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"Fission-Fusion Dynamics in an Urban Population of Crows (*Corvus corone ssp.*)"

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Abstract

Animal species living in dynamic social groups face cognitive challenges like keeping track of individuals and social relationships. Effects of fission-fusion dynamics, i.e. changes in group size and composition, on socio-cognitive skills have mainly been studied in large-brained mammals. Comparably little is known about the dynamics of birds. This study investigates fission-fusion dynamics of a flock of Carrion and Hooded Crows (*Corvus corone sp.*) in an urban environment. Wild crows often form seemingly anonymous flocks; yet recent studies from captivity suggest that groups may be structured by different types of social bonds. I observed wild crows living in and around the Tiergarten Schönbrunn (Zoo Vienna), Austria, over the course of one year. Individual information on over 300 birds was available, as these birds had been caught, measured and marked. I was interested in i) which individuals were present, when and where in the zoo, ii) whether or not the crows were found in groups (i.e. within five metres of one another crow) and iii) which environmental factors (i.e. weather, temperature, time, date, and number of visitors) could explain patterns of flock and group formation, respectively. As expected, the size of the local flock varied strongly over the course of the year, with few birds being present in the zoo during the breeding period. The composition of the local population also changed over time and crows could be categorized according to their residency pattern as locals or as different types of visitors. The time of day, season, temperature and weather had strong influences on the size of the local flock. In contrast, the area of the zoo, the age class of the birds, the season of the year as well as the time of the day affected the group formation within the flock. These findings suggest that several environmental factors may have significant effects on group formation, as well as on group structure, by influencing the chances of individuals interacting.

Introduction

The social intelligence hypothesis states that one of the main driving forces for cognitive skills is living in complex groups with conspecifics (Dunbar, 1998). There are different factors contributing to social complexity: group size, as an increasing number of individuals in the group leads to an increase in memory capacities, and the keeping track of social relationships becomes more and more demanding (Dunbar & Bever, 1998; Dunbar, 1998); variation in relationship quality, as social bonds between particular individuals may serve as alliances, which affect the outcome of conflicts and lead to dependencies in dominance rank (Braun & Bugnyar, 2012; Holekamp et al., 1997); fission-fusion dynamics, as the likelihood of meeting particular individuals more often than others may lead to improved inference or inhibition skills (Amici, Aureli, & Call, 2008; Aureli et al., 2008).

Most research on the aforementioned factors has so far been done on mammals, in particular on primates. In recent years birds' social complexity has also been studied, albeit to a lesser extent (Beauchamp & Fernández-Juricic, 2004; Bond, Kamil, & Balda, 2003; Fraser & Bugnyar, 2010b). With regard to primates, group size has been found to be correlated with forebrain size (Dunbar, 1998). In birds, correlations between forebrain size and group size are so far unsupported (Beauchamp & Fernández-Juricic, 2004). Indeed, group size is hardly indicative of social complexity in species outside of primates (Byrne & Bates, 2007). Social relations between individuals can lead to the formation of alliances which are found in a variety of taxonomic groups, e.g., bottlenose dolphins (Connor, Smolker, & Richards, 1992); spotted hyenas (Holekamp et al., 1997), and birds (Emery, Seed, von Bayern, & Clayton, 2007a). These alliances are useful support for individuals in conflicts. While mammalian alliances are often built around kinship (Holekamp et al., 1997; Parsons et al., 2003), non-related individuals can also form long term pair bonds, which are common in many bird species, i.e. in ravens (Braun & Bugnyar, 2012) and carrion crows (Richner, 1989). Keeping track of the hierarchy and alliances among individuals in a group can lead to the development of higher cognitive skills such as transitively inferring dominance ranks (Paz-y-Mino, Bond, Kamil, & Balda, 2004). The complexity of this track-keeping is likely increased in systems with high fission-fusion dynamics, as individuals meeting each other only from time to time still have to remember their relationships.

Since the introduction of the term by Kummer (1971), the research on fission-fusion dynamics was mostly focused on mammals with studies on a wide variety of species, e.g., dolphins (Bräger, 1999); bats (Kerth & König, 1999); giraffes (Carter, Seddon, Frère, Carter, & Goldizen, 2013); elephants (Wittemyer, Douglas-Hamilton, & Getz, 2005); hyenas (Holekamp et al., 1997); non-human primate species: chimpanzees (Boesch & Boesch-Achermann, 2000; Mitani, Watts, & Muller, 2002), spider monkeys (Chapman, Wrangham, & Chapman, 1995), bonobos (Hohmann & Fruth, 2002); and

humans (Marlowe, 2005). Yet, fission-fusion dynamics have been studied to a lesser extent than the aforementioned factors of group size and social relations influencing social complexity. This holds especially true for birds, which have been the focus of only few studies in this respect so far, e.g., in ravens (Braun & Bugnyar, 2012; Braun et al., 2012; Loretto et al., 2015), monk parakeets (Hobson, Avery, & Wright, 2014), brown-headed cowbird (Kohn et al., 2015) and sea birds (Beauchamp, 2011). Considering the strong dynamics occurring in many avian species, this is surprising, as at least during non-breeding season many species of birds form large flocks. Silk et al. (2014) argue that foundations for studies in avian social systems are already laid and that such studies could contribute greatly to our understanding of fission-fusion dynamics.

Many species of birds are gregarious and the groups they form can serve multiple purposes. These purposes are often protection from predation or increasing foraging efficiency (Krause & Ruxton, 2002). Group sizes usually have an optimum, above which joining a group ceases to have a meaningful positive effect for the individual (Krause & Ruxton, 2002). Studies on seabirds showed species and context specific saturation for group-sizes with regard to the population density, where most foraging parties had an optimum and most flying parties did not (Beauchamp, 2011). The organisation of avian groups is highly variable, from animals mostly living in dyads, with the young of the year, to large groups of birds living communally (Bond et al., 2003). These large groups can also feature different kinds of fission-fusion dynamics, e.g. Ravens flocking in large numbers at night roosts and splitting up into small subgroups during the day (Braun et al. 2012), or Eurasian Nutcrackers congregating at a food-source but normally only living in small groups in their territories (Vander Wall & Balda, 1977). Studies on magpie-jays have found ecological effects with regard to food availability on group size (Langen & Vehrencamp, 1998), where more food in a territory could sustain a higher number of birds. Such effects were also found in spider monkeys and chimpanzees (Chapman et al., 1995), red colobus and black-and-white colobus (Chapman & Pavelka, 2005), as well as in lions (Caraco & Wolf, 1975). Another ecological factor that can influence group size is the openness of the habitat that proved to be of importance in moose (Peek, LeResche, & Stevens, 1974) and fallow deer (Thirgood, 1996). Both social and environmental effects can play an important role in group formation and group size, yet the impact of environmental effects on groups is considerably less studied.

Corvids show interesting social behaviours and socio-cognitive abilities. They can form alliances (Emery, Seed, von Bayern, & Clayton, 2007b; Fraser & Bugnyar, 2010b, 2012), console partners after conflicts (Fraser & Bugnyar, 2010a; Seed, Clayton, & Emery, 2007), learn to judge others in food caching contexts (Bugnyar, Schwab, Schloegl, Kotrschal, & Heinrich, 2007), use deception when competing for food (Bugnyar & Kotrschal, 2002; Emery, Dally, & Clayton, 2004), use their social

relations when learning form others (Schwab et al., 2008, Kulahci et al., submitted), and they are able to infer the social dominance from observations of other individuals' interactions (Paz-y-Mino et al., 2004). In addition to these studies on captive birds, studies on free ranging ravens show that individuals in non-breeder flocks can form subgroups (Braun et al., 2012) and be split into different structural levels concerning their sociality (Braun & Bugnyar, 2012). Therefore it is likely that non-breeder flocks are not entirely anonymous. Activity range in ravens also differs greatly from sometimes small territories of pair-bonded individuals to large range sizes during dispersal (Loretto, Schuster, & Bugnyar, 2016; Loretto et al., 2015).

Crows (*Corvus corone ssp*.) are similar to ravens with regard to their life history as well as their ecology. Both species are highly opportunistic generalists utilising a wide range of habitats, though crows are more likely to follow humans into densely populated urban habitats (Goodwin, 1976). On one hand crows, like ravens, develop neophobia from a sub-adult age onwards, making them less explorative (Miller, Bugnyar, Pölzl, & Schwab, 2015), on the other hand young and subordinate crows profit from the exploration behaviour of dominant birds (Chiarati, Canestrari, Vera, & Baglione, 2012). Crows have been tested in a variety of cognitive tasks, e.g. understanding object permanence (Hoffmann, Rüttler, & Nieder, 2011), distinguishing object sizes (Moll & Nieder, 2014) and being aware of inequity in getting rewarded (Wascher & Bugnyar, 2013). In most of these tests, they perform similarly to ravens; however, there are also results that call for caution concerning equalizing crow's cognitive skills with those of ravens, for instance in inhibition tasks (Mikolasch, Kotrschal, & Schloegl, 2012; Wascher, Dufour, & Bugnyar, 2012). These differences in performance might be linked to their social structure, as an association between the degree of fission-fusion dynamics and inhibitory skills was found in primates (Amici et al., 2008). While cognitive abilities of crows and ravens have recently received comparable attention, crows are lacking behind in terms of detailed studies on their social system. Crow aggregations show hierarchies determined by age, sex and body size (Richner, 1989), regulating the access to food and other resources. Earlier studies present evidence for fission-fusion societies in American crows (Stouffer & Caccamise, 1991). In *Corvus corone ssp*. the extent of fission-fusion dynamics has not yet been studied.

The current study focused on a flock of free ranging crows situated in the Vienna Zoo, Tiergarten Schönbrunn, Austria. This flock has been part of a monitoring program involving the colour-banding of > 300 birds for individual identification. The study area in general is ideal to study fission-fusion dynamics as the zoo is regularly frequented by crows, which use the area extensively to forage on a wide variety of foods available. Also the birds in the area are habituated to humans and can therefore be approached closely and still show natural behaviours.

The aim of this study is to examine fission-fusion dynamics in crows and to investigate influencing factors on group and flock size, respectively. I address the following hypotheses: (1) The size of the local flock varies over the year. (2) The local flock has a non-random social structure. Environmental factors influence the size of (3) the local flock and (4) the foraging groups of crows present at the zoo. My predictions are: (1) Higher numbers of crows should be found in the zoo outside the breeding season as territorial pairs should fend off non-breeding birds during breeding season. (2) The flock should be structured in a manner resembling the organisation found in raven non-breeder flocks, which can be characterized by local birds, regular visitors and infrequent visitors (Braun & Bugnyar, 2012; Heinrich, Kaye, Knight, & Schaumburg, 1994). (3) Environmental factors that influence the flock size should be: weather, with less birds being present in adverse weather conditions; season, with a decline of birds during breeding season and a spike during summer months, as observations from previous years showed an influx of juvenile birds into the zoo after breeding season (Schwab, personal comment); time of the day, as birds are more likely to arrive when the zoo animals are getting fed in order to be able to exploit the food; number of visitors present, where higher numbers of visitors could lead to more food being available at the zoo, as people drop food or even actively feed the birds. (4) Overall population size should have an effect on group size; however also factors concerning the surroundings of the birds should play an important role, as larger groups could be expected in larger open areas for predator protection (Jarman, 1974). Additionally, I expect an influence in terms of ontogeny with younger birds showing a stronger tendency to form groups than adult birds or even pair-bonded birds.

Methods

Study site and population

The study was carried out at the Vienna Zoo, the Tiergarten Schönbrunn, Austria and its immediate surroundings (see Figure 1). The local population of crows consists of carrion crows, hooded crows, and their hybrids since Vienna lies in the overlapping range of the two subspecies across Central Europe (de Knijff, 2014; Glutz von Blotzheim, 1993). Since 2010, approximately 300 crows were caught using Walk-In- and Larsen-traps (Kirchmeir, Uhl, Bugnyar, & Schwab, n.d.), and then marked with unique coloured bands for individual identification. At the beginning of the observations the number of marked birds was 297, at the end 322.

Figure 1. Study area. The area relevant to the observations, Vienna Zoo plus immediate surroundings, is outlined in red. The black line represents the route along which the observations were made. Dotted lines represent paths of the observations that were not always taken as they were not always accessible due to construction work and/or hazardous weather conditions during winter. The map was provided by the MA41.

Data collection

Data were collected from 8.1.2014 to 31.12015. The observations were confined to daylight hours. During winter (8.1.2014 to 17.4.2014 and 17.10.2014 to 31.1.2015) there were two observational sessions: one starting between 9am and 1pm ("Morning") and one starting between 1pm and 4pm ("Afternoon"). When daylight hours increased (23.4.2014 to 14.10.2014) we ran three observational sessions: between 8am-12pm ("Morning"), 12pm-3pm ("Noon"), 3pm-7pm ("Afternoon").
Data collection was done via scan observations along a set route through the zoo that ensured full coverage of the study area (see Fig. 1). There were changes to the route, as some paths were closed at times. The starting point of the route was fixed, the start time of observational sessions, however, varied as well as the direction (clockwise/counter-clockwise).

Scan protocols consisted of observations along the route through the zoo. Crows that were present at a location were assigned via a MobileMapper® 10 by Spectra Precision using ArcGIS® ArcPAD® 10.2 by ESRI® onto a map of the Zoo area. Furthermore, for each crow sighting several behavioural and environmental parameters, as well as parameters concerning the crows themselves (subspecies, age, ID), were recorded which can be found in Table 1. In addition, I noted per scan the group sizes in the respective zoo area. A group was defined as being within 5 metres of one another and having direct sight to at least one other member of the group. The total number of scan protocols was 271 (104 morning, 60 noon, 107 afternoon) which took place on 122 days with an average of 2.22 (SE: ±0.06) scans per day.

Table 1. Parameters that were collected for each crow and their definition. Most fields also had the option of using a question mark if the parameter could not be determined with the desired accuracy or were generally not attainable. Categories of parameters are given in bold letters, single parameters in the preceding category in regular letters. The direction of interactive behaviours was determined by recording the initiator of a behaviour and the recipient of a behaviour.

Category	*Parameter*	*Definition*
General Info		
Date		Date of the observation
Time		Time of the observation
Observer		Initials of the observer
Temperature	Cold	<5°C
	Warm	5-25°C
	Hot	>25°C
Weather	Sun	Sun shines, few if any clouds
	Clouds	Heavily overcast skies, also foggy days
	Rain/Snow	Precipitation
Visitors	Many	Perceived amount of visitors present.
	Some	
	Few	
Crow Parameters		
Marking	Marked/Unmarked	Banded crows are entered as "marked", Unbanded Crows as “unmarked”
Phenotype	C	Carrion
	H	Hooded
	HY	Hybrid
	HH	Hooded-Hybrid (for those hybrids closer to hooded crows)
	CH	Carrion-Hybrid (for those hybrids closer to Carrion Crows)
Age	Juvenile	Young birds, still red in their beaks, first plumage
	Sub-adults	Birds that are not juvenile any more, but still have their juvenile flight feathers, may be still red in their beaks
	Adults	Birds with adult plumage
Individual	ID	If ID-Number of a bird is known to the observer, then it can be entered into a special box.
Behavioural Categories		
	Autopreening	Cleaning or smoothing the feathers by means of bill and feet.
	Feeding	Picking up food and feeding on it. This means the food item disappears in bill, therefore storing of food in throat pouch is counted as feeding as well. Manipulating a food object (e.g. a nut) for later consumption is regarded as feeding as well.
	Foraging	Walking around and looking for food. This can be recognized via the birds often picking at the ground as well as turning over leaves and stones
	Object Manipulation	Picking or manipulating a non-food object with the bill.
	Nest Building	Carrying nesting material or manipulating a nest.

Show-off-walk	Bird walking around with puffed feathers, stiff legs
Tail fanning	Briefly fanning the wings/tail feathers (count fequencies)
Co-Feeding	Feeding within half a metre of another crow.
Begging	Begging another crow for food.
Transport Active/Bill Feeding	Bill to bill food transfer done voluntarily
Stealing	Taking an item (food/non-food) from another bird and leaving with it
Displacing from item	Crow A approaching another crow sitting close to some food/eating, which in turn leaves, crow A obtains food item/object
Item sharing	Two crows manipulate the same food item
Wait and watch	A approaches B who is manipulating food, A watches B nothing happens
Allopreening	Preening another bird for at least 3 consecutive seconds.
Threat	Crow hitting other crow with beak, pulling on the feathers or grasping it with its legs, no one leaves
Fight	Two birds aggressively interacting, both pecking each other
Contact sitting	Two crows sitting in close proximity of one another for at least 3 seconds
Displacement	A approaches B without aggression, B leaves
Aggressive Displacement	A approaches B, B leaves, aggression involved
Approach	A crow walking up to another crow, nothing else happens
Follow	Crow A leaves a location Crow B follows, keeping close distance (<0.5m)
Affirmation	After show off walk, A to B touches, soft calls either on request or voluntarily
Call	Bird makes distress calls either during interaction with other bird or alone (frequencies)
None	No behaviour observable, bird is stationary
?/Unidentified Behaviour	Behaviour does not fit any of the above categories

Analysis

Data were analysed in ESRI® ArcGIS® ArcMap™ 10.0 as well as in R Version 3.2.1 (R Core Team 2015). We added information on the localities for each of the crow sightings via Spatial Join in ArcGis 10. The study area was split up in several categories based on the local conditions, with regard to the openness of the area, as the study area in the zoo also features a forested part. In addition the zoo area was divided into areas of higher or lower danger in the zoo, thereby describing whether an enclosure held animals that could potentially prey on crows. Furthermore, the study site held different possibilities of encountering different foods. Therefore the foods were split up into 4 categories that represent the nutrient levels of the food in the respective area. Lastly we also took

into account the structure of the area that a bird was found in with regard to man-made structuring of the environment. The information added is listed in Table 2. Additionally we split the data into three seasons according to the birds breeding ecology: the breeding season (February to May), the paternal care season (June to September) and the non-breeder season (October to January). The breeding season lasts from beginning of February, as then the adults start building their nests, to end of May when parents with their chicks start forming bigger groups. Paternal care season starts with aforementioned formation of bigger groups of juvenile birds with their parents and ends with the second migratory period of the year in end September, when juveniles become independent of their parents. The non-breeder season is starting with October when the juveniles are independent and ends with end of January when breeding season starts.

Table 2. Information on the surroundings of each sightings added to the Parameters in ArcMap. Note that each sighting contains information on all categories.

Category	Parameter	Description
Forested Area	In forest	Forested area of the Zoo
	Out of forest	Non-forested area of the Zoo
Dangerous Enclosure	Dangerous	Enclosure inhabited by animals that could prey on or kill a crow
	Non-dangerous	Enclosure inhabited by animals that are harmless to a crow
Food in Enclosure	1	Only grass fed to animals in enclosure
	2	Grass and Fruits fed to animals in enclosure
	3	Mainly vegetarian food fed to animals, but also meat
	4	Mainly meat fed to animals in enclosure
On Building	On	Rooftop or man-made structure that cannot be accessed by visitors
	Off	On the floor or on trees
Area	Enclosure	Inside animal enclosure
	Gastronomical area	Areas that are close to food-stands or restaurants
	Other	Areas that do not fall into the other categories

We calculated a daily estimate for the flock size based on the number of crows seen at the zoo. Unmarked crows could not be reliably identified, therefore it is possible that unmarked birds were sighted several times at different locations during an observational session. We therefore used the ratio of resightings of marked birds to correct for such resightings via this formula:

$$CF = \frac{CM_{res} - CM_{abs}}{CM_{res}}$$

CF is the estimate for the resightings of unmarked birds. CM_{abs} is the absolute number different marked birds seen that day, CM_{res} is the total number of sightings of marked birds including resightings.

Using this correction factor we then calculated a flock size estimate:

$$FS_e = CM_{res} + \mathrm{CU} - \mathrm{CU} \times CF$$

FS_e is the flock size estimate per day. CU is the total number of unmarked crows seen over the course of a day. We conducted this analysis for each day by combining the numbers of crows from all two or three scan rounds conducted on the same day.

We analysed the local flock size according to the calculated estimate. In order to investigate flock size changes between seasons we compared flock size estimates of different seasons with a Kruskal-Wallis test and then proceeded to pairwise comparisons via Two-tailed Mann-Whitney U tests and adjusted the p-Values via Bonferroni corrections.

We looked at the temporal presence of the marked birds and determined categories the crows can be assigned to with regard to their presence at the Zoo. For this, we looked at the information we had gathered concerning breeding individuals as well.

We used generalised linear mixed models (GLMM) to test which factors influenced the number of crows present at the zoo, as well as which factors influence group size. For the former the response variable was the number of crows seen per scan (corrected for re-sightings of individuals as it was done for the flock size estimate). We included date as random factor into the model and included fixed factors were: weather, temperature, time of day, season, number of visitors, age of the crow, forested area, food in enclosure, on building and area. For the latter our response variable was group size. We included date as random factor into the model and included fixed factors were: weather, temperature, time of day, season, number of visitors, number of crows present that day, marking, age, forested area, dangerous enclosure, food in enclosure, on building and area.
Akaike's information criterion (AIC) were used for model selection (Anderson & Burnham, 2002; Burnham & Anderson, 2004). Model averages were then formed from the estimates of the models that were within an ΔAICc of 2 of the best fitting model (Anderson, 2008). The parameter used for the assessment of the factors influencing the flock size is a variation of the flock size estimate, i.e. an estimate of the number of crows per scan instead of an estimate for the whole day. The parameter used in the analysis of the influencing factors on the group-size was the observed group-size minus one. This transformation was chosen because in the dataset we had group sizes of 1 to 33 birds. To fit the data to the negative binomial distribution for further analysis we subtracted one as we had no group-size of zero.

Results

Number of crows visiting the Zoo area

The flock size estimate, ergo the estimate for the number of different individuals seen per day over all days of data collection (n = 122) was on average 55 ± 23 crows (mean ± SD). Visual inspection of the data shows strong fluctuations during migratory periods (February/March, September/October) (Figure 2).

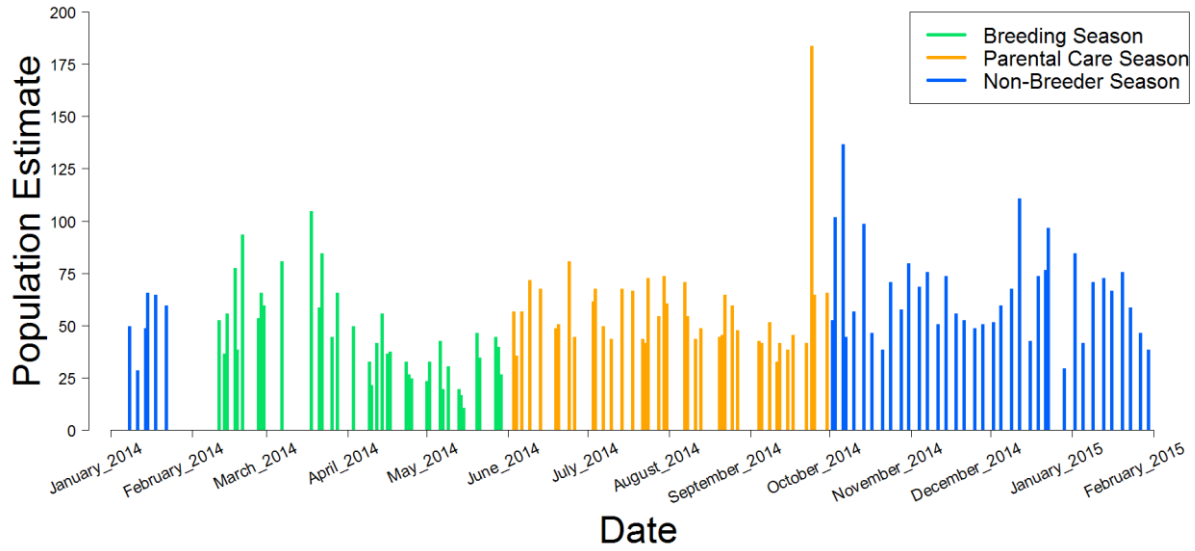


Figure 2. The flock size estimates per observation day throughout the entire observational period. The different colours represent the different seasons during the year.

As predicted, the size of the local flock differed significantly between seasons with the least number of birds being present at the zoo during the breeding season (Kruskal-Wallis, $H(2) = 17.649$, $p < 0.001$). Pairwise comparisons of the flock size estimate showed a highly significant difference between the Non-Breeder Season and the Breeding season (Wilcoxon $W = 1219.5$, $p < 0.001$), as well as a significant difference between Breeding Season and Paternal Care Season (Wilcoxon $W = 1076$, $p = 0.01$) and no significant difference between Non-Breeder and Paternal Care Season (Wilcoxon $W = 1102.5$, $p = 0.15$) (see Figure 3).

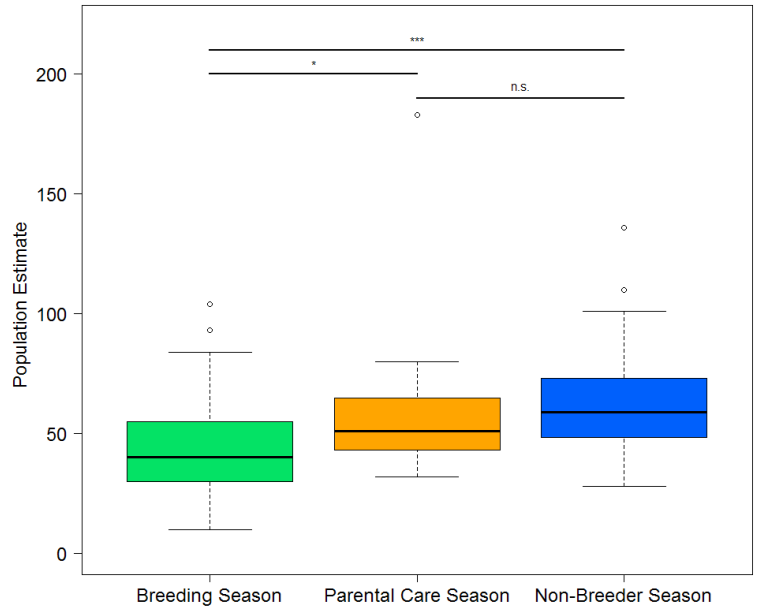


Figure 3. The flock size estimates of the seasons with significance levels added (*p<0.05, ***p<0.001).

Temporal presence of crows

Out of 322 banded and identifiable crows that were part of a colour-ring project in Vienna, 129 individuals were observed at the zoo during the observational period. Details to these individuals can be found in Table 3.

Table 3. Information on the birds that were part of the colour-ring project and the individuals that were observed.

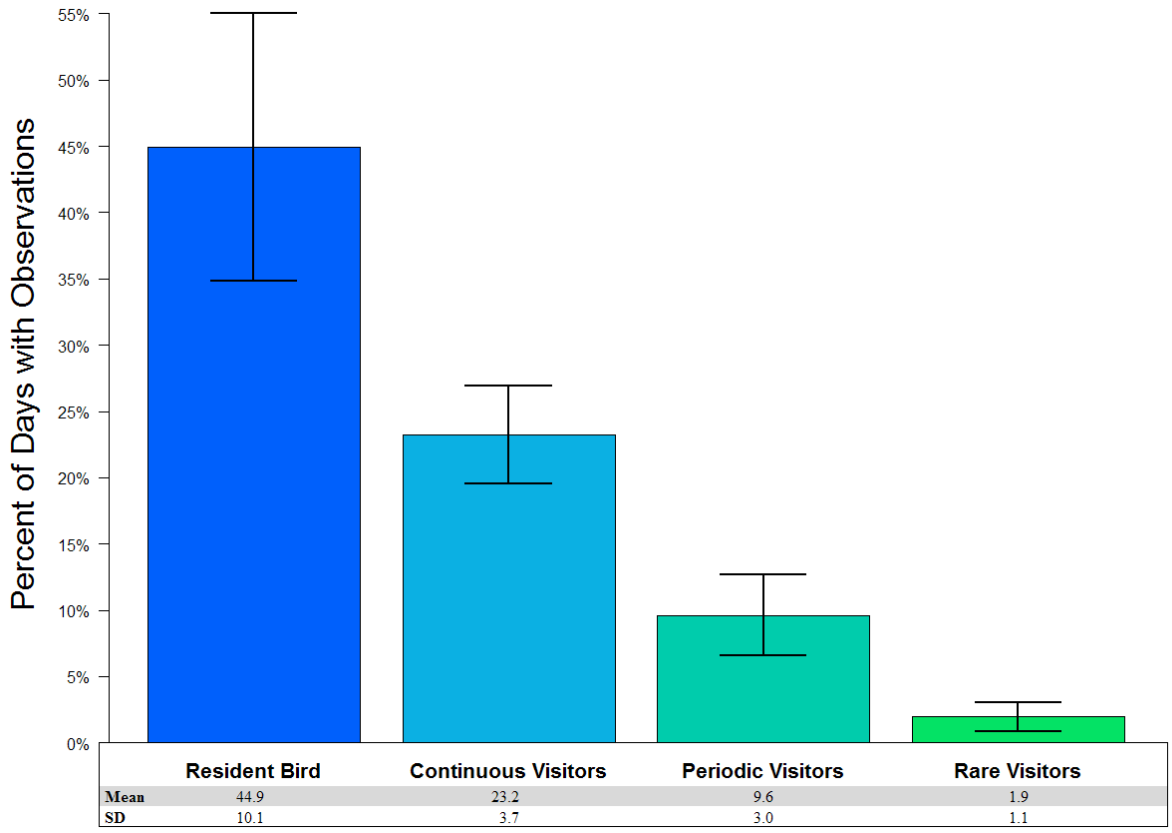
		All Ringed Birds	Observed Individuals
Sex	Male	163	81
	Female	118	40
	Unknown	41	8
Subspecies	Carrion	55	25
	Carrion-Hybrids	34	24
	Hybrids	17	3
	Hooded-Hybrids	96	40
	Hooded	101	35
Total Number		322	129

The marked individuals that could be identified account for 86.2% (2894 out of 3356) of all sightings of marked birds. The rest of sightings of marked birds could not be identified, as lighting and environmental conditions, such as high grass, leaves and the distance to the crow, as well as several birds losing rings prevented discrimination. How often individuals were seen varied strongly, ranging from 67.2% of all observational days (sightings on 82 out of 122 days) to 0.8% of all observational days (sighted on one day only).

We classified the birds into three presence categories: resident birds that have been observed ≥30% of observational days (n=25), frequent visitors that have been observed <30 to ≥5% of observational

days (n=48) and finally rare visitors that have been observed on < 5% of observational days (n=56, Figure 4). We then added information on the birds` breeding status at the zoo (breeder were defined as occupying a nest at the zoo independent of breeding success) and visually inspected the birds` presence pattern. This allowed us to further differentiate the category of frequent visitors into continuous visitors (n=16), whose presence was roughly evenly distributed over the entire observational period and into periodic visitors (n=32), whose presence showed a patterning over the observational period with lacks of sightings that spanned several months (Figure 5).

The overall number of sightings of marked and identified individuals can be split up into the different groups, with 1800 (62.2%) sightings of resident birds, 540 (18.7%) sightings are accounted for by continuous visitors, 418 (14.4%) sightings can be attributed to periodic visitors and 136 (4.6%) sightings were made for rare visitors (Figure 4).



	Resident Bird	Continuous Visitors	Periodic Visitors	Rare Visitors
Mean	44.9	23.2	9.6	1.9
SD	10.1	3.7	3.0	1.1

Figure 4. Mean presence of each class of marked individuals at the zoo in percent of the days with observations (122 days) and the standard deviations.

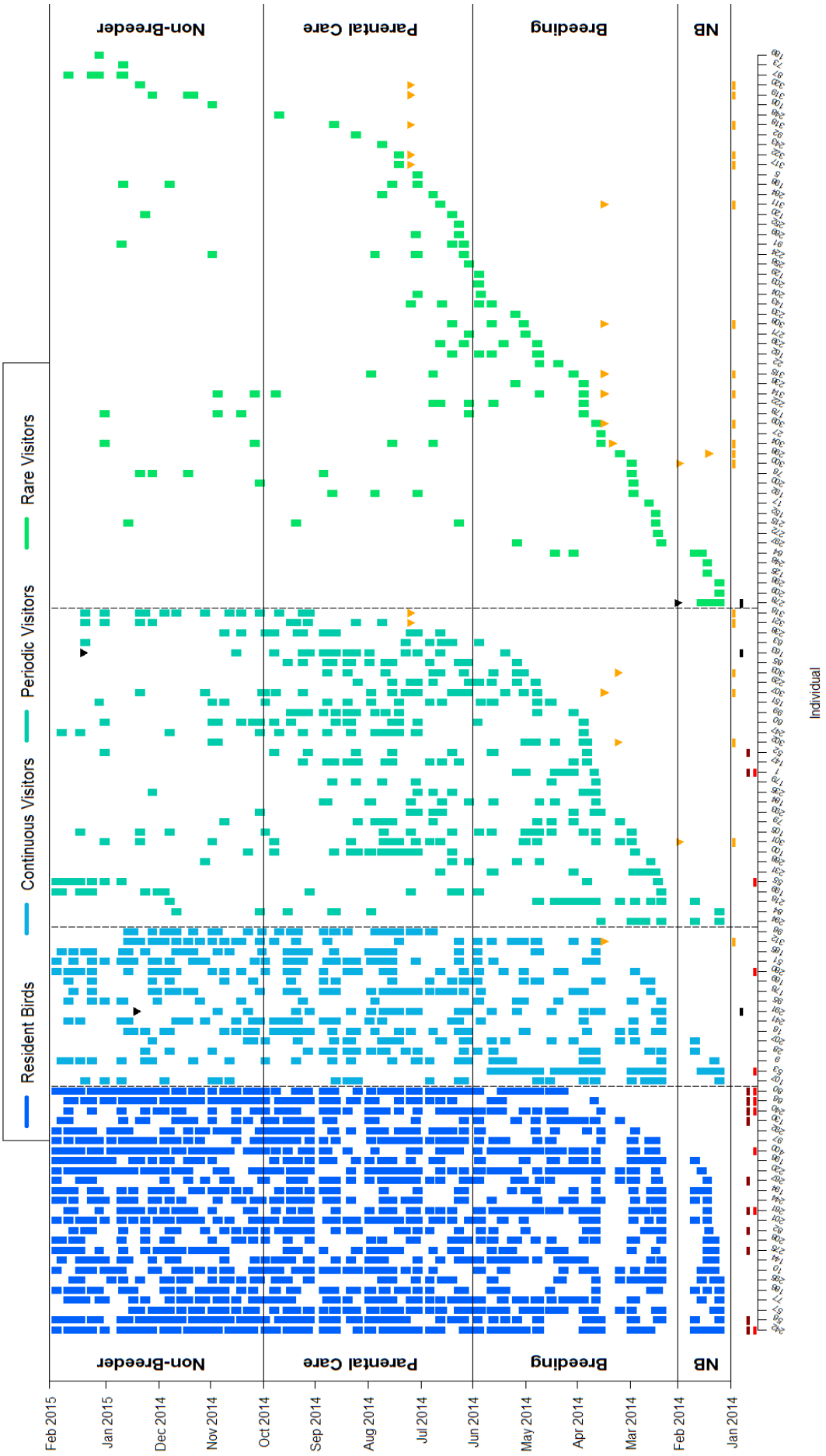


Figure 5. Days the marked birds were seen at the zoo. The breaks indicate the categories according to percentages. The classes were sorted for each birds' date of first sighting at the Zoo. The lines found between the x-axis and the line at the bottom of the graph signify breeders (2014 bright red, 2013 dark red), birds we know died (black), and birds marked throughout the year (orange). The inverted triangles show the dates at which birds either died (black) or were marked (orange).

Influences on flock size

In total we obtained 17645 observations (out of which 2894 were observations of marked individuals that were uniquely identifiable) between 8.1.2014 to 31.1.2015. The models that best explained the flock size estimation were averaged. The models best describing the response variable included several factors which are detailed in Table 4. The results of the analysis are presented in Table 5. The factors with the strongest effects estimates are the time of day (Noon Estimate -0.021 SE: 0.006, Afternoon Estimate: 0.531 SE: ±0.004), followed by season (Breeding Season Estimate: -0.288 SE: ±0.074, Parental Care Season Estimate: 0.138 SE: ±0.072), temperature (Warm Estimate: -0.282 SE: ±0.014, Hot Estimate: -0.282 SE: ±0.014), and weather (Clouds Estimate: 0.147 SE: ±0.011, Sun Estimate: 0.170 SE: ±0.012).

The factors influencing flock size most strongly, i.e. time of day, season, temperature and weather, can also be found as graphs in the appendix (Figure A).

Table 4. The models that were best explaining the dataset regarding flock size, with the factors included in the models. The factors are sorted in descending order of effect.

Model 1	**Model 2**	**Model 3**	**Model 4**
Time of Day	Time of Day	Time of Day	Time of Day
Season	Season	Season	Season
Temperature	Temperature	Temperature	Temperature
Weather	Weather	Weather	Weather
Interaction: Visitors/Season	Interaction: Visitors/Season	Interaction: Visitors/Season	Interaction: Visitors/Season
Dangerous Enclosure	Dangerous Enclosure	Dangerous Enclosure	Dangerous Enclosure
On Building	On Building	On Building	On Building
Food in Enclosure	Food in Enclosure	Food in Enclosure	Food in Enclosure
Age	Age	Age	Age
Visitors		Visitors	
Area	Area	Area	Area
Forested Area	Forested Area		

Table 5. Model coefficients with standard-errors for the models that best explain which of the factors influence the flock size in the research area. Calculations were generalized linear models (family = negative binomial, link = log). The table is sorted by the average estimates from higher values to lower values by category. The categories are differentiated via the shading of the fields.

Model	1	2	3	4	Average
AICc	145610.1	145610.1	14569.9	14569.9	
ΔAICc	0.2	0.2	0	0	
Model Weight	0.24	0.24	0.26	0.26	
(Intercept)	4.001	4.001	4.008	4.008	4.005
	±0.053	±0.053	±0.052	±0.052	±0.053
Noon	-0.021	-0.021	-0.021	-0.021	-0.021
	±0.006	±0.006	±0.006	±0.006	±0.006
Afternoon	0.531	0.531	0.531	0.531	0.531
	±0.004	±0.004	±0.004	±0.004	±0.004
Breeding Season	-0.288	-0.288	-0.288	-0.288	-0.288
	±0.074	±0.074	±0.074	±0.074	±0.074
Parental-Care Season	0.138	0.138	0.138	0.138	0.138
	±0.072	±0.072	±0.072	±0.072	±0.072
Temperature - Warm	-0.282	-0.282	-0.281	-0.281	-0.282
	±0.014	±0.014	±0.014	±0.014	±0.014
Temperature - Hot	-0.184	-0.184	-0.183	-0.183	-0.184
	±0.020	±0.020	±0.020	±0.020	±0.020
Weather - Clouds	0.147	0.147	0.147	0.147	0.147
	±0.011	±0.011	±0.011	±0.011	±0.011
Weather - Sun	0.170	0.170	0.170	0.170	0.170
	±0.012	±0.012	±0.012	±0.012	±0.012
Non-Breeder Season : Visitors - Some	0.000	0.006	0.000	0.006	0.003
	±0.000	±0.009	±0.000	±0.009	±0.004
Non-Breeder Season : Visitors - Many	0.000	0.030	0.000	0.032	0.016
	±0.000	±0.135	±0.000	±0.135	±0.068
Visitors - Some :	-0.043	-0.037	-0.042	-0.036	-0.040
Breeding Season	±0.013	±0.010	±0.013	±0.010	±0.012
Visitors - Many :	0.002	0.032	0.002	0.034	0.018
Breeding Season	±0.137	±0.020	±0.137	±0.020	±0.078
Visitors - Some :	0.006	0.012	0.006	0.012	0.009
Parental-Care Season	±0.010	±0.005	±0.010	±0.005	±0.008
Visitors - Many :	-0.004	0.026	-0.006	0.026	0.011
Parental-Care Season	±0.136	±0.011	±0.136	±0.011	±0.073
Predator Enclosure	0.031	0.031	0.030	0.030	0.031
	±0.007	±0.007	±0.007	±0.007	±0.007
Not On Building	0.030	0.030	0.028	0.028	0.029
	±0.006	±0.006	±0.006	±0.006	±0.006
Vegetarian Food	-0.007	-0.007	-0.007	-0.007	-0.007
	±0.005	±0.005	±0.005	±0.005	±0.005
Mixed Food	-0.023	-0.023	-0.023	-0.023	-0.023
	±0.008	±0.008	±0.008	±0.008	±0.008
Mainly Meat	0.004	0.004	0.002	0.002	0.003
	±0.009	±0.009	±0.009	±0.009	±0.009
Non-Juvenile	-0.017	-0.017	-0.017	-0.017	-0.017
	±0.006	±0.006	±0.006	±0.006	±0.006
Visitors - Some	0.006	0.000	0.006	0.000	0.003
	±0.009	±0.000	±0.009	±0.000	±0.004
Visitors - Many	0.030	0.000	0.032	0.000	0.016
	±0.135	±0.000	±0.135	±0.000	±0.068
Gastronomical Area	-0.001	-0.001	0.000	0.000	-0.001
	±0.007	±0.007	±0.007	±0.007	±0.007
Enclosure	-0.017	-0.017	-0.015	-0.015	-0.016
	±0.004	±0.004	±0.004	±0.004	±0.004
Non-Forested Area	0.007	0.007	0.000	0.000	0.003
	±0.005	±0.005	±0.000	±0.000	±0.002

Group Size

The observed group sizes were in the range of 1 to 33 individuals (Figure 6). The mean group size was 1.85 SE ±0.02 individuals (Quantiles: 0%: 1; 25%: 1; 50%: 1; 75%: 2; 100%: 33). If considering only group sizes of 2 individuals or more the mean was 3.07 SE ±0.03 (Quantiles: 0%: 2; 25%: 2; 50%: 2; 75%: 3; 100%: 33).

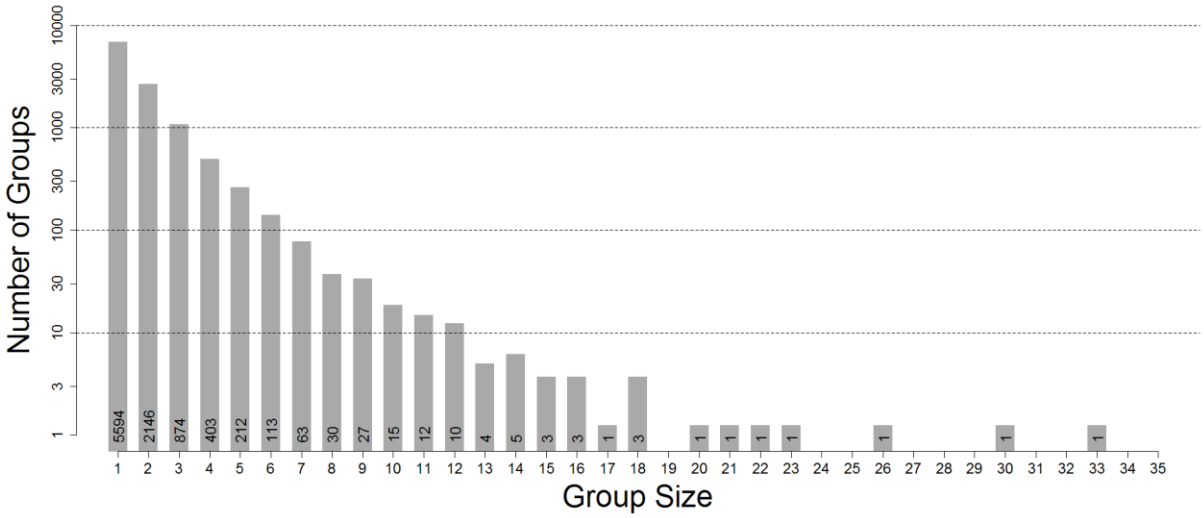


Figure 6. The group sizes that were observed with the amount of observations of each size. The group size describes the number of individuals in an observed group. The y-axis is log transformed for readability. The number of observed groups of each group size is added at the bottom of the bars.

Influences on group size

The data included in this analysis is the same as in the analysis before, with a change of the response variable to the observed group-size minus one. The models that best explained the changes in group-size were averaged. The full results can be seen in Table 6. The factors with the highest influence on group-size according to our analysis are the forestation of the area (Non-Forested Area Estimate: 0.512 SE: ±0.035), their location relative to manmade structures (Not on Building Estimate: 0.373 SE: ±0.042), the weather (Clouds Estimate: 0.318 SE: ±0.064, Sun Estimate: 0.109 SE: ±0.067), the food available in a location (Vegetarian Food Estimate: 0.311 SE: ±0.028, Mixed Food Estimate: -0.127 SE: ±0.049, Mainly Meat: 0.121 SE: ±0.044) the of the Crows (Non-Juvenile Estimate: -0.413 SE: ±0.034), the season (Breeding Season Estimate: -0.381 SE: ±0.056, Parental Care Season Estimate: -0.116 SE: ±0.052) and whether the birds were marked (Marked Estimate: -0.372 SE: ±0.030).

The factors influencing group size most strongly can also be found as graphs in the appendix, where they are split in 4 graphs starting with temperature (Figure B), the environmental factors' effects (season, weather, time of day and visitors) (Figure C), the effects factors regarding the locality in the zoo have on group size (Figure D), and the effects of the individuals age and marking as well as the interaction of marking with season (Figure E).

Table 6. The models that were best explaining the dataset regarding group size, with the included factors included in the models. The factors are sorted in descending order of effect.

Model 1	**Model 2**	**Model 3**	**Model 4**
Forested Area	Forested Area	Forested Area	Forested Area
	Season		Season
On Building	On Building	On Building	On Building
Marking	Marking	Marking	
Weather	Weather	Weather	Weather
Food in Enclosure	Food in Enclosure	Food in Enclosure	Food in Enclosure
Time of Day	Time of Day	Time of Day	Time of Day
Interaction: Marking /Season	Interaction: Marking /Season	Interaction: Marking /Season	Interaction: Marking /Season
Area	Area	Area	Area
Visitors	Visitors	Visitors	Visitors
Temperature	Temperature	Temperature	Temperature
Dangerous Enclosure			
Crows per Scan	Crows per Scan	Crows per Scan	Crows per Scan

Table 7. Model coefficients with standard-errors for the models that best explain which of the factors influence the group size in the research area. Calculations were generalized linear models (family = negative binomial, link = log). The table is sorted by the average estimates from higher values to lower values by category. The categories are differentiated via the shading of the fields.

Model	1	2	3	4	Average
AICc	65397.28	65396.08	65396.08	65396.08	
ΔAICc	1.21	0	0	0	
Model Weight	0.16	0.28	0.28	0.28	
(Intercept)	-0.333	-0.333	-0.333	-0.333	-0.333
	±0.145	±0.145	±0.145	±0.145	±0.144
Non-Forested Area	0.513	0.512	0.512	0.512	0.512
	±0.035	±0.035	±0.035	±0.035	±0.035
Non-Juvenile	-0.413	-0.413	-0.413	-0.413	-0.413
	±0.034	±0.034	±0.034	±0.034	±0.034
Breeding Season	0.000	-0.676	0.000	-0.676	-0.381
	±0.000	±0.099	±0.000	±0.099	±0.056
Parental-Care Season	0.000	-0.206	0.000	-0.206	-0.116
	±0.000	±0.091	±0.000	±0.091	±0.052
Not on Building	0.373	0.373	0.373	0.373	0.373
	±0.042	±0.042	±0.042	±0.042	±0.042
Marked	-0.517	-0.518	-0.518	0.000	-0.372
	±0.041	±0.041	±0.041	±0.000	±0.030
Weather - Clouds	0.316	0.318	0.318	0.318	0.318
	±0.064	±0.064	±0.064	±0.064	±0.064
Weather - Sun	0.108	0.109	0.109	0.109	0.109
	±0.067	±0.067	±0.067	±0.067	±0.067
Vegetarian Food	0.306	0.312	0.312	0.312	0.311
	±0.029	±0.028	±0.028	±0.028	±0.028
Mixed Food	-0.130	-0.126	-0.126	-0.126	-0.127
	±0.049	±0.049	±0.049	±0.049	±0.049
Mainly Meat	0.093	0.126	0.126	0.126	0.121
	±0.055	±0.042	±0.042	±0.042	±0.044
Noon	-0.145	-0.142	-0.142	-0.142	-0.143
	±0.036	±0.036	±0.036	±0.036	±0.036
Afternoon	0.245	0.246	0.246	0.246	0.246
	±0.025	±0.025	±0.025	±0.025	±0.025
Marked : Non-Breeder Season	0.000	0.000	0.000	-0.518	-0.146
	±0.000	±0.000	±0.000	±0.041	±0.012
Marked : Breeding Season	-0.299	0.375	-0.301	-0.143	-0.066
	±0.111	±0.067	±0.111	±0.053	±0.082
Marked : Parental-Care_Season	0.157	0.361	0.155	-0.157	0.126
	±0.102	±0.056	±0.102	±0.038	±0.071
Unmarked : Breeding_Season	-0.675	0.000	-0.676	0.000	-0.295
	±0.099	±0.000	±0.099	±0.000	±0.043
Unmarked : Parental-Care_Season	-0.204	0.000	-0.206	0.000	-0.090
	±0.091	±0.000	±0.091	±0.000	±0.040
Gastronomical Area	-0.193	-0.192	-0.192	-0.192	-0.192
	±0.045	±0.045	±0.045	±0.045	±0.045
Enclosure	0.205	0.205	0.205	0.205	0.205
	±0.028	±0.028	±0.028	±0.028	±0.028
Visitors - Some	-0.097	-0.097	-0.097	-0.097	-0.097
	±0.025	±0.025	±0.025	±0.025	±0.025
Visitors - Many	0.197	0.196	0.196	0.196	0.197
	±0.055	±0.055	±0.055	±0.055	±0.055
Temperature - Warm	0.157	0.160	0.160	0.160	0.159
	±0.069	±0.069	±0.069	±0.069	±0.069
Temperature - Hot	0.082	0.082	0.082	0.082	0.082
	±0.105	±0.105	±0.105	±0.105	±0.105
Predator Enclosure	0.041	0.000	0.000	0.000	0.006
	±0.044	±0.000	±0.000	±0.000	±0.007
Number of Crows Present	0.004	0.004	0.004	0.004	0.004
	±0.002	±0.002	±0.002	±0.002	±0.002

Discussion

The aim of this study was to shed light on the social dynamics and influencing factors thereof in wild crows. As expected, the composition of our study flock of crows changed considerably throughout the year. As for our hypotheses we found that our predictions were supported by our data. Firstly the flock size was significantly lower during breeding season than during the rest of the year. Secondly the local flock showed structure that resembled the social structure previously found in ravens (Braun & Bugnyar, 2012). Thirdly the influence of environmental factors on the size of the local flock was substantial with strong effects for time of day, season, temperature and weather. Fourthly environmental effects on group size also had strong effects, in particular the structure of the surroundings, age class, weather, and season.

Seasonal changes in Flock Size

The flock size differed most strongly between the breeding season and the rest of the year. On the one hand we had a strong negative effect of the breeding season with a lower number of birds being present. This effect could be explained by the increased territoriality of the crow breeding pairs that try to defend food resources exclusively for their offspring (Marzluff & Heinrich, 1991; Webb, Marzluff, & Hepinstall-Cymerman, 2012). As breeding territories covered most of the zoo area, the effects of the increased territoriality during breeding season could prevent non-breeders from using most parts of the zoo. The effect of territoriality could be diluted outside of the breeding season, however, as the abundance of food in the zoo area is generally high and accessible to many crows. The fact that the zoo is highly attractive to numerous crows might explain why territorial breeding pairs only defended their territories during the breeding season as it would be too difficult to defend the territories held within the zoo area year round. On the other hand, the parental care season had a positive effect on flock size in our model calculation. However, pairwise comparisons indicated a trend with flock size being marginally lower during parental care season than during non-breeder season. This discrepancy is based on the nature of two types of analysis, as model calculations take other factors into account, while the pairwise comparison only compared the values of the flock sizes for each season. One explanation could be the higher temperatures that occur during the parental care season have strong negative effects on the flock size.

Temporal presence of Crows

The crows present at the zoo could be split into four groups: resident birds, continuous visitors, periodic visitors and rare visitors. This was a more detailed differentiation than the classes defined in a similar situation in ravens (Braun & Bugnyar, 2012). Not only did we discriminate the groups by the percentage of days present and the temporal patterns of their presence in the zoo, we also incorporated the information we had on breeding birds as an approximation for territorial breeding pairs of crows at the zoo. Resident birds were at the study site without longer breaks and included a

high number of breeders. Note that not all birds we determined to be resident birds were known breeders in the zoo. We also found several birds that were in other categories to be breeders at the zoo either in 2013 or 2014. These cases could represent birds that only come to the zoo to breed. The differentiation between the resident birds and the continuous visitors was mainly chosen by the larger timeframes that the continuous visitors were absent from the zoo when compared to the resident birds. These birds might visit the zoo for foraging purposes and hold territories in the surroundings of the zoo. Periodic visitors were found to visit the zoo mainly during specific periods and are then absent during the rest of the year. Rare visitors were only sighted during less than 5 percent of days. The sightings of these visitors were not concentrated in migratory periods therefore these birds could be vagrant birds that use large areas similar to individuals found in ravens (Loretto et al., 2016). The presence of crows in the study area could be assumed to be organised in different levels with breeding birds staying and holding territories in the zoo, as well as others that use the zoo to forage either whenever they do not find enough food in the surrounding area or use it as a stopover.

Factors influencing flock size and group size

Flock size was influenced by fewer factors than group size. Firstly, flock size and group size were linked by the number of crows present in the study area. This could be expected as higher numbers of birds present at the zoo increase the possibility of bigger groups forming. When there were only few birds present in the study area, most of them represented breeding pairs that usually do not form bigger groups. The group size therefore increased with the number of birds present in the study area which is in accordance to what is found in other species (Beauchamp, 2011).

Secondly, the flock size and the group size were affected in a similar manner with regard to the time of day. The flock size and the group size were substantially higher during afternoon sessions. During noon sessions there was a small decrease in flock size and a higher decrease in group size. These lower numbers could be explained by the birds' ecology, as the activity levels are lower during noon sessions and the crows could therefore be less likely to engage in social activities. Flock size and group size increase during afternoon sessions could be explained by the feeding regime at the zoo as the animals do get fed during the day increasing the number of feeding sites accessible throughout the day. Also the afternoon increase in flock size could be explained by birds coming into the zoo area to feed on what visitors drop of their food in the zoo, getting picked up by the crows when the number of visitors decreases. The increase in group size in the afternoon could also be explained by more and more birds arriving at the zoo in the afternoon increasing the chances of social interaction. Both flock and group size numbers throughout the day were likely driven by the availability of food in the study area.

Thirdly, the weather also influenced the flock size and the group size in a comparable manner. Both cloudy and sunny weather lead to an increase in flock size and group size. Looking at the data in more detail, however, showed a difference between the flock size and the group size. While there was some difference between the group size between cloudy and sunny weather, the increase in flock size remained largely the same when compared to rainy/snowy weather. This could be because less birds frequented the zoo during rainy weather than during other conditions. It is possible, though, that our results were confounded by our impaired vision by rain or snow. During cloudy periods the crows could rely more on the anti-predator protection of a group, as the likelihood to spot an airborne predator increases in larger groups and clouds could present difficult conditions to spot such an attack. The strongest effect on both the flock size and group size was found during periods of precipitation.

Fourthly the effects of the temperature differed between the flock size and the group size While warm temperatures had a strong negative effect on the overall flock size, group sizes were higher during periods with warmer temperatures than in cold temperatures. The hot temperatures had a negative effect on the flock size when compared to cold temperatures, group size on the other hand showed no difference between hot and cold weather. The time of the year could play an important role for flock size, as cold temperatures were only found during winter when the number of crows was generally higher in the zoo. Food availability is lower during colder periods outside the zoo, i.e. food abundance is higher outside the zoo if the temperatures are warmer. The food fed to the zoo animals could attract more crows during colder temperatures. The increase in group size during warm periods could be accounted for by higher sociality in periods were food is easy to gain access to. Overall the differing effects of temperature on the flock and group size were likely linked to the season and the overall food abundance.

While there are the similarities between the factors influencing both the group size and the flock size, the factors influencing flock size are mainly the ones already discussed with only small effect sizes for the rest of the factors in the analysis. For group size, however, a larger number of factors had strong effects.

Factors influencing Group Size

The biggest effect on group size was whether the birds were in the forested area of the zoo or in the more open and structured part of the zoo. Bigger groups were more likely to form in the more open, non-forested part of the zoo, which could on the one hand be explained by protection from predation that comes with forming larger groups in more open areas (Jarman, 1974). On the other hand the availability and distribution of food could be of importance. The biggest recorded group, for

example, was found in an enclosure with widely scattered food. This distribution of food allowed for a large group of birds to forage and feed at the same time, while lowering the chances of conflicts, similar to findings in spider monkeys (Asensio, Korstjens, & Aureli, 2009; Asensio, Korstjens, Schaffner, & Aureli, 2008). This is supported by the fact that the group-size tended to be larger in the mainly vegetarian enclosures of the zoo, where food was often distributed over larger areas. In contrast we also observed a slightly higher likelihood of group formation in enclosures of large predators that mainly got fed with meat (e.g. polar bears). This was most likely due to the quality of the food available in such enclosures, as meat fed to predators is attracting larger numbers of crows, in addition to larger groups providing more protection from such predators. This is similar to the results found in lions where higher food quality allows for bigger foraging parties (Caraco & Wolf, 1975). The results found in white throated magpie jays are also similar with larger groups found in areas with higher food availability (Langen & Vehrencamp, 1998). The group sizes also were more likely to be smaller on buildings. This is likely accounted for by the scarcity of food on buildings lowering the chance of crows to aggregate on buildings in general. Also the propensity of finding groups of crows in enclosures was higher than in other areas of the zoo accessible to visitors. In the parts of the zoo and its surroundings accessible to visitors we categorised two different types of areas: gastronomical areas and normal visitor areas. The effect on group size is negative in gastronomical areas compared to the normal visitor area. Therefore the group sizes in gastronomical areas are smaller than in the rest of the area open to visitors. This could be explained by the fact that visitor densities in such gastronomical are higher making bigger groups of crows less likely to occur as the crows often got shooed by the visitors. Also groups in such areas could not be entered as a group as the individuals could be forced to split farther apart in order to avoid the visitors. Overall the surroundings played an important role in the formation and size of groups in crows in our study by determining the abundance and availability of food.

The second most influential factor for group size was the age-class of the birds. In the field it was only possible to separate age into juvenile and non-juvenile, as adult and sub-adult birds were hard to distinguish in our observation protocol. The lower likelihood found for non-juvenile birds to form groups was explicable via the birds' ecology in that crows form bonds with other individuals and become territorial (Goodwin, 1976). Therefore they are often found alone or with their partner. This was supported by the fact that marked crows are less likely found in bigger groups. Sightings of marked birds in our sample were largely non-juvenile birds (ca. 80%). Therefore we assume that most of the sightings of marked birds represent older individuals; these birds were less likely to spend time in big juvenile flocks and more likely to try establishing territories. These results suggest that older individuals are less likely to be found in groups.

Territoriality seemed to be of different importance throughout the year as could be seen in our analysis of both the impact of season as well as the interaction term of season and marking. A general effect of seasons on the group formation could be found. There was a similar negative effect of breeding season on group size as on flock size and could be explained in the same manner. The territoriality of the breeding pairs at the zoo prevented non-breeders from forming larger aggregations in the zoo and the birds present at the zoo were local breeding pairs, which were then often sighted foraging on their own. In addition, groups of unmarked crows at the zoo tended to be smaller in the breeding season than during the rest of the year. During paternal care season, however, marked birds showed a higher likelihood of forming groups which could be explained by the fact that they were then often found with their offspring. In contrast unmarked birds showed a lowering effect on group-size in the paternal care season. The results show an impact of the seasonal effects and an impact of territoriality that changes throughout the year.

The number of visitors present also had an effect on group size. A slight decrease in group size was recorded in cases where the number of visitors was average, and a slight increase in group size was observed when many visitors were around. The crows potentially used more of the zoo area when there were fewer visitors around to disturb them, causing them to be farther apart leading to lower group sizes. More visitors on the other hand can lead to more concentration of the crows inside enclosures, therefore a higher potential for group formation. Hence, the number of crows present at the zoo was influenced by the number of visitors, with the crows tending to form larger groups when confronted with large numbers of visitors.

Conclusion

Overall the findings of our study suggest that crows in our study area form a flock with high fission-fusion dynamics. The local flock and its dynamics are influenced by environmental factors, like weather and time of day influencing the flock and group size in the same manner, or the temperature with different effects on flock or group-size. The implications of these findings can be very useful in planning and setting up studies on crows and other corvid species with a similar social structure that live in close proximity of humans. Our knowledge of the relative importance of basic environmental factors can be used to control for these effects in follow-up studies.

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Appendix

Zusammenfassung

Tierarten die in dynamischen sozialen Gruppen leben begegnen verschiedenen kognitiven Herausforderungen, wie etwa sich die anderen Mitglieder der Gruppe und deren sozialen Beziehungen einzuprägen. Fission-Fusion Dynamiken, ergo die Veränderungen von Gruppengröße und Gruppenzusammensetzung, haben Effekte auf die sozio-kognitiven Fähigkeiten von Säugetieren mit großen Gehirnen, die bereits das Thema verschiedener Studien waren. Im Vergleich dazu ist in Vögeln wenig über diese Dynamiken und deren Effekte bekannt. Diese Studie untersucht die Fission-Fusion Dynamiken einer Schar von Krähen (*Corvus corone ssp.*) in einem urbanen Habitat. Frei lebende Krähen formen oftmals scheinbar anonyme Scharen, jedoch deuten neue Studien aus der Gefangenschaft darauf hin, dass diese Gruppen soziale Strukturen haben könnten. Ich habe frei lebende Krähen in und um den Wiener Zoo, Tiergarten Schönbrunn, Österreich, über ein Jahr hinweg beobachtet. Information zu über 300 Krähen war vorhanden, da diese Vögel zuvor gefangen, vermessen und markiert worden waren. Meine Untersuchungen sollten zeigen (i) welche Individuen wann und wo im Zoo waren, (ii) ob die Krähen in Gruppen anzutreffen waren (ergo innerhalb von fünf Metern zu einer anderen Krähe) und (iii) welche Umweltfaktoren (zum Beispiel Wetter, Temperatur, Tageszeit, Saison und Zahl der Besucher) die Struktur der lokalen Krähenschar und Gruppenformation in eben dieser beeinflussen. Wie zu erwarten schwankte die Größe der lokal anzutreffenden Krähenschar über das Jahr hinweg stark, wobei während der Brutsaison besonders wenige Krähen im Untersuchungsgebiet anzutreffen waren. Auch die Zusammensetzung der Krähen-Schar änderte sich mit verlauf der Zeit. Ich konnte zudem die Krähen entsprechend ihrer Anwesenheit im Zoo entweder als „Locals“, oder als verschiedene Kategorien von „Visitors“ einordnen. Die Tageszeit, Saison, Temperatur und das Wetter hatten einen starken Einfluss auf die Größe der im Untersuchungsgebiet anzutreffenden Krähenschar. Demgegenüber war die Formation von Gruppen in dieser Schar den Effekten der Umgebung, der Altersklasse der Krähen, der Saison und der Tageszeit unterworfen. Diese Ergebnisse deuten darauf hin, dass Umweltfaktoren einen signifikanten Einfluss auf die Gruppenbildung und auch auf die Gruppenstruktur haben können, da sie die Chancen von verschiedenen Individuen zu interagieren beeinflussen.

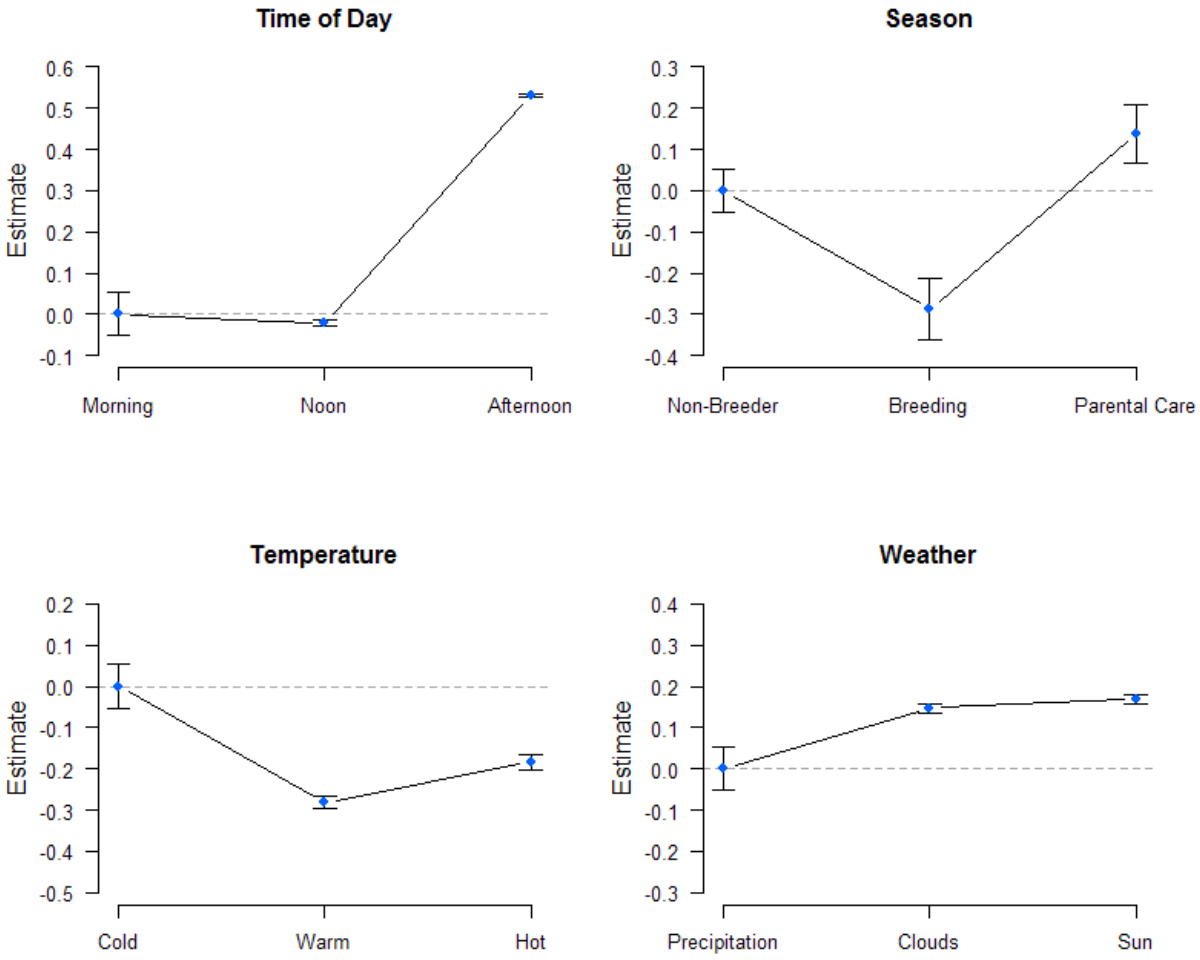

Figure A.: Flock Size influencing factors. The factor expressed in the intercept (actual value: 4.005) is expressed as 0. The error-bars describe the standard error.

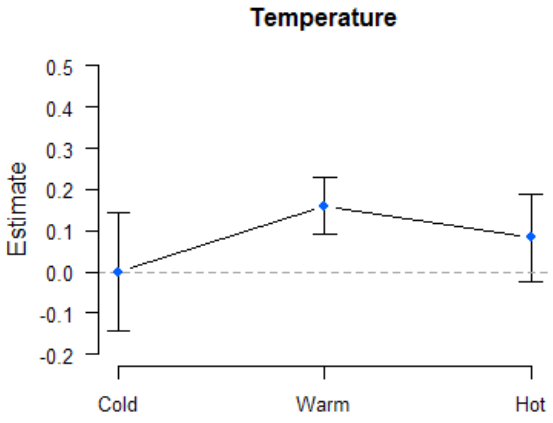

Figure B.: The effects of temperature on group-size. The factor expressed in the intercept (actual value: -0.333) is expressed as 0. The error-bars describe the standard error.

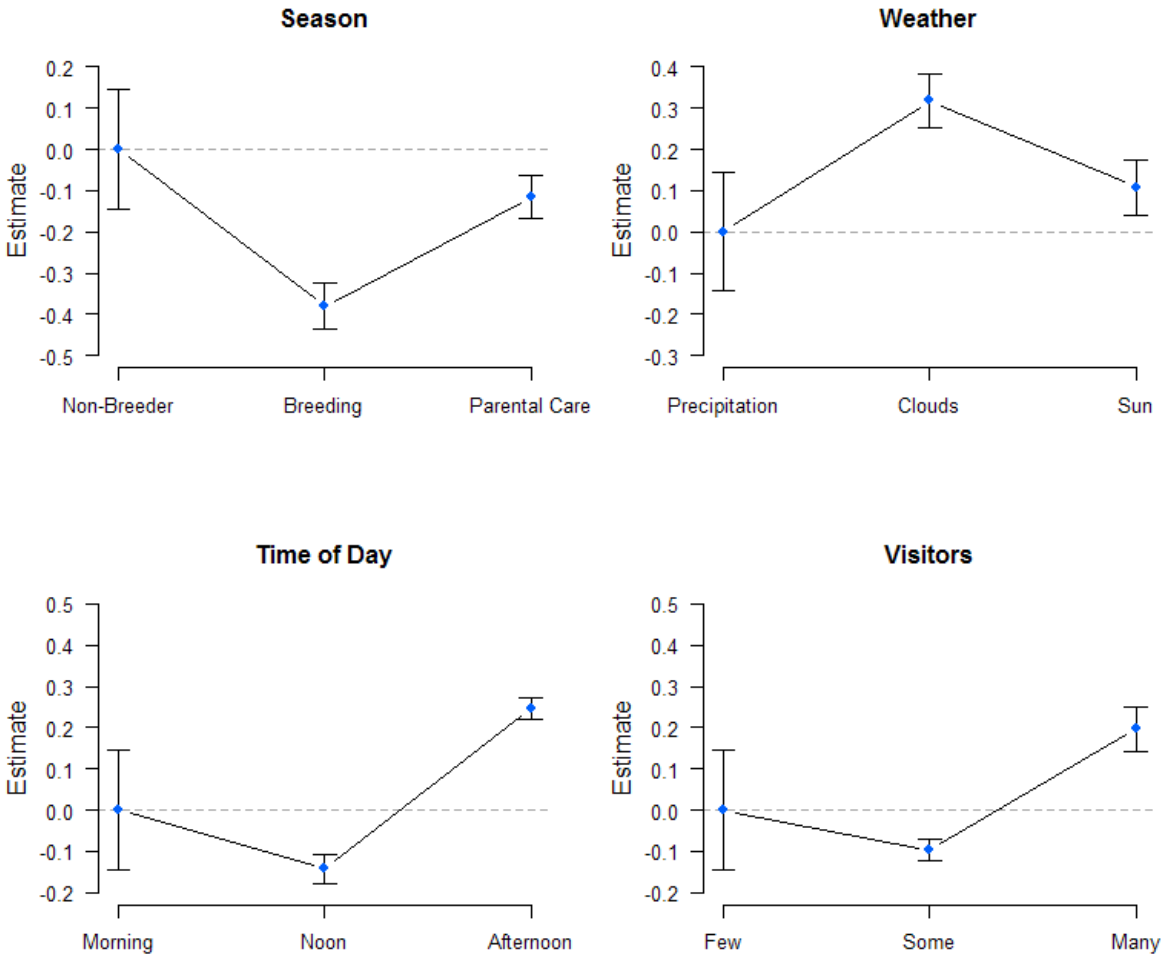

Figure C.: Group-size influencing environmental factors. The factor expressed in the intercept (actual value: -0.333) is expressed as 0. The error-bars describe the standard error.

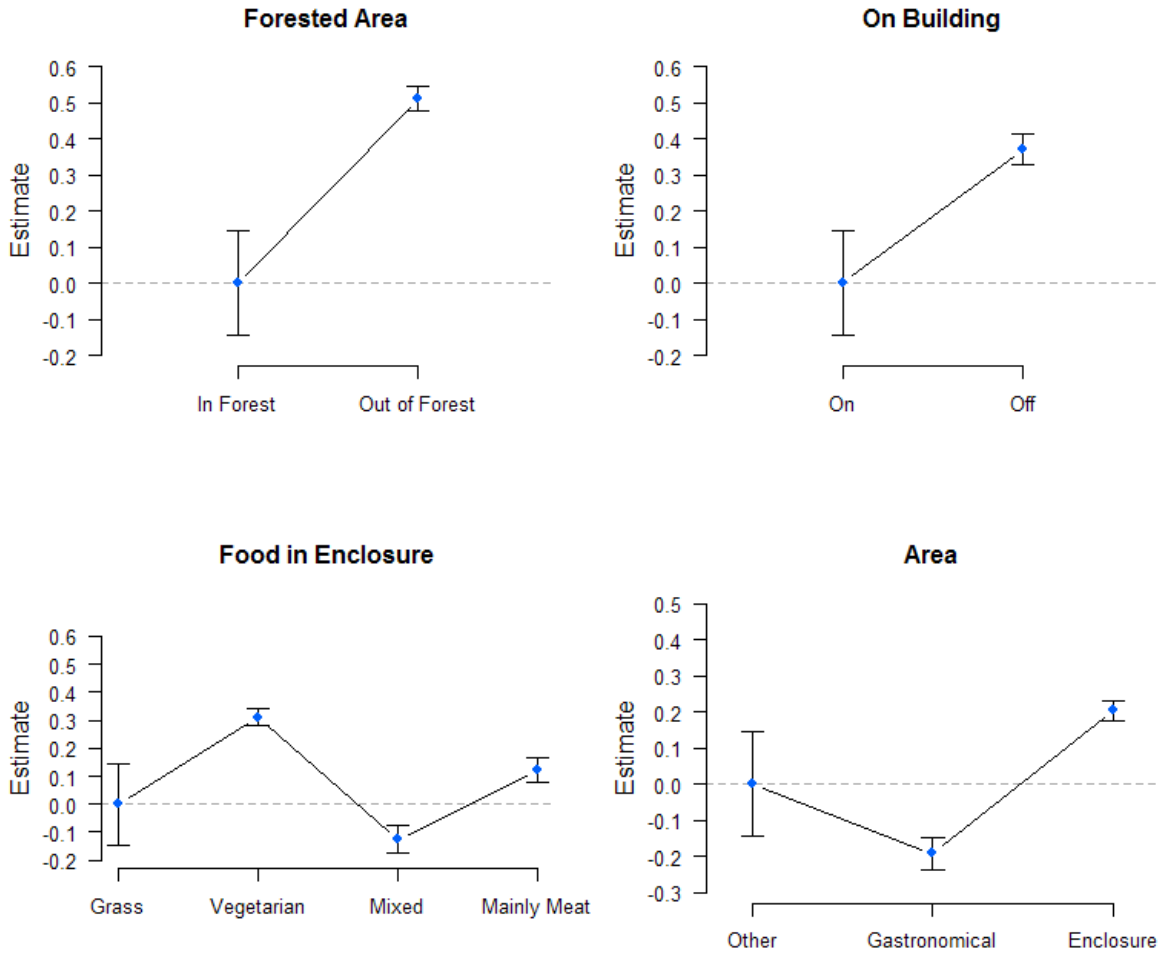

Figure D.: Group-size influencing factors of the locality. The factor expressed in the intercept (actual value: -0.333) is expressed as 0. The error-bars describe the standard error.

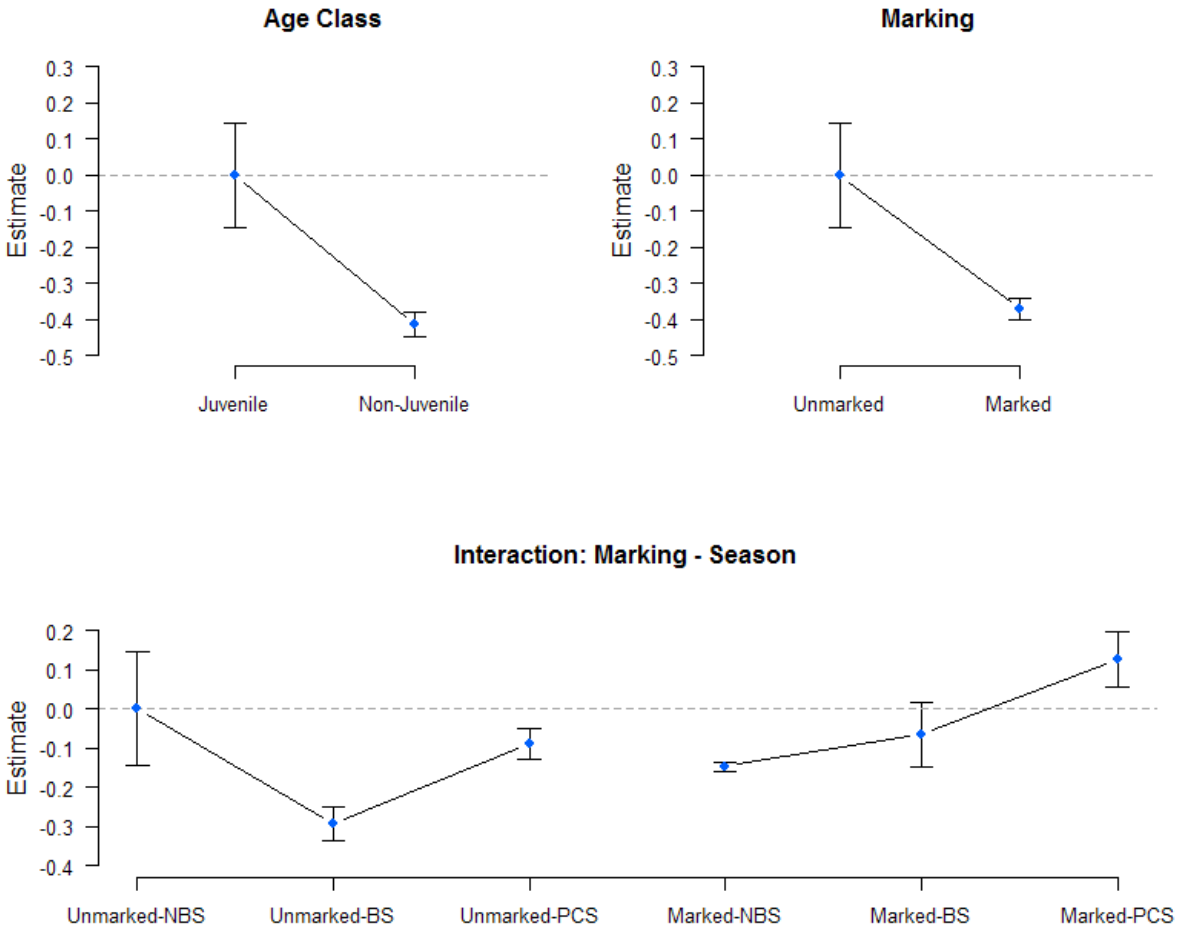

Figure E.: Group-size influencing individual factors. The factor expressed in the intercept (actual value: -0.333) is expressed as 0. The error-bars describe the standard error.