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“Effects of resource availability and distribution on grouping dynamics and foraging strategies in an urban population of crows (*Corvus corone ssp.*)”

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Abstract

Social systems of many animal species are strongly depending on ecological and social conditions and therefore, spatial cohesion and composition of groups vary constantly depending on their environment. Such called fission-fusion societies are extensively studied in primates, but to a lesser extent in avian species. The degree of fission-fusion dynamics differs characteristically among species and is known to positively correlate with cognitive abilities. Birds of the corvid family exhibit strong grouping dynamics and are known for their high cognitive skills. This study examines the environmental effects influencing fission-fusion dynamics and foraging strategies of a wild population of crows (*Corvus corone ssp.*) at the Schönbrunn Zoo in Vienna, Austria. Data were collected by means of the citizen science app KraMobil (Spotteron), a project conducted by the Department of Behavioural and Cognitive Biology of the University Vienna, the Konrad Lorenz Research Center, and the Schönbrunn Zoo. The chances and limitations of citizen science data in research will be discussed. I identified group size and zoo area as the main factors influencing grouping dynamics within the zoo. In animal enclosures, crow group size, the number of enclosed species and the related risk, and the quality and distribution of food resources had the greatest impact on crow grouping dynamics and behaviour. Against my predictions, aggressive behaviour was mostly exhibited in small groups and foraging group size was not enhanced in predator enclosures. Moreover, I did not find any correlation between food distribution and group size. Overall, these findings indicate that the observed crow population exhibits pronounced fission-fusion dynamics depending on ecological and social factors.

1. Introduction

Living in groups is widely spread among animal species (Krause & Ruxton, 2002) and offers several benefits, like reduced predation and improved foraging success (Davies et al., 2012; Krause & Ruxton, 2002; Silk et al., 2014). Despite the benefits, group-living is also associated with costs, such as increased resource competition (Ebensperger & Hayes, 2016; Rubenstein, 1978) and exposure to pathogens and parasites (Davis et al., 2012, Ward & Webster, 2016). Consequently, animals form groups if the related benefits on the individuals' inclusive fitness outweigh any associated costs (Majolo & Huang, 2017). Although maintenance of cohesion represents an important aspect of many group-related benefits, there are contexts in which temporarily splitting is more advantageous than staying together (Jacobs, 2010). Therefore, animal groups do not necessarily remain together constantly but rather vary in spatial cohesion and composition (Aureli et al., 2008) to adjust group size to changing ecological conditions (Dunbar, 1996).

Such modulation of group size by temporarily splitting into subgroups was first described by Hans Kummer (1971), who established the term “fission-fusion society” to characterize the flexible and dynamic social system of chimpanzees (*Pan troglodytes*), geladas (*Theropithecus gelada*), and hamadryas baboons (*Papio hamadryas*) (Aureli et al., 2008). So far, fission-fusion dynamics have not only been studied in non-human primates, but also in other mammalian species like spotted hyenas (*Crocuta crocuta*) (Holekamp et al., 1997), Bechstein's bats (*Myotis bechsteinii*) (Kerth & König, 1999), dolphins (*Tursiops spp.*) (Connor et al., 2000), elephants (*Loxodonta africana*) (Wittemyer et al., 2005), giraffes (*Giraffa camelopardalis sp.*) (Bercovitch & Berry, 2012; Carter et al., 2012) and to a lesser extent in avian species e.g., ravens (*Corvus corax*) (Loretto et al., 2015) and crows (*Corvus corone ssp.*) (Uhl et al., 2018). Spatiotemporal variation in group cohesion,

size and composition is a common quality of animal societies, while the degree of fission-fusion dynamics varies characteristically between species (Aureli et al., 2008, Couzin & Laidre, 2009) and can range from extremely cohesive to vastly fluid (Aureli et al., 2008). Furthermore, the extent of fission-fusion dynamics within an animal society significantly correlates with cognitive abilities, as for instance primate species with higher fission-fusion dynamics have been shown to be more successful in inhibition tasks (Amici et al., 2008).

The social brain hypothesis (Dunbar, 1998; Jolly, 1966) assumes that sociality and associated requirements for living in complex social groups have substantially driven the evolution of cognition. In previous studies group complexity has primarily been defined by quantitative means, e.g. group and brain size (Bergman & Sheehan, 2013), since memory capacities seem to increase with the number of social relationships (Dunbar, 1998; Dunbar & Bever, 2010). While several studies support a positive correlation between forebrain and group size in mammals (Byrne & Corp 2004; Dunbar, 1992; Dunbar & Bever, 2010; Kudo & Dunbar, 2001; McComb et al., 2001, Sawaguchi & Kudo, 1990), so far this concept could not be proven to apply for birds (Burish et al., 2004; Emery & Clayton, 2004; Iwaniuk & Arnold, 2004). Other studies emphasize the importance of relationship qualities in social complexity (Dunbar & Shultz 2007; Emery et al., 2007). To combine quantitative and qualitative aspects, Bergman & Beehner (2015) suggest defining social complexity by the number of differentiated relationships maintained.

Cognitive demands increase within societies characterized by high fission-fusion dynamics, as individual recognition and keeping track of relationships and their nature gets more challenging in a flexible social environment where individuals interact repeatedly in different contexts (Amici et al., 2008; Aureli et al., 2008; Bergman & Sheehan, 2013). In many mammalian species individuals tend to form alliances based on differentiable social

relationships that they can take advantage of in case of conflicts (Connor et al., 1992; Holekamp et al., 1997; Parsons et al., 2003). Within avian species, lifelong pair bonds have been identified as drivers for the evolution of large brains (Dunbar, 2009; Dunbar & Shultz, 2007). This is particularly true for complex social avian species, e.g., corvids (Corvidae) and parrots (Psittaciformes) where the bonded pairs behaviour simulates those alliances found in primates and dolphins (Emery et al., 2007).

However, social systems may vary depending on location and ecological pressures. Grouping dynamics are strongly related to ecological factors like resource availability and distribution or predation risk (Couzin & Laidre, 2009). The effect of food availability on group size has been extensively studied in primates (Chapman, 1990; Chapman & Chapman, 1995; Chapman et al., 1993; Chapman & Pavelka, 2005) where the number of group members positively correlates with increasing food abundance. Similar effects have been found in white-throated magpie-jays (*Calocitta formosa*), which form larger groups in territories with greater food availability (Langen & Vehrenkamp, 1998). Transiently splitting into smaller subgroups therefore represents an appropriate response to limited or patchily distributed food and reduces competition among individual group members (Couzin & Laidre, 2009). Differences in predation pressure can also lead to considerable variation in group size, with higher predation risk favouring for example larger groups in cercopithecoid primates (Hill and Lee, 1998) and larger groups having remarkably reduced predation risk in chestnut-crowned babblers (*Pomatostomus ruficeps*) (Sorato et al., 2012).

The effects of the ecological environment on fission-fusion mediated group dynamics have been studied primarily focused on primates and other mammals and have been recognized comparatively less in avian species. There is knowledge about strong grouping dynamics in birds, like the corvid family, including ravens and crows (Silk et al.,

2014). While for ravens, literature suggests their dynamic social structures are based on fission and fusion (Braun et al., 2012), there is a deficit of studies on the extent of fission-fusion dynamics in crows. Both species share a similar life history being opportunistic generalists that take advantage of various food resources. Crows more than ravens are adapted to live in urban environments, where their populations can grow large if resources are sufficient (Goodwin, 1976). Typically, flocks of non-breeders form communal roosts and foraging groups to roam larger areas together (Baglione et al., 2002). Sex, age, and body size determine the hierarchy within those flocks (Richner, 1989). Crows are monogamous birds, that will leave the flock and form life-long pair bonds once the individual finds a mate (Braun & Bugnyar, 2012). Breeding pairs can be highly territorial and typically breed unassisted, while in case of some crow species cooperative breeding can occur under certain environmental conditions (Baglione et al., 2002).

Corvids are known for their high cognitive skills and the social brain hypothesis has been applied to this family (Bond et al., 2003). Comparing relative forebrain sizes, corvids show remarkably larger brains than most other bird species (Emery & Clayton, 2004). They access episodic-like memory in food-caching contexts by recalling information about location, type, and perishability of cached goods, as well as respective social contexts (Emery & Clayton, 2004), and use deception in food competing (Bugnyar & Kotrschal, 2002). They know how to make use of tools (Bird & Emery, 2009; Hunt, 1996; Weir et al., 2002), solve object permanence tasks (Pollok et al., 2000; Zucca et al., 2007), are aware of inequity when getting rewarded (Wascher & Bugnyar, 2013), and successfully distinguish objects by size (Coburn, 1914). Although they perform equally well in named cognitive tasks, there is evidence that ravens cognitive abilities exceed those of crows e.g., in inhibition tasks (Mikolasch et al., 2012; Wascher et al., 2012). As mentioned before, Amici

et al. (2008) connected primates' performance differences in inhibition tasks to the extent of their fission-fusion dynamics, which might also be true for ravens and crows. Overall, studying grouping dynamics in avian species could contribute greatly to our understanding of fission-fusion social systems and the evolution of complex cognitive abilities.

Previous studies on grouping dynamics of free-ranging crows at the Schönbrunn Zoo in Vienna, Austria have shown, that environmental factors not only influence the size of crow subgroups, but also group composition. Time of the day, season, temperature, and weather were identified to impact the local flock size in this crow population (Uhl et al., 2018). Since 2020, the citizen science project KraMobil (Spotteron) aims to gain further knowledge on the behaviour and grouping dynamics of this population of free-ranging crows at the Schönbrunn Zoo. Citizen science engages the public in gathering authentic scientific information (Bonney et al., 2009; Dickinson et al., 2012), and its role in research has increased over the last years (Lukyanenko et al., 2016). While the integration of non-professionals in scientific data collection represents a great possibility to collect large amounts of data over long time spans (Bonney et al., 2009), there has been concerns about data quality and accuracy (Kosmala et al., 2016). However, other studies have proven the comparability of citizen scientist's data quality to that of professionals (Kosmala et al., 2016).

This study intends to investigate the impact of food availability and distribution as well as predation risk on grouping dynamics and foraging strategies in a wild population of crows (*Corvus corone ssp.*) at the Schönbrunn Zoo in Vienna, Austria. My hypotheses are that 1) group size varies between different animal enclosures (characterised by quality and

distribution of food resources, and ‘predation’ risk of the housed species) and 2) crows perform different types of behaviour depending on respective group size and enclosure. I predict that 1) groups will be bigger in predator enclosures and enclosures with high-quality food resources, due to enhanced vigilance and reduced predation risk of larger groups, but also because of the valuable food resource itself. Patchily distributed food should lead to smaller sub-groups, to limit intra-specific competition. 2) Individuals in large groups will show more aggressive behaviour than individuals in small groups, due to increased intra-specific competition over resources with rising group size. Furthermore, the vicinity of predator zoo species will lead to larger foraging groups compared to zoo animals that do not present any risk to the crows.

Methods

2.1 Study location and population

Data were collected at Schönbrunn Zoo in Vienna, Austria (48° 11' 6.486" N 16° 18' 45.3348" E). Founded in 1752, Schönbrunn is the world's oldest existing zoo and was declared a UNESCO world heritage site. With an area of 17 hectares the zoo provides habitat for more than 650 animal species, including some critically endangered ones. The Schönbrunn Zoo is strongly involved in nature and animal conservation, and some of their endangered species are part of international breeding conservation programs. A variety of research is conducted at the Schönbrunn Zoo, including studies on visual communication in foot-flagging frog species (*Staurois spp.*), raven cognition, and some social science and historical studies.

The Schönbrunn Zoo is used by a population of more than 300 (Uhl et al., 2018) free-ranging crows (*Corvus corone ssp*) to forage and socialise (they mainly roost in the surrounding park, Schönbrunn). This population consists of breeder and non-breeder carrion crows (*Corvus corone corone*), hooded crows (*Corvus corone cornix*) and, due to Vienna being a zone of overlap of both subspecies, various hybrid forms (Short, 1969). Schönbrunn Zoo provides optimal conditions for monitoring crow behaviour, since the area is characterized by great resource availability (via the food provided in the zoo enclosures), and thus represents permanent and qualitative foraging opportunities for the birds (Kövéř et al., 2019; Miller et al., 2014). Moreover, crows that are breeding or foraging within the zoo are used to human presence (Deventer et al., 2016) and therefore suitable subjects for behaviour observations at close distance.

2.2 Data collection

The observations took place from March to November 2021 during the zoo's regular opening times from Monday to Sunday. Opening hours varied between 9 a.m. to 4:30 p.m. from April to September and 9 a.m. to 6:30 p.m. from October to March. Data were collected by means of the smartphone app "KraMobil" (Spotteron). The app is part of a project conducted by the Department of Behavioural and Cognitive Biology of the University Vienna, the Konrad Lorenz Research Center, and the Schönbrunn Zoo and makes use of the citizen science approach. Zoo visitors can download the app on their smartphone for free and use it to collect data about free-living corvids within the zoo area. "KraMobil" users can take photos and provide different details about their observations. Besides some general information (coordinates, date, time, user), the app acquires information about the observed individual itself, including species classification, group size, position, zoo area, behaviour, vicinity of zoo animals or visitors and possible interactions with the latter (Table 1). Detailed descriptions of the behavioural categories are presented in Table 2. In addition to the data I collected between March and November 2021, KraMobil observations from citizen scientists between April 2020 and November 2021 were included. Therefore, the total number of observations conducted is 12992, composed of 887 own observations (6,83%) and an additional 12105 observations by 224 citizen scientists (93,17%). To ensure data reliability, citizen scientists' observations were checked for accuracy by reviewing each observation.

Table 1: Collected parameter for each observation in the KraMobil App

<i>Parameter</i>	<i>Category</i>
Coordinates	
Date	
Time	
User ID	
Species	Carrion Crow Hooded Crow Hybrid
Group Size	1 2 3-5 6-10 11-20 21-50 51-100 100+
Position	On ground In the air On structure/tree Other
Area	Enclosure Pathway Restaurant/Resting area Other
Behaviour	Foraging Sitting/Resting Comfort/Cleaning Affiliation Aggression Other
Vicinity	No Zoo animals Persons
Interactions	Yes No

Table 2: Behavioural categories and detailed descriptions

Behavioural Category	Description
Foraging	Moving or standing/sitting on the ground/structure/tree while actively searching for food with head down towards ground or collecting food resources with beak. Taking up food items with beak and feeding. Possible manipulation of grass, stones, branches etc. to find resources.
Sitting/Resting	Motionless in squatting position or lying down, usually perched on structure/tree. Feathers can be fluffed up and head turned around with beak in feathers. Eyes can be open or closed.
Comfort/Cleaning	Touching feathers with beak or cleaning beak by rubbing/scratching against structure/tree. Scratching of body parts with foot or against structure/tree. Stretching wings and legs in the air or shaking. Standing in or moving in water and bathing.
Affiliations	Touching of another bird's body with head or by sitting on or besides it. Touching or running through feathers of another bird with the beak. Active transfer of food item from one bird's beak to the beak of another.
Aggressions	Pecking other bird with beak. Rushing towards another bird flying in the air or running on the ground. Pulling feathers of other bird with the beak or hitting it with the feet/beak.
Other	Any other behaviour

2.3 Analysis

For further evaluation in R (Version 4.2.2 (2022-10-31)) Data were processed in Microsoft Office Excel (Version 16.67). With respect to observations within zoo animal enclosures, the coordinates were used to determine the housed species and thereby, based on information provided by the Schönbrunn Zoo, the number of individuals within the enclosure, the risk of the species, as well as the quality and distribution of food resources. Beforementioned parameters concerning animal enclosures are listed and described in Table 3. Additionally, each observation was assigned to year, month and season, divided into a breeding season from March to June inclusively, and a non-breeding Season from July to February (Preininger et al., 2019). To reduce parameter levels of group size, they were summarized into 3 categories: solo (one individual), small group (2-5 individuals) and large group (>6 individuals). The behavioural categories sitting/resting, and comfort/cleaning were combined into the category self-directed behaviour. Throughout this study, the parameter species, position, vicinity, and interaction were excluded from further analysis. Only data within months with a sampling effort of more than 80 observations were included in the analysis. Consequently, spots within April, March, and December 2020, as well as January and March 2021 were not considered in the analysis. This leads to a total of 11598 analyzed observations, composed 838 of my own observations (7,2%) and 10760 observations by 213 citizen scientists (92,8%).

Table 3: Additional parameter for observations within zoo animal enclosures

Parameter	Category	Description
Enclosure species		Name of housed species
Number of individuals	1-10	Number of individuals housed in the enclosure
	11-50	
	>50	
	NA	
Risk	Predator	Enclosure houses predator species
	Non-predator	Enclosure houses non-predator species
Food quality	Vegetarian	Grass, fruit, and seeds fed to housed species
	Mixed	Grass, fruit, seeds and meat or fish fed to housed species
	Mainly meat	Mainly meat and fish fed to housed species
Food distribution	Clumped	Food clustered within enclosure
	Evenly	Food evenly distributed within enclosure
	Patchy	Food placed at one or multiple fixed locations within the enclosure
	Inaccessible	Food not available for crows, housed species fed by hand or indoors

Model 1. Generalized linear mixed models (GLMM) with the frequency of spots as response variable and the number of users per month as an offset were used to test for possible group size differences between the different zoo areas and animal enclosures. Group size, zoo area and season as well as the interaction between group size and zoo area were included as fixed factors. Year and month were used as random factor.

Model 2. To access group size differences within the different enclosures, group size, season, the number and the risk of enclosed species, food quality and food distribution, as well as the interaction between group size and enclosure species risk were included as fixed factors, while year and month were determined random factors.

Model 3. To account for effects of zoo area and group size on behaviour, GLMMs with the frequency of spots for each behavioural category (4 GLMMs in total) as response variable and group size, zoo area, the interaction between group size and zoo area and season as

fixed factors were performed. Year and month were included as random factor and the number of users as offset.

Model 4. GLMMs with the frequency of spots for each behavioural category as response variable were performed to examine effects of group size and enclosure species on the behaviour. Here the fixed factors included group size, enclosure species risk, the number of enclosed species, food quality, food distribution and season. Furthermore, I included the interaction between the risk of the enclosure species and group size. Again, the number of users was used as an offset and year and month as random factor. In this case the number of aggression observations was too small for proper model adjustment, hence this behaviour was excluded from further analysis.

All statistics were performed with a significance threshold of $\alpha = 0.05$ and Akaike's information criterion (AIC) was used for model selection in all cases.

Results

1.1 Effects of zoo area and crow group size

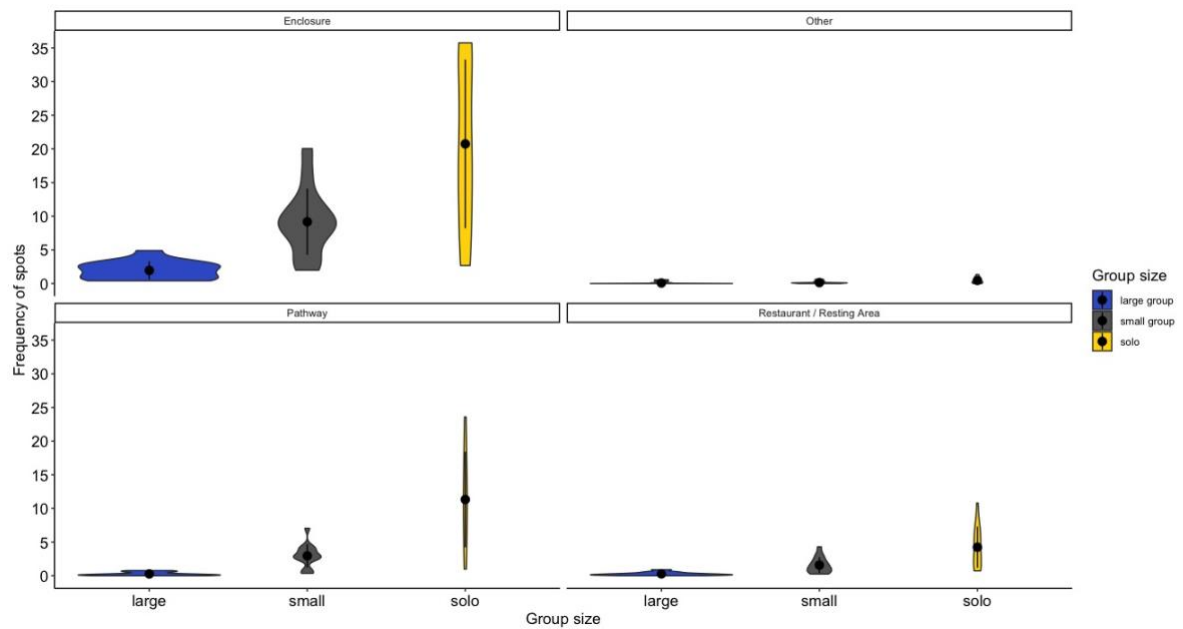


Figure 1: Average monthly frequency of spots per group size within the different zoo areas

The spot frequency estimate varies significantly between group size and zoo area categories (Table 4 Appendix) and data suggests strong interaction between those factors (Full-Reduced-Anova, $p = 1.004e-08$, $\Delta AIC = 36.3$). Irrespective of group size, the highest number of observations occurred at animal enclosures with a monthly average of 496.928 ± 293.670 (mean \pm SD), followed by pathways (222.286 ± 157.351), restaurant and resting areas (97.286 ± 59.899), and lastly other areas (11.928 ± 12.168). Within animal enclosures crows were mostly spotted as solo individuals, while small groups were spotted about half as frequently. Large groups represented the lowest proportion of spots. This pattern repeats within other and restaurant/resting areas, while in relation the share of large groups at pathways was noticeably reduced.

1.2 Effects of animal enclosure properties

1.2.1 Group Size

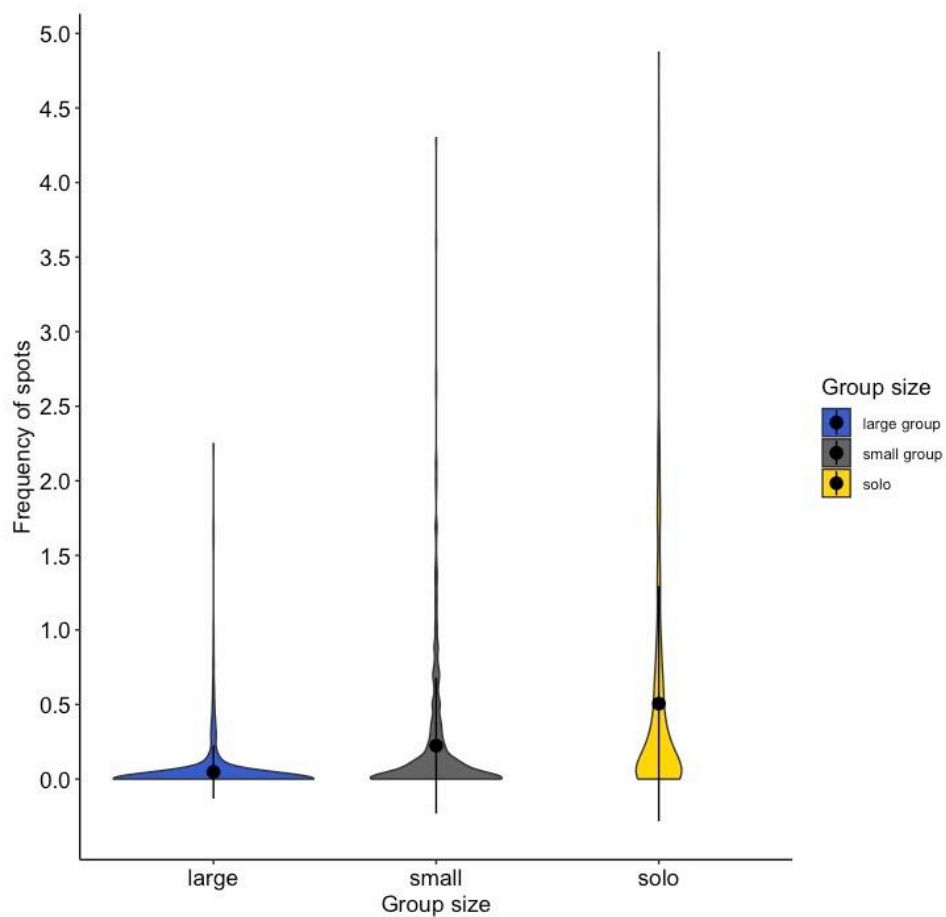


Figure 2: Average monthly frequency of spots per group size within animal enclosures

Within animal enclosures, crows were predominantly spotted as solo individuals, with an averaged frequency of 0.506 ± 0.789 . Small groups were approximately half as likely (0.224 ± 0.455) and large groups had the smallest proportion (0.048 ± 0.179). This frequency distribution is consistent with the one outlined in the previous paragraph. Pairwise comparison of the spot frequency estimate shows highly significant divergence between large and small groups (Tukey post-hoc, $p < 1e-0.8$), large groups and solo

individuals (Tukey post-hoc, $p < 1e-0.8$), and small groups and solo individuals (Tukey post-hoc, $p < 1e-0.8$).

1.2.2 Food Quality

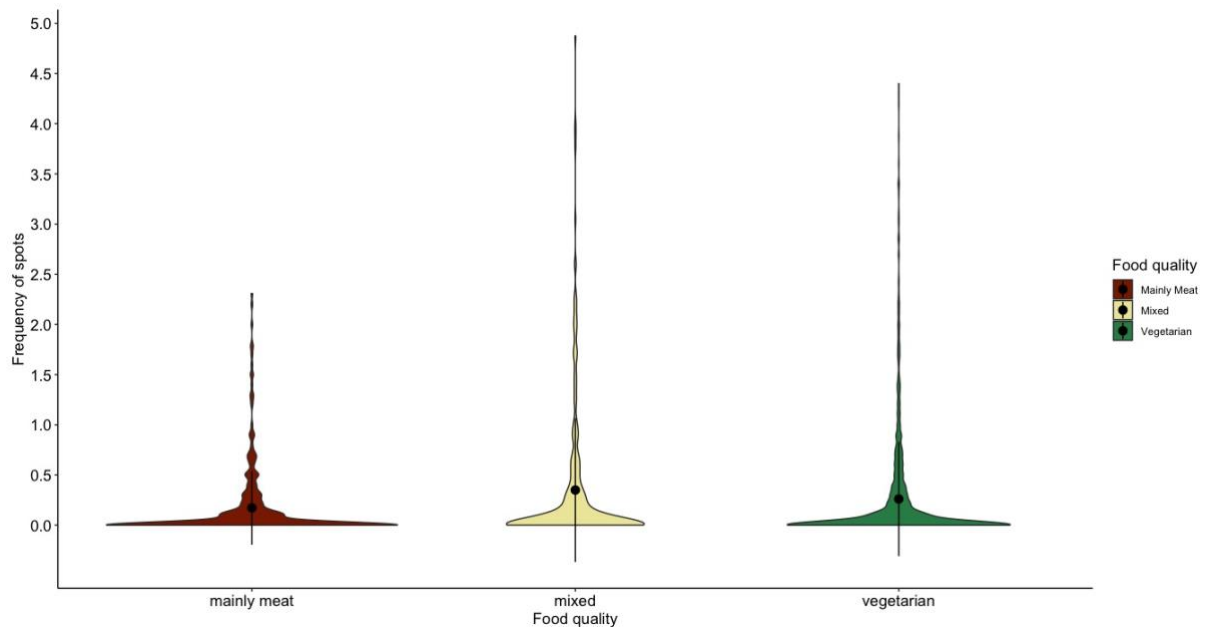


Figure 3: Average monthly frequency of spots per food quality within animal enclosures

The quality of food significantly influenced the frequency of crow spots within zoo animal enclosures (Table 5 Appendix). Spots in enclosures with mixed foods had the highest frequency with an average of 0.350 ± 0.717 , followed by strictly vegetarian food resources (0.261 ± 0.569) and mainly meat (0.173 ± 0.368). Estimate comparisons of spot frequency demonstrate significant differences between the categories mainly meat and mixed (Tukey post-hoc, $p = 0.0118$) and no significant differences between vegetarian and mainly meat (Tukey post-hoc, $p = 0.0858$), and vegetarian and mixed (Tukey post-hoc, $p = 0.1874$).

1.2.3 Number of enclosure species

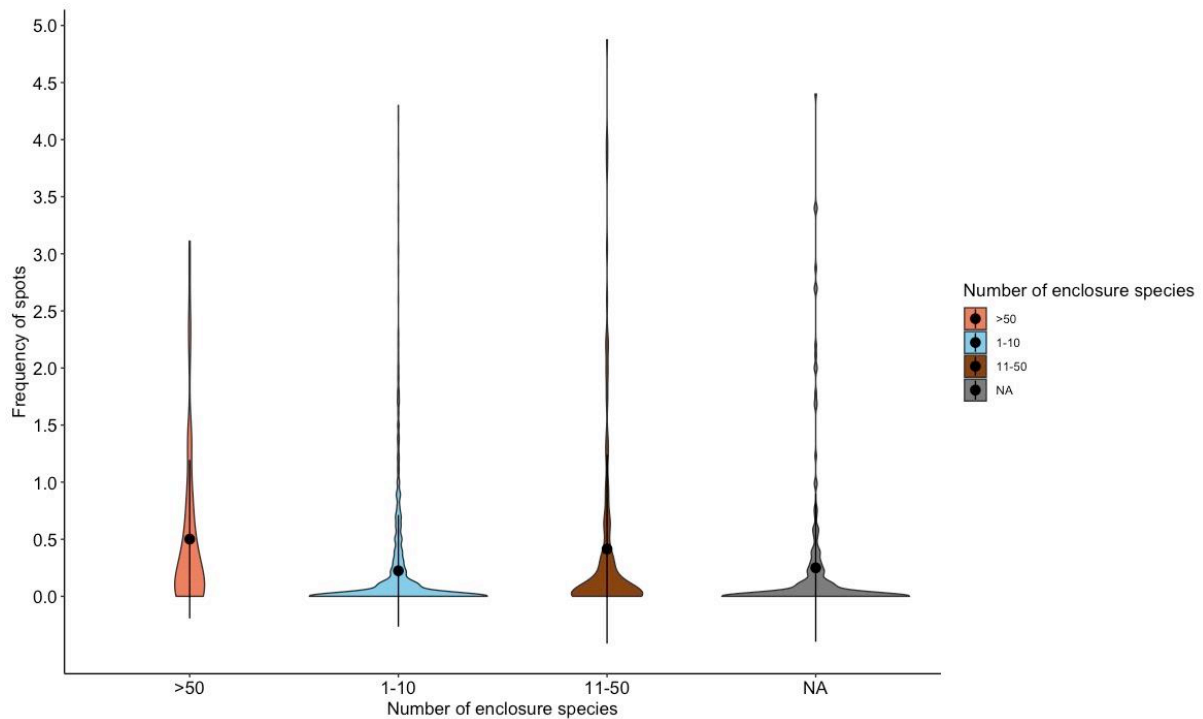


Figure 4: Average monthly frequency of spots per number of enclosures species within animal enclosures

The frequency of crow sightings within animal enclosures was strongly depending on the individual number of housed species (Table 5 Appendix). With an average monthly frequency of 0.501 ± 0.695 , observations in enclosures with >50 individuals represented the highest proportion of spots, closely followed by enclosures with 11-50 individuals with an average of 0.414 ± 0.827 . The average frequency of spots in enclosures with no further information on the number of housed species was 0.250 ± 0.649 and observations in enclosures with 1-10 individuals depicted the smallest fraction of all spots, with an average of 0.224 ± 0.490 . Pairwise comparisons of the spot frequency estimate demonstrate highly significant differences between enclosures with 1-10 and >50 housed individuals (Tukey post-hoc, $p < 0.001$), significant differences between enclosures with 11-50 and >50 individuals (Tukey post-hoc, $p = 0.0148$) and no significant differences between enclosures with 11-50 and 1-10 individuals (Tukey post-hoc, $p = 0.1038$).

1.2.4 Interaction between enclosure species risk and food distribution

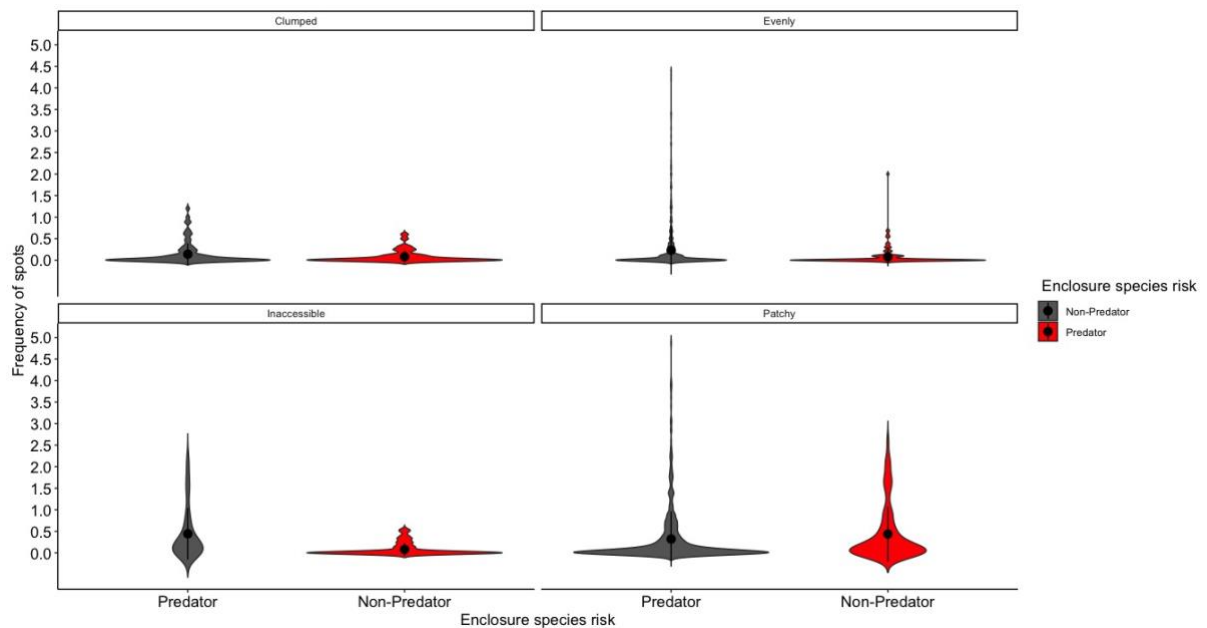


Figure 5: Average monthly frequency of spots per risk of the enclosure species and distribution of food resources

The risk of the enclosed species alone did not have any significant effect on the frequency of crow observations (Table 5 Appendix) and the pair-wise comparison of the spot frequency estimate does not show any significant differences between predator and non-predator enclosures (Tukey post-hoc, $p = 0.466$). However, in interaction with food distribution, the impact was highly significant (Full-Reduced-Anova, $p < 2.2e-16$, $\Delta AIC = 96$). The average monthly frequency of spots was always elevated in predator enclosures unless food was distributed patchily. Pair-wise comparisons of the spot frequency estimate indicate highly significant differences between all distribution categories (Tukey post-hoc, $p < 0.001$), except for patchy and inaccessible food resources (Tukey post-hoc, $p = 0.0857$).

1.3 Effects of zoo area on crow behaviour

1.3.1 Foraging behaviour

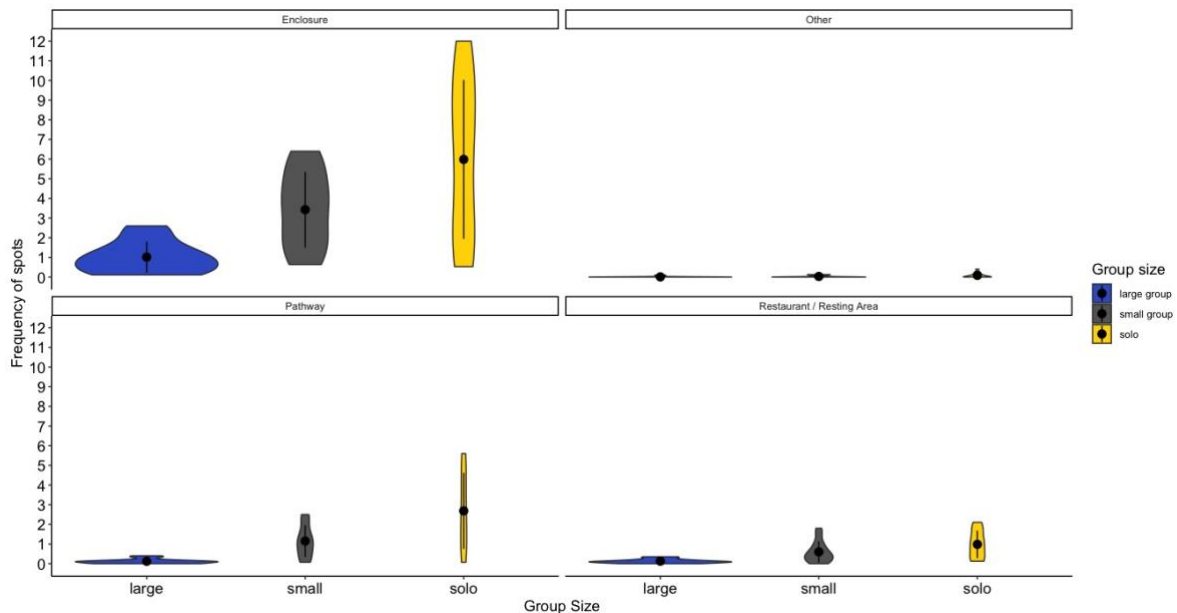


Figure 6: Average monthly frequency of foraging behaviour per group size within the different zoo areas

The interaction between group size and zoo area did influence the frequency of foraging spots in a highly significant manner (Full-Reduced-Anova, $p = 0.0002123$, $\Delta AIC = 14.11$). The estimate of spot frequency varied significantly between group size and zoo area categories (Table 6 Appendix). The highest number of monthly observations were recorded in zoo animal enclosures (162.5 ± 109.304), followed by pathways (58.714 ± 48.898), restaurant and resting areas (28.428 ± 21.936) and other areas (1.643 ± 2.170). Within enclosures crows were mostly observed as solo individuals, about half as often in small groups and least likely in large groups. This pattern repeats within the other areas, while again the likelihood of large groups was comparably lower within pathways and this time also other areas of the zoo.

1.3.2 Self-directed behaviour

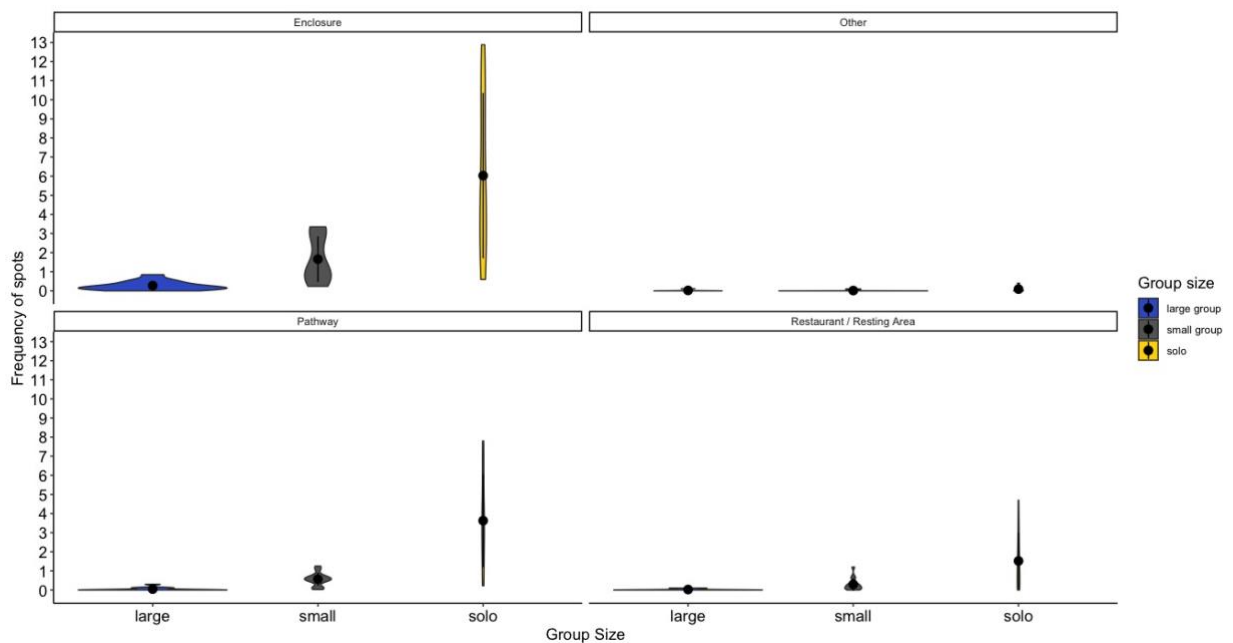


Figure 7: Average monthly frequency of self-directed behaviour per group size within the different zoo areas

Within self-directed behaviours the frequency of spots was strongly depending on the interaction effects between zoo area and group size (Full-Reduced-Anova, $p < 2.2e-16$, $\Delta AIC = 212.8$) and pair-wise comparisons of the spot frequency estimate shows highly significant differences between group size and zoo area categories (Table 6 Appendix). Again, the highest proportion of spots every month were located within animal enclosures (118.571 ± 77.220), followed by pathways (62.786 ± 46.565), restaurant and resting areas (26.357 ± 19.061) and other areas (2.071 ± 2.759). Within enclosures, on pathways and in restaurant and resting areas crows were predominantly spotted as solo individuals, to a lesser extent in small groups and least likely in large groups. This distribution diverges within other areas of the zoo, while still most of the crows were observed as solo individuals, the lowest proportion of spots was represented by small groups.

1.4 Aggressive behaviour

1.4.1 Group size

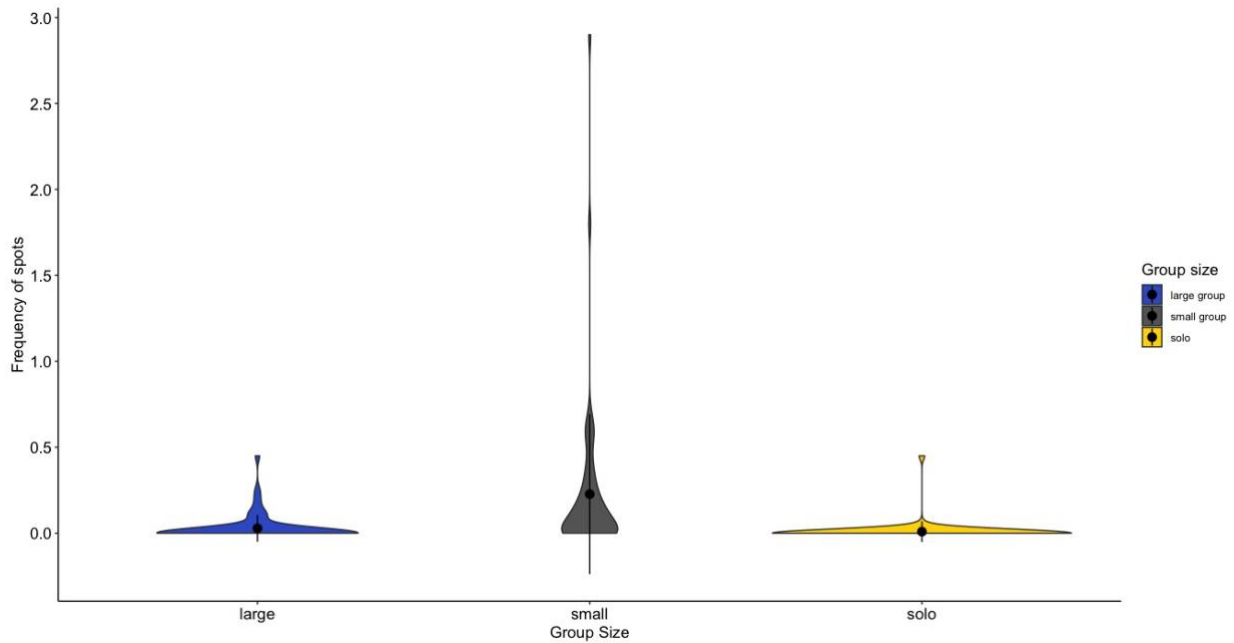


Figure 8: Average monthly frequency of aggressive behaviour per group size

The spot frequency for aggressive behaviour was strongly affected by crow groups size (Table 6). The average monthly frequency was highest for small groups (0.228 ± 0.466), followed by large groups (0.0282 ± 0.078) and solo (0.009 ± 0.060) individuals. Pairwise comparisons of spot frequency estimates present highly significant differences between small and large groups (Tukey post-hoc, $p < 0.001$), small groups and solo individuals (Tukey post-hoc, $p < 0.001$) and no significant differences between solo individuals and large groups (Tukey post-hoc, $p < 0.148$).

1.4.2 Zoo area

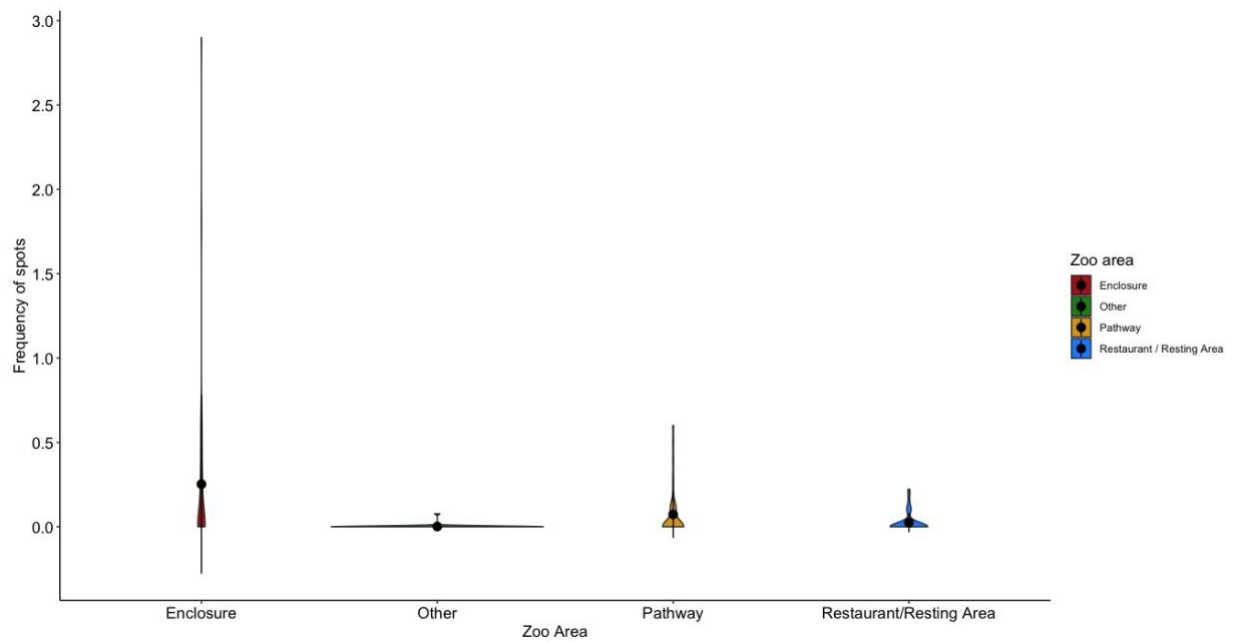


Figure 9: Average monthly frequency of aggressive behaviour within the different zoo areas

The frequency of spots for aggressive behaviour was also depending on the zoo area (Table 6 Appendix). Crows were most likely exhibiting aggressive behaviour within animal enclosures (0.253 ± 0.530), followed by pathways (0.073 ± 0.140), restaurant and resting areas (0.024 ± 0.056) and lastly other areas (0.002 ± 0.012). Pair-wise comparison of the spot frequency estimate for aggressive behaviour was only significant between pathways and animal enclosures (Tukey post-hoc, $p < 0.0167$).

1.5 Effects of animal enclosure properties on crow behaviour

1.5.1 Foraging behaviour

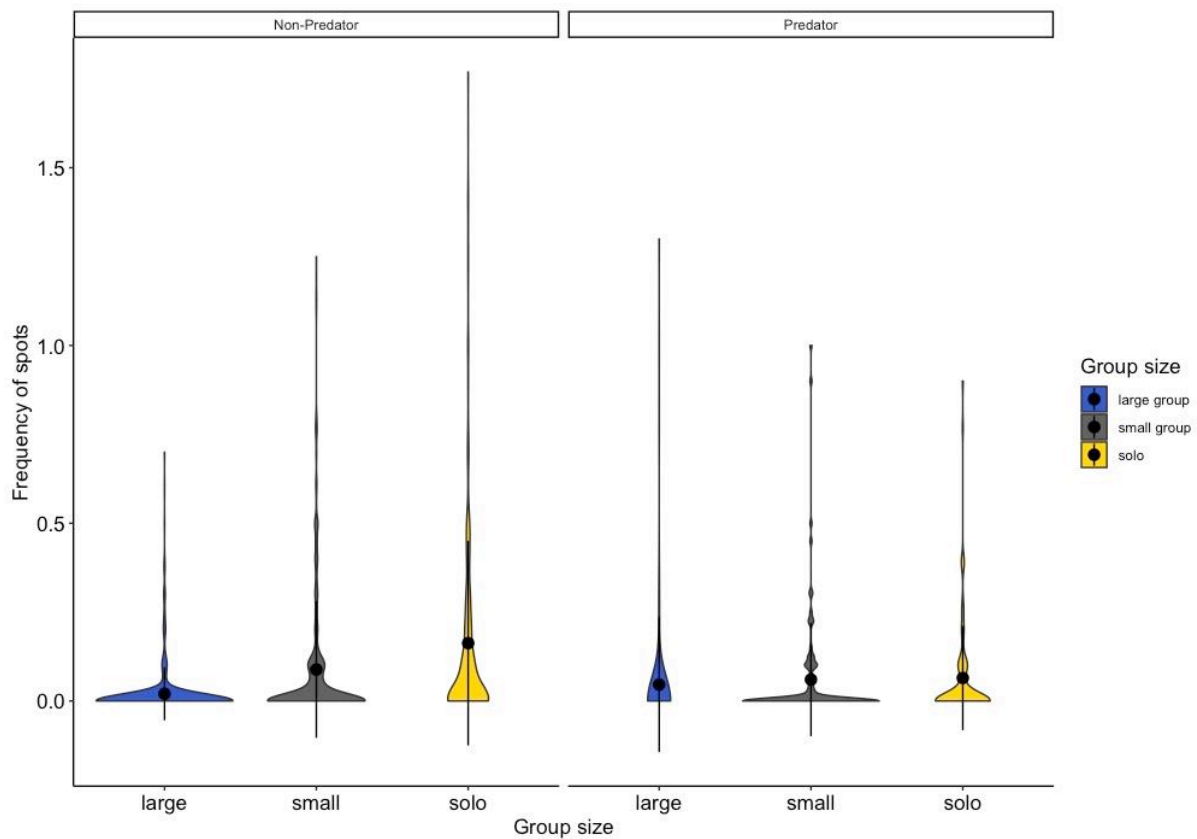


Figure 10: Average monthly frequency of foraging behaviour per group size within animal enclosures

The frequency of foraging behaviour within animal enclosures was significantly influenced by interaction effects between the risk of the housed animal species and the group size (Full-Reduced-Anova, $p = 4.771e-15$, $\Delta AIC = 61.9$). Foraging crows were more likely to be spotted in non-predator enclosures with an average frequency of 1.420 ± 3.134 , compared to predator enclosures with an average of 0.840 ± 2.143 . In non-predator enclosures, the highest number of crows were spotted as solo individuals (0.163 ± 0.288),

followed by small (0.088 ± 0.192) and then large groups (0.020 ± 0.075). This distribution recurs within predator enclosures, where crows were most likely spotted as solo individuals (0.064 ± 0.147), to a lesser extent in small groups (0.060 ± 0.159) and least likely in large groups (0.046 ± 0.190).

1.5.2 Self-directed behaviour

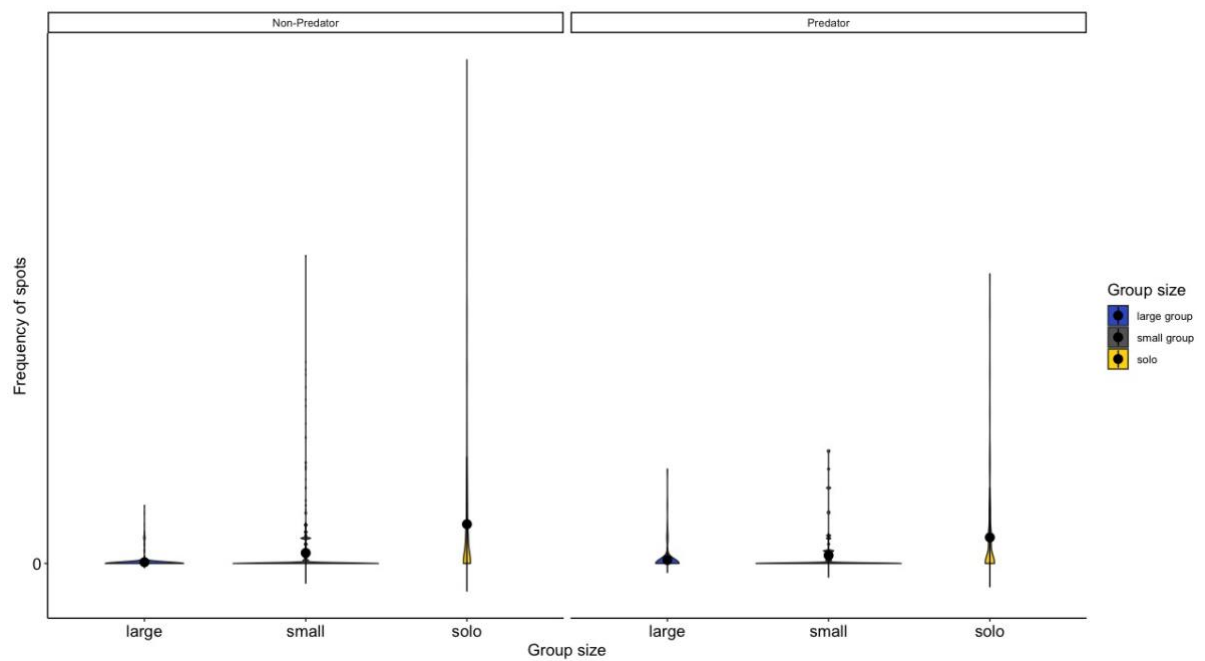


Figure 11: Average monthly frequency of self-directed behaviour per group size and risk of the enclosure species

Interactions between risk of enclosed species and crow group size significantly influenced the spot frequency of self-directed behaviours (Full-Reduced-Anova, $p = 0.003527$, $\Delta AIC = 7.3$). With an average of 0.997 ± 2.433 spots in non-predator enclosures were slightly more frequent than those in predator enclosures with averagely 0.803 ± 2.327 . Frequency distribution patterns were similar for predator and non-predator enclosures, with solo individuals representing the highest proportion of spots followed by small groups and then large groups.

2. Discussion

The aim of this study was to evaluate environmental effects influencing fission-fusion dynamics and foraging strategies of a wild population of crows at the Schönbrunn Zoo in Vienna, Austria. Although the data did not support the predictions of my suggested hypotheses, I identified several factors influencing grouping dynamics of the studied population.

Crow group size and zoo area had significant effects on the observation frequency in general and of the different behaviours. For every area of the zoo, the frequency of observations decreased with increasing crow group size and in comparison, the share of large groups on pathways was remarkably reduced. The likelihood of observations was highest in animal enclosures, followed by pathways, restaurant and resting areas, and lastly other areas, regardless of the crows' exhibited behaviour.

Furthermore, the frequency of observations within animal enclosures was strongly depending on crow group size, the number and risk of the enclosed species, and the quality and distribution of food resources. Again, increased crow group size negatively impacted observation frequency. Crows preferred enclosures with mixed food resources over enclosures housing zoo species with a vegetarian or mainly meat diet. Non-predator enclosures, as well as the number of housed animals positively affected observation frequency. The likelihood of observations for different behaviours in animal enclosures was depending on crow groups size and the enclosure species risk. Regardless of the exhibited behaviour, crows preferred to stay in non-predator enclosures and act as solo individuals.

2.1 General environmental effects

2.1.1 Grouping Dynamics

Group size and zoo area significantly influenced the grouping dynamics of free ranging crows at the zoo. Regardless of exhibited behaviours, crows were mostly observed within animal enclosures, followed by pathways, restaurant and resting areas and lastly other areas. This might be due to considerably stable resource abundance within animal enclosures (Kövért et al., 2019; Miller et al., 2014) but could also be a result of citizen scientists favouring observations while simultaneously watching zoo species or potential interactions. This potential bias could prospectively be prevented by specifically training citizen scientist and a follow-up reliability study might help to identify the most common source of error. The reduced number of observations within other areas was to be expected and can be explained by being the only option to choose, if the site of the observation did not fit into any of the defined zoo areas. Based on my data, a reasonable and more detailed specification of zoo areas might be taken into consideration for following studies.

Predominantly, crows were spotted as solo individuals, to a lesser extent in small groups (2-5 individuals) and least common in large groups (>6 individuals). This was applicable for all zoo areas and observations of foraging and aggression, while during self-directed behaviour crows were least likely to be in small groups. Crows were comparably less likely to stay on pathways when being part of large groups, which might reflect the limited space provided, as pathways are more narrow than other sites and have highest visitor densities. Moreover, food resources are very limited and are only represented by trash bins and food dropped by visitors (Kövért et al., 2019).

2.1.2 Behaviour

Crow group size and area of the zoo also affected crow behaviour. During foraging and self-directed behaviours crows were most likely observed as solo individuals and to a lesser extent in small and large groups. The proportion of large groups foraging at pathway sites was again considerably reduced. However, aggression was mostly shown in small and large groups while it was rarely exhibited by solo individuals. These findings suggest that most of the observed aggression occurred intraspecific among the members of a crow group, and that conflicts with zoo animals or other free-ranging species at the zoo were scarce. It could also be the consequence of another potential observation bias, in case two individuals were aggressively interacting and classified as a small group while technically being part of a bigger group. Moreover, the fact that aggression was mostly exhibited by individuals in small groups is against the prediction, that large groups will encourage aggressive behaviour due to increased competition over resources (Couzin & Laidre, 2009).

2.2 Effects of enclosure parameter

2.2.1 Grouping dynamics

Although group size, the quality and distribution of food resources within animal enclosures, and the risk and number of the enclosed animal species significantly impacted grouping dynamics and behaviour of free ranging crows, the data did not confirm my predictions that groups should be bigger in predator enclosures and in enclosures with high quality food resources. The model did neither detect interaction between crow group size and resource distribution nor group size and food quality. This is against the prediction that patchily distributed and limited food resources should lead to smaller subgroups in crows

to prevent resource competition (Couzin & Laidre, 2009; Langen & Vehrenkamp, 1998). In animal enclosures the frequency of observations decreased with increasing crow numbers. Crows preferred enclosures with mixed food resources over vegetarian choices and mainly meat. The frequency of observations seemed to increase with the number of housed animals. However, those findings are hard to interpret since it included enclosures with no information on species numbers but also because the numbers of enclosed animals changed during the observation period for this study. Non-predator enclosures had a positive effect on observation frequency according to model calculations, meaning crows favoured non-predator enclosures over predator enclosures. Presuming predators represented mainly carnivore species, this supports our finding that crows were least likely to visit enclosures with mainly meat resources but contradicts with the prediction that meat will be the preferred source of nutrition. Interestingly, patchily distributed food positively affected the frequency of spots within predator enclosures. Patchy resources might encourage crows to form various smaller foraging groups, to reduce the individuals' risk within a group, by dividing the predator's attention. Therefore, predator enclosures with patchy resource distribution might be able to sustain a higher number of crows in total.

2.2.2 Behaviour

Crow group size and the risk of the enclosure species significantly influenced the frequency of foraging and self-directed behaviour, while other enclosure related environmental conditions did not have any impact. Regardless of the exhibited behaviour, crows were most frequently visiting non-predator enclosures. Against our prediction that possible predation pressure will lead to larger foraging groups to make use of shared vigilance (Davies et al., 2012; Hill and Lee, 1998; Krause & Ruxton, 2002; Silk et al., 2014; Sorato

et al., 2012), crows preferred to act as solo individuals. Thus, the enhanced protein content of food resources did not seem to offset predation risk in predator enclosures. The huge variety of resources within the zoo might not require crows to take predation risk while foraging. The lack of data for aggressive behaviour within animal enclosures could be a consequence of crows primarily acting as solo individuals, since our data suggests that aggression is more likely to occur intraspecific in small and large groups.

Conclusion

Altogether, the findings of this study indicate that the observed crow population exhibits pronounced fission-fusion dynamics based on varying ecological and social factors. Grouping dynamics and behaviour were strongly linked to crow group size and area of the zoo. Enclosure properties that affected grouping dynamics included species related factors like the number and the risk of the housed animal species, but also the quality and distribution of food resources. Crow behaviour within animal enclosures was connected to the number of conspecifics present and the predation risk. This study represents an example for the chances, but also limitations of citizen science data in research. While citizen science projects offer the possibility for large scaled data, ensuring data quality and reliability is essential. My findings provide a base for following studies on fission-fusion corvid societies and might help to further control for or identify environmental and social factors involved.

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Appendix

Table 4: Statistical values of the generalized linear mixed model analysing the effects on spot frequency

<i>Model 1</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>z-value</i>	<i>Pr(> z)</i>
(Intercept)	0.3906	0.3786	1.032	0.302193
Small	1.6084	0.1265	12.714	<2e-16
Solo	2.3042	0.1265	18.352	<2e-16
Other	-3.3473	0.2837	-11.800	<2e-16
Pathway	-2.0533	0.1871	-10.973	<2e-16
Restaurant/Resting Area	-1.9068	0.1793	-10.633	<2e-16
Non-Breeding	0.1130	0.4355	0.260	0.795179
Small:Other	-0.8923	0.3552	-2.512	0.011995
Solo:Other	-0.3537	0.3201	-1.105	0.269101
Small:Pathway	0.8167	0.2233	3.657	0.000255
Solo:Pathway	1.4286	0.2194	6.511	7.48e-11
Small:Restaurant/Resting Area	0.1537	0.2191	0.701	0.483170
Solo:Restaurant/Resting Area	0.3342	0.2146	1.558	0.119313

Table 5: Statistical values of the generalized linear mixed model analysing the effects on spot frequency within animal enclosures

<i>Model 2</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>z-value</i>	<i>Pr(> z)</i>
(Intercept)	-3.366075	0.461139	-7.299	2.89e-13
Small	1.803208	0.112713	15.998	<2e-16
Solo	2.655915	0.112800	23.545	<2e-16
Predator	-0.260660	0.357477	-0.729	0.465900
1-10	-1.091310	0.173146	-6.303	2.92e-10
11-50	-0.763161	0.241159	-3.165	0.001553
Mixed	0.660835	0.232713	2.840	0.004516
Vegetarian	0.303511	0.144491	2.101	0.035680
Evenly	0.197133	0.191464	1.030	0.303195
Inaccessible	1.366856	0.316775	4.315	1.60e-05
Patchy	0.734158	0.189379	3.877	0.000106
Non-Breeding	-0.007241	0.438339	-0.017	0.986820
Predator:Evenly	-1.340514	0.441137	-3.039	0.002375
Predator:Inaccessible	-1.535827	0.505784	-3.037	0.002393
Predator:Patchy	1.717794	0.456115	3.766	0.000166

Table 6: Statistical values of the generalized linear mixed model analysing the effects behaviour frequency

Model 3

Foraging				
	<i>Estimate</i>	<i>Std. Error</i>	<i>z-value</i>	<i>Pr(> z)</i>
(Intercept)	-0.32274	0.45794	-0.705	0.48095
Small	1.31870	0.13458	9.799	<2e-16
Solo	1.72320	0.13225	13.029	<2e-16
Other	-4.71483	0.72045	-6.544	5.98e-11
Pathway	-2.07993	0.23311	-8.923	<2e-16
Restaurant/Resting Area	-1.86975	0.21875	-8.547	<2e-16
Non-Breeding	0.06037	0.52934	0.114	0.90920
Small:Other	-0.38552	0.85606	-0.450	0.65246
Solo:Other	0.37031	0.77107	0.480	0.63105
Small:Pathway	0.84653	0.26695	3.171	0.00152
Solo:Pathway	1.23054	0.26070	4.720	2.36e-06
Small:Restaurant/Resting Area	0.09637	0.26035	0.370	0.71127
Solo:Restaurant/Resting Area	0.13299	0.25406	0.523	0.60064
Self-Directed				
	<i>Estimate</i>	<i>Std. Error</i>	<i>z-value</i>	<i>Pr(> z)</i>
(Intercept)	-1.57281	0.47119	-3.338	0.000844
Small	1.88631	0.19720	9.565	<2e-16
Solo	3.03949	0.19129	15.890	<2e-16
Other	-2.67461	0.53686	-4.982	6.30e-07
Pathway	-2.07924	0.42526	-4.889	1.01e-06
Restaurant/Resting Area	-2.45538	0.48792	-5.032	4.85e-07
Non-Breeding	-0.01706	0.52444	-0.033	0.974043
Small:Other	-1.66197	0.71398	-2.328	0.019925
Solo:Other	-1.46027	0.59783	-2.443	0.014582
Small:Pathway	0.91234	0.45791	1.992	0.046328
Solo:Pathway	1.57964	0.44615	3.541	0.000399
Small:Restaurant/Resting Area	0.75982	0.52211	1.455	0.145593
Solo:Restaurant/Resting Area	1.01810	0.50859	2.002	0.045306
Aggression				
	<i>Estimate</i>	<i>Std. Error</i>	<i>z-value</i>	<i>Pr(> z)</i>
(Intercept)	-2.7879	0.5725	-4.870	1.12e-06
Small	2.1307	0.2429	8.770	<2e-16
Solo	-0.7472	0.4051	-1.844	0.06513
Other	-20.0444	5172.8831	-0.004	0.99691

Pathway	-1.5581	0.5508	-2.829	0.00467
Restaurant/Resting Area	-20.0449	5174.1451	-0.004	0.99691
Non-Breeding	-0.3342	0.6289	-0.531	0.59517
Small:Other	14.9693	5172.8832	0.003	0.99769
Solo:Other	0.7513	7308.0115	0.000	0.99992
Small:Pathway	0.2896	0.5761	0.503	0.61514
Solo:Pathway	-0.6391	1.1904	-0.537	0.59137
Small:Restaurant/Resting Area	17.5347	5174.1451	0.003	0.99730
Solo:Restaurant/Resting Area	0.7517	7309.2271	0.000	0.99992

Table 7 Statistical values of the generalized linear mixed model analysing the effects behaviour frequency within animal enclosures

Model 4

Foraging				
	<i>Estimate</i>	<i>Std. Error</i>	<i>z-value</i>	<i>Pr(> z)</i>
(Intercept)	-2.533786	1.215484	-2.085	0.0371
Small	1.558145	0.095772	16.269	<2e-16
Solo	2.055483	0.092451	22.233	<2e-16
Predator	-0.396863	1.454026	-0.273	0.7849
1-10	-1.312054	0.802825	-1.634	0.1022
11-50	-1.118495	0.982464	-1.138	0.2549
Mixed	-0.712235	0.938465	-0.759	0.4479
Vegetarian	-0.613476	0.674780	-0.909	0.3633
Evenly	-1.126896	0.808736	-1.393	0.1635
Inaccessible	0.011822	1.428385	0.008	0.9934
Patchy	0.006507	0.791091	0.008	0.9934
Non-Breeding	-0.181583	0.519628	-0.349	0.7268
Small:Predator	-1.176777	0.198068	-5.941	2.83e-09
Solo:Predator	-1.674115	0.196484	-8.520	<2e-16
Predator:Mixed	14.955954	447.025136	0.033	0.9733
Predator:Evenly	-13.769941	447.024816	-0.031	0.9754
Predator:Inaccessible	0.230868	2.058003	0.112	0.9107
Predator:Patchy	-11.747901	447.027253	-0.026	0.9790
Self-Directed				
	<i>Estimate</i>	<i>Std. Error</i>	<i>z-value</i>	<i>Pr(> z)</i>
(Intercept)	-5.67874	1.12944	-5.028	4.96e-07
Small	2.11296	0.18287	11.555	<2e-16
Solo	3.35679	0.17571	19.104	<2e-16
Predator	0.48000	1.32587	0.362	0.717331
1-10	-0.30554	0.71954	-0.425	0.671107

11-50	-0.24148	0.88648	-0.272	0.785312
Mixed	-0.59449	0.84564	-0.703	0.482055
Vegetarian	-0.49878	0.60058	-0.831	0.406254
Evenly	-0.32922	0.72969	-0.451	0.651856
Inaccessible	1.19392	1.27111	0.939	0.347589
Patchy	0.74370	0.71411	1.041	0.297676
Non-Breeding	0.05021	0.53540	0.094	0.925277
Small:Predator	-0.86020	0.35194	-2.444	0.014518
Solo:Predator	-1.13604	0.32989	-3.444	0.000574
Predator:Mixed	2.37336	1.62010	1.465	0.142937
Predator:Evenly	-1.18592	1.56719	-0.757	0.449217
Predator:Inaccessible	-2.11464	1.85257	-1.141	0.253677
Predator:Patchy	-0.37598	2.02568	-0.186	0.852752

Zusammenfassung

Soziale Systeme im Tierreich hängen stark von ökologischen und sozialen Faktoren ab, wodurch die Größe und Zusammensetzung von Tiergruppen ständiger Variation unterliegen. Während sogenannte Fission-Fusion Dynamiken bei Primaten bereits ausgiebig untersucht wurden, sind dementsprechende Studien bei Vogelarten selten. Der Grad von Fission-Fusion Dynamiken ist artspezifisch und es wird angenommen, dass dieser positiv mit den kognitiven Fähigkeiten einer Art korreliert. Rabenvögel zeigen stark ausgeprägte Gruppendynamiken und sind für ihre hohen kognitiven Fähigkeiten bekannt. Diese Studie untersucht den Einfluss von Umweltfaktoren auf Fission-Fusion Dynamiken und die Nahrungssuche einer frei-lebenden Population von Krähen (*Corvus corone ssp.*) im Tiergarten Schönbrunn in Wien. Die Daten wurden mit Hilfe der Citizen Science App KraMobil (Spotteron) gesammelt. Gruppengröße der Krähen und Zoo Areal hatten den größten Einfluss auf die Gruppendynamik der Krähen im Zoo. Innerhalb der Tiergehege wirkten sich Gruppengröße der Krähen, Anzahl der Individuen, die in einem Gehege beherbergt sind und das von ihnen ausgehende Risiko, sowie die Qualität und Verteilung der angebotenen Nahrung auf die Gruppendynamik und das Verhalten der Krähen aus. Die

Ergebnisse deuten darauf hin, dass die untersuchte Krähen Population starke Fission-Fusion Dynamiken aufweist und diese von ökologischen und sozialen Faktoren abhängig sind.