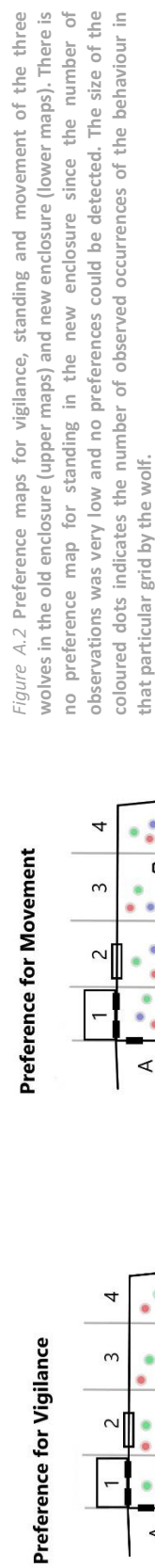


Figure A.2 Preference maps for vigilance, standing and movement of the three wolves in the old enclosure (upper maps) and new enclosure (lower maps). There is no preference map for standing in the new enclosure since the number of observations was very low and no preferences could be detected. The size of the coloured dots indicates the number of observed occurrences of the behaviour in that particular grid by the wolf.