MASTERARBEIT

Titel der Masterarbeit

Individuality and Foraging Strategies in free ranging crows (*Corvus corone corone; C.c. cornix*)

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Contents

Abstract

As feeding generalists, both subspecies of carrion crows (*Corvus corone corone, C. c. cornix*) are common in the area of Vienna Zoo. Anecdotal reports suggest that foraging crows frequently interact with both the visitors and the Zoo animals. The aim of this study was to investigate the foraging strategies of crows, focusing on individual preferences for given feeding techniques and specific sites within the Zoo. Crows were captured with drop-in traps, measured, sexed and individually marked with leg bands. In addition, each bird was subjected to a tonic immobility test, measuring its propensity for actively dealing with an unpleasant situation and allowing us to characterize whether individuals are fast or slow at coping with an experimental challenging situation. Tagged birds were observed on a daily basis for five months using a combination of focal, scan and ad-lib sampling. Results show that crows have individual preferences for using particular areas of the Zoo and, within these areas, for using specific enclosures. Interestingly, these preferences are dependent on the birds' social class (breeder/ non-breeder) and copying style. These findings suggest that the crows prefer certain locations.

1. Introduction

1.1. Urban environment and personality

During the last few decades, the number of species living in urban habitats has increased. Many of these species are nowadays referred to as “undesirable species” as they can cause problems, such as damage to buildings/ crops, when they occur in large numbers. In the UK, the damage caused by badgers is a huge source of human–wildlife conflict when the badgers excavate burrows close to man-made structures (e.g. houses, roads) or on agricultural land (e.g. crops, forestry) (Davison et al., 2011; Delahay et al., 2009). In urban areas, toxic faecal droppings and excessive noise from roosting birds can be a significant issue (Raatikainen et al., 1989). In big cities the aggressive nest/ fledging defence behaviour of hooded crows (*Corvus corone cornix*) is considered frightening by local people and can even lead to physical injury (Vuorisalo et al., 1997, 2003). A study on the American crow (*Corvus brachyrhynchos*) conducted by Knight et al. (1987) shows that rural crows tend to behave less aggressively in nest-defence than urban crows. In former times, the American crow has been persecuted as a pest and hunted for sport. In recent decades, American crows, which in the past were typically rural birds, have begun nesting in cities where ordinances prohibit the discharge of firearms. As a result of this colonization of urban areas, two adjacent crow populations exist in many regions, a persecuted rural one and a protected urban one. Similar patterns seem to occur in different parts of the (western) world.

Animals in urban habitats seem to be more often bold in the presence of humans than animals in rural areas (Metcalf et al., 2002). Such boldness may arise due to a variety of reasons. One may be that urban animals learn, through repeated exposure, that passing humans do not represent a threat (Evans et al. 2010). Different means of learning like habituation (Hinde, 1970), associative learning (e.g. classical conditioning) (Pavlov, 1903, 1927) and/ or social learning (Fritz & Kotrschal, 1999) may play a role. Several experiments have demonstrated that corvids are able learners. For instance, captive ravens (*Corvus corax*) quickly solve feature and position discriminations (Range et al., 2008).

Another mutually, though not exclusive, explanation for the increasing boldness of urban living animals is a genetic predisposition, where the genes can influence either the species or an individual. A study about zebra fish (*Danio rerio*) was one of the first to show the influence of genes on social interactions and vice versa. It assessed the global gene expression in relation to the complicated behaviours involved in the establishment and maintenance of dominance hierarchies within groups of individuals. Gene expression profiles may be to some extent controlled by the social relationships within a group thus providing some evidence that predicts that an individual’s genotype is also influenced by its interactions with conspecifics (Sneddon et al., 2011). The genetic influence could also be on an individual level and therefore be described as the individuality or personality

(Pervin & John, 1999) of an animal. The existence of consistent individual differences in behaviour, often referred to as differences in temperament, coping style or behavioural syndroms (Sih et al., 2004), seem to appear in a wide range of animal species. A basic definition of personality is that it represents suites of correlated behaviours that are expressed across different situations (Carere & Eens, 2005). There is also clear evidence that the personality of an animal influences their behaviour (Dingemanse et al., 2003, 2005; Minderman et al., 2009; Hollander et al., 2007). Rooks (*Corvus frugilegus*) were tested individually to measure a number of behavioural parameters related to boldness, which correlateed well with corticosterone levels under stress (Scheid & Noë, 2010). In a study on barnacle geese (*Branta leucopis*), leadership is closely related to some aspects of personality. The movement patterns of individuals living in groups are also affected by the personality traits of other group members. This finding suggests that the movement patterns of a group, may be shaped by the mix of personality types present in the group (Kurvers et al., 2009).

The bold-shy continuum is a fundamental axis of behavioural variation in humans and some other species. The study of shyness and boldness adds an interesting new dimension to behavioural ecology by focusing on the nature of continuous behavioural variation that exists within the familiar categories of age, sex and size. These categories may differ in their average degree of shyness and boldness. The tonic immobility test is a measurement of the animals' propensity of actively dealing with an unpleasant situation, and can be used to categorize animals along a bold-shy continuum (Wilson et al., 1994). The tonic immobility is an unlearned response characterized by a catatonic-like state of reduced responsiveness to external stimulation. It is elicited by a relatively brief period of physical restraint (Jones, R.B., 1986). Some studies indicate that, in other species, individual differences in tonic immobility predict behaviour. For instance, in a study with domestic pigs, individuals who did not become immobile during the tonic immobility and struggled immediately when turned on their backs, moved faster in the raceway than pigs that stayed immobile in the tonic immobility test. This variation in test findings may reflect differences in behavioural strategies rather than in responsiveness. In this respect, the authors concluded that tonic immobility test is one possible way of assessing whether individual piglets are more likely to adopt a more active or passive behavioural strategy in a challenging situation (Erhard et al., 1999).

Complex cognition or intelligence in animals is usually defined by exclusion, rather than by some positive assessment of the mechanisms underpinning it. Identifying intelligence in animals in practice typically amounts to observing the presence of sophisticated behaviours in the species' natural environment, and looking for evidence of behavioural flexibility or the appearance of novel solutions that are not part of the animals' repertoire (Roth & Dicke 2005). In the last decade, the main focus in cognitive research has been on captive birds like parrots (e.g. Pepperberg 2006), great tits (e.g. Dingemanse et al., 2002, 2004) and several corvids such as nutcrackers (*Nucifraga coumbina*) (e.g. Jones et al., 2002), jackdaws (*Corvus monedula*) (e.g. Schwab et al., 2008b) and ravens (*Corvus corax*) (e.g. Heinrich & Bugnyar, 2005; Bugnyar et al., 2002; Range et al., 2008; Schwab et al., 2008a). The main focus in corvid research has been on the physical and social effects of cognition (e.g. causation and social learning). For instance, a string pulling study with captive ravens suggests that success in a string-pulling task may not only be due to learning (e.g. sorting out options for how to get the reward, improvement of motor skills such as placement of feet in holding string etc.). Instead, it may also involve some kind of understanding of means–end relationships, i.e. an apprehension of a cause–effect relation between string, food and certain body parts (Heinrich & Bugnyar, 2005). A study by Schwab et al. (2008a) indicates the importance of social dynamics for social learning in common ravens (*Corvus corax*). The results support the hypothesis that affiliate relations between individuals affect the transmission of information and may lead to directed social learning, even when experimentally controlling for spatial proximity (Schwab et al., 2008a).

1.2. Corvids

The increase in the size of corvid populations/ number of corvids throughout the world is inextricably linked to the activities of humans. Most Corvidae are "human commensals" and thrive in highly disturbed habitats including agricultural, suburban and urban areas (Marzluff et al. 1994). This may be due to two reasons. Firstly, most of the corvid species are feeding generalists. In addition to this, as these birds are highly flexible in their behaviour, they are able to easily colonize new habitats. Previous studies have also indicated that these species are cognitively smart and suggest that cognitive skills in corvids are even comparable to those of primates (e.g. Marzluff et al. 1994 and Emery & Clayton, 2004).

Little is known about the cognitive skills of birds in the wild. Marzluff et al. (2010) experimental work with wild American crows (*Corvus brachyrhynchos*) has shown that conditioned and observational learning of a specific threat (e.g. wearing a dangerous mask during banding) allows local birds to develop aversions towards individual people. Other significant studies on free ranging crows have focussed on their ecology and, in particular, cooperative breeding (Baglione et al., 2002). It was shown that non-cooperative carrion crows of Swiss ancestry could express delayed natal dispersal and helping behaviour when reared in a cooperatively breeding population of the same species in Spain. The study was based on the transfer of carrion crow eggs from a Swiss non-cooperative population to the Spanish cooperative one, in order to rear Swiss chicks in Spanish foster nests (Baglione et al., 2002). Some research has also concentrated on the influence of hybridization on egg size, chick growth and the survival of the population across a hybrid zone (Saino & Villa, 1992a/ b).

As Austria is directly on the hybridization belt between carrion and hooded crows (*Corvus corone corone and C. c. cornix*), studies about the hybridization grade with these species' exist (Saino &

Villa, 1992b), but behavioural studies on wild crows are still missing. However, there does appear to be good opportunities for behavioural research. In urban areas in particular, the presence of easy to access food sources (e.g. human rubbish) encourages the gathering of large number of crows within close viewing distance of researchers. For instance, in Vienna, with the high grade of hybridization between carrion and hooded crows, big flocks of both subspecies can be found in parks like Augarten, Donauinsel and in the area of the Palace of Schönbrunn, including Vienna Zoo (Sachslehner, 2006). The present study was therefore conducted within Vienna Zoo focusing on carrion crows and their hybrids. Anecdotal reports suggest that there is a lot of interaction between the crows and the zoo animals, as well as the crows and the visitors – which are always strongly food related (Zoo staff, personal comment). Hence, Vienna Zoo is a perfect location to observe crows at a close distance, as they are used to being around humans. Within the Zoo area are both breeding and non-breeding crows. If a crow becomes part of a breeding pair, it then starts defending a territory against other crows; in contrast the non-breeding crows form big flocks and share foraging areas (Bossema & Benus, 1985).

1.3. Aim and hypothesis

The aim of this study was to investigate the foraging strategies of carrion crows in Vienna Zoo with a focus on individual preferences for specific techniques and sites. Based on the reported anecdotes, it was hypothesized that the population of crows strongly depends on food provided for the zoo animals and by visitors. These anecdotes are supported by individual observations of crows, which seem to feed mostly on human-related food sources. It was also expected that particular crows might specialize at specific sites, as it had been reported that some crows might follow specific hunting strategies to catch offspring of zoo animals. This specialisation could be due to social and/ or individual learning and could also being linked to the birds' personality. One hypothesis is that bolder birds may forage in areas with higher risk. There, they will probably receive high-energy food like meat and fish, as animals that are more dangerous (e.g. cheetah, polar bear, marabou) are typically predators. It was also expected that the way of dealing with challenging situations could be influenced by social class (breeders/ non-breeders). As breeders were expected to stay around their nesting areas and defend these areas, the expectation was that breeders and non-breeders would be found in different areas. Therefore bold and shy birds would be found either at entirely different sites, or the shy birds would primarily be found more in high crow density areas, whilst bold birds would also use areas with few crows around. In addition, an experiment was conducted to test for social/ individual influences when a bird approached a novel object that included a food reward. It was expected that territorial breeding crows would approach novel objects first. The reason for this expectation could be that those individuals holding territories would also be more likely to take higher risks when approaching food, due to the demands of feeding their offspring. Another reason may be that territorial birds are more aggressive towards conspecifics, preventing the non-breeders from having access to novel food sources.

2. Material and Methods

2.1. Subjects

The subjects were free ranging carrion crows (*Corvus corone),* including the subspecies' *Corvus corone cornix* and *Corvus corone corone* and their hybrids. The main living habitat of the birds was the urban area of Vienna Zoo (Tiergarten Schoenbrunn/ Austria) and the surrounding parks. Over a period of three months, 115 crows were captured, individually marked and released immediately after the handling procedure.

Table 1: List of marked crows including individual information on species, social status and sex.

Subspecies	**n total**	**n social status**		**n sex**	
		breeder	non-breeder	male	female
Carrion crows	5	1	4	5	0
Hooded crows	42	4	38	28	14
Carrion/ Hooded hybrids	68	6	62	33	24
Total	115	11	104	66	38

2.2. Marking procedure

Crows were caught with a 3x2 m² drop-in "Reusen" trap (see Figure 1) for individual marking. The mean marking rate per month was 38.3 birds. For individual recognition in the field, leg bands were used – between two and three for each bird (one EAZA band from the Zoo, one or two small metal bands with different colours plus the official band of the Austrian ornithological station Radolfzell). For kinship analyses, 1µl blood was taken from the elbow vein by using a 1µl capillary. For the conservation of the blood, 95% ethanol was used. To sex the crows, 2 feathers were taken and analyses were done by IMDB (Institut fuer Molekulare Diagnostik Bielefeld).

Figure 1: Crow trap in the kangaroo enclosure with one hooded crow sitting in front and one inside the trap (Picture © Martina Schiestl)**.**

During the handling procedure the crows were weighed and the wing, tarsus and bill were measured with a digital calliper (Fixpoint, RS232S-Serialoutput, accuracy as per DIN 862, 0 – 150 mm measuring range) (Heinrich, 1994a, b). The age of the bird was estimated by looking at the inner colour of the bill. This age discrimination was based on Bugnyar & Kotrschal (2002): juveniles (birds in their first summer, with blue eyes and a pink oral cavity), sub adults (birds in their second or third summer, changing in colour to adults but still retaining parts of their juvenile features) and adults (birds older than three summers, with brown eyes and a dark oral cavity). The procedure took between five and ten minutes for each bird.

2.2.1. Ethical statement

It is obligatory to have an animal experiment permission for the handling and the blood taking of wild birds. This permission was received prior to the start of catching in April 2010 (License number: BMWF-66.006/0005-II/10b/2010). In addition, permission for catching and ringing activity was received from MA22. Care was taken to ensure the well being of the birds during the whole handling procedure, as well as in the ongoing studies. To the best of our knowledge, this research has not had any damaging effects on the crows.

2.3. Duration and time schedule

All observations and experiments took part from April until November 2010 in the area of Vienna Zoo, which was entered by visitors on a daily basis from 0900 hours to 1830 hours. The traps were placed inside the zoo in March. To ensure a habituation time of at least one month, the catching period ran from April until July 2010. The scan observations were collected from April to August 2010, and the focal observations started after the first marking procedures and ended in September 2010. The experimental phase started in July and was conducted until November 2010.

2.4. Observation procedure

All observational data were collected with binoculars and a Dictaphone/ tape recorder and took place in the area of Vienna Zoo (Coordinates: 48° 10′ 56″ N, 16° 18′ 9″ E). The Zoo was divided into eight scan sampling areas, which were named after the biggest enclosures within them: flamingo, cheetah, kangaroo, seriema, penguins, spectacled bear, polar bear and peccaries (see Figure 2).

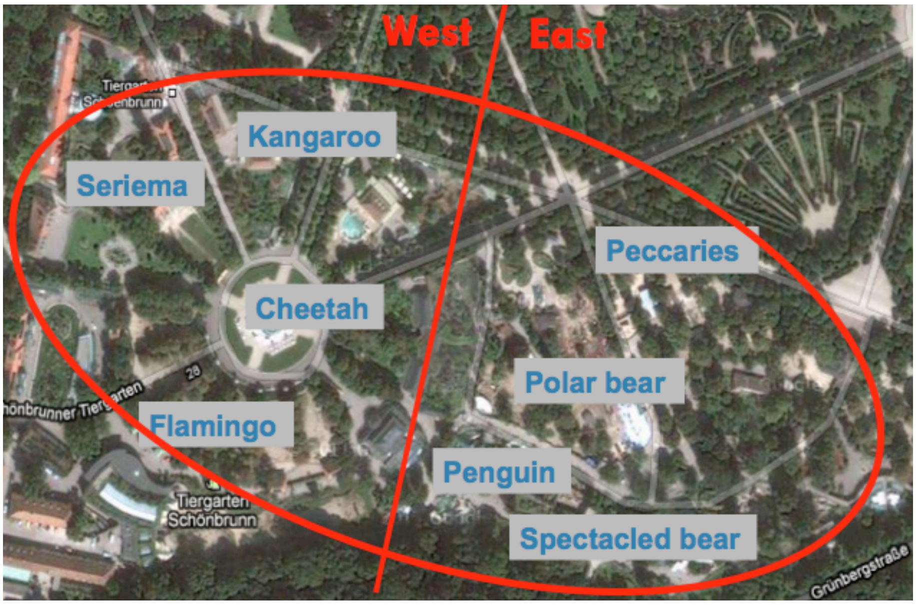

Figure 2: Scan sampling areas of Vienna Zoo[1]. The division of the Zoo in East and West was only done after the first results showed such an individual bisectional use of areas (see Figure 6).

2.4.1. Scan sampling

Scan protocols were conducted to examine the location and behaviour of the crows at certain times to observe where the crows were and what they were doing at certain times. Protocols were taken in eight different observation areas at a maximum of three different times a day between five to seven days a week: morning round (0900 hours - 1100 hours), lunch round (1300 hours - 1500 hours) and evening round (1800 hours - 2000 hours). Every round consisted of three scans in each area with five-minute break between the scans. During the scans, data about the current situation such as the number of crows per subspecies, foraging behaviour and other specific behaviours were recorded (see Appendix 1).

2.4.2. Focal sampling

One-minute focal sampling protocols on each marked crow were done during the five-minute break between the scans, as well as on any other occasion and in any place a marked individual was spotted. Behaviours are defined and listed in the table below (see Table 2).

Throughout the observations, a classification of the social class of the birds (breeder/ non-breeder) was done. Breeders were defined as individuals that were observed more than once in a breeding or breeding related context (e.g. nest building, feeding offspring, close distance to other adult crow during such processes etc.). Accordingly, non-breeding crows were defined as crows that did not show any breeding or breeding related behaviour during all observations.

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[1] Original Map Source: http://maps.google.at/maps?q=Sch%C3%B6nbrunn&oe=utf-8&rls=org.mozilla:en-US:official&client=firefox-a&um=1&ie=UTF-8&sa=N&hl=de&tab=wl

Table 2: List of behaviours used for focal observations.

Behaviour category	**Behaviour**	**Description**
Individual/ Movement	Mobile	Moving from one location to another, no other behaviour visible
Individual/ Movement	Stationary	Remaining stationary, either on or off ground, alert (feathers upright) or passive (feathers smooth, relaxed posture), may be looking around the surrounding area, not directly food related
Individual/ General	Object manipulation	Touching/ pulling/ carrying a non- food object
Individual/ General	Nest build	Removing twig/branch from ground or off ground (i.e. tree) and carrying in bill for over 30 seconds
Individual/ General	Drink	Taking water up in the bill
Individual/ Foraging	Feed	Consuming food item, food disappears into bill, includes food storing in throat pouch
Individual/ Foraging	Search	Digging in/on substrate/ moving around on the ground, head generally directed towards ground
Individual/ Foraging	Watch	Observing others searching or others with food, “others” includes conspecifics, other species as well as humans, on or off ground
Individual/ Foraging	Carry	Holding food item visibly in bill and moving from one location to another, on or off ground
Individual/ Foraging	Cache	Hiding single or small amounts of food or other items in different areas, on/in substrate
Individual/ Foraging	Cache retrieval	Recovering a food or other item from a cache, this may then be re- cached (cached again in a different location) or consumed
Social/ Agonistic	Cache raid	Recovering a food or other item from the cache of another bird, which may then be re-cached or consumed
Social/ Agonistic	Displace	Crow A- crow B (food), crow A approaches crow B, crow A obtains food, crow <u>B</u> leaves (without food). Crow A is alert (feathers upright), may involve harsh vocals and physical contact from Crow A to B. Must

		include transfer of food. Crow B may be substituted for another species including human.
Social/ Agonistic	Steal	Crow A- crow B (food), crow A approaches crow B, crow A obtains food, crow A leaves (with food). Crow A is alert (feathers upright), may involve harsh vocals and physical contact from Crow A to B. Must include the transfer of food. Crow B may be substituted for another species including human.
Social/ Affiliative	Co- feed	Feeding on same spot as another individual(s) within 0.5m2
Social/ Affiliative	Share	Feeding on same item within 0.5m2
Social/ Affiliative	Offer	Crow A- crow B (food), crow A approaches crow B, crow A obtains food, crow A or B may leave (with/ without food), crow B initiates, involves transfer of item between individuals, may result in success/ fail. Crow B may be substituted for another species including human.
Social/ Affiliative	Beg	Crow A- crow B (food), crow A approaches crow B, crow A obtains/ is given food, crow A or B may leave (with/ without food). Crow A initiates, involves transfer of item between individuals, may result in success/ fail. Crow B may be substituted for another species including human.
Social/ Affiliative	Bill feed	Crow B (adult) has transfers food directly from bill to bill to crow A (adult/ chick). May follow a beg.
Individual/ General	Defecate	Producing faeces
Individual/ Self directed	Bathe	Dipping body repeatedly under water
Individual/ Self directed	Auto-preen	Self- preening: the action of cleaning or smoothing the feathers using the bill/ feet, including scratching
Individual/ Self directed	Bill- wipe	Moving the bill in one or both directions

		against a substrate
Individual/ Self-directed	Tail fan	Briefly lifting the tail feathers so that they spread out, may occur repeatedly, on or off ground
Social/ Agonistic	Approach- retreat	Crow A approaches crow B and crow B immediately moves away (at least 1 step away) or leaves area, no contact occurs, takes place on or off ground (level 1). (No transfer of food)
Social/ Agonistic	Approach- forced retreat	Crow A approaches crow B and crow B moves away (at least 1 step) or leaves area, includes physical contact, may include harsh vocalisations, aggression displays (feathers upright), takes place on or off ground (level 2). (No transfer of food).
Social/ Agonistic	Approach- no retreat	Crow A approaches crow B and crow B does not leave (at least immediately), occurring on or off ground. May lead to fight or chase (level 3)
Social/ Agonistic	Fight	Crow A pecks, feather pulls or physically attacks crow B, either on or off ground (level 4)
Social/ Agonistic	Chase	Crow A follows crow B in flight, may follow or precede a fight
Social/ Affiliative	Touch	Contact with bill or body part, lasting less than 3 seconds
Social/ Affiliative	Allo-preen	One bird preening another with the bill, occurring simultaneously or one-way, bill to body contact lasting over 3 seconds
Social/ Affiliative	Contact sit	2 birds sitting together within distance of body length (approx 30cm)
Individual/ Vocal	Vocalisation	Vocalising individually
Social/ Vocal	Separate location vocalisation	Vocalising simultaneously with another bird at different locations (on perch or on ground)
Social/ Vocal	Same location vocalisation	Vocalising simultaneously with another bird whilst perched or standing together on ground

2.4.3. Ad-lib sampling

For rare events such as predation by crows on other animals, ad-lib observations were taken. The protocol was therefore used in the same way as it was during the scan and focal sampling procedures.

2.5. Tonic immobility test

The tonic immobility test, which measures the crows' propensity of actively dealing with an unpleasant situation, allows observers to characterize individual personality along the bold-shy continuum as cited in Wilson et al. (1994). The tonic immobility procedure was used to determine if a crow was a fast or a slow coper in an unpleasant situation. To do this, the crow was turned on its backside and pinned down on the ground for 2 seconds, after which the experimenter stepped back and recorded how long it took the crow to right itself and take off (see Appendix 2). After a maximum of 60 seconds, the experimenter turned the crow over and gently pushed it. The experimenter thus stayed in close proximity (+/- one metre) to the bird during the entire period of the test.

2.6. Novel object exploration experiment

The experiment was designed to test how crows explore and manipulate novel food related objects, taking into account their personality and the social context. The tasks in this experiment were of differing complexity, with each task presented in a known foraging area for the crows:

- A motor task: crows were required to use their bills or feet to open an opaque box. The box offered them two different access possibilities to the food source inside – one was a cover, which had to be pulled up, and the other was a drawer, which had to be pulled out.
- A motor coordination task: string pulling is a task often used to investigate the problem solving abilities of different avian species. The crows had to use their bill and legs in order to gain access to a reward at the end of a string (Heinrich & Bugnyar, 2005). In the set-up, the string was tied to a branch to which they had easy access.
- A discrimination task: the goal of this task was to find out how precisely crows learn to discriminate between objects with different features. Three cups of different colours (red, green and yellow) were used. In the testing phase, only the red cup contained a food reward, which was place underneath the upside down cup. The cups were placed directly on the ground.

2.6.1. Experimental set-up

Each object was placed at each of the three chosen locations for 20 minutes per test session, counterbalancing the order of the presentation of the tasks to ensure each object had an equal chance of being observed by the crows at each location. The exact locations were as follows:

- Location 1: Flamingo enclosure - inside the enclosure, which was usually used as common feeding site for the cranes and the crows as co-feeders, within the view of visitors.

- Location 2: Seriema - inside the enclosure, usually used as common feeding site for the cranes and the crows as co-feeders, half hidden and half within the view of visitors.
- Location 3: Pelican pond - outside the enclosure on a small oneway street, closed to visitors during the experiments, close to the area of the water birds feeding ground.

As all of the tasks included novel objects and Corvids are known to be neophobic (Heinrich et al., 1995b), the experiment started with a training phase to get them used to the objects, as well as the video camera. During the training phase, no food was involved in the presentation of the objects, but on the fourth day, a "food only" day was done, where high quality food was placed in exactly the same locations as where the objects were usually placed (see Appendix 4).

After a training phase of 20 days, the experiment started and the tasks were set up the same way as during the training phase, but this time including a food reward, which was visible for the crows and placed in, on or under the object. The only change was that there were no more "food only" days. For further analyses, the experiments were audio-visually recorded to ensure proper identification of the birds and that nothing important was missed. During the experiments, the area was observed with binoculars from a distance of 20 to 30 meters, so someone being around the food source would not distract the crows.

2.7. Data analysis

All GLMM analyses were conducted using R (R Development Core Team (2011) and other parts of the analyses were done with IBM SPSS Statistics 19.0.0. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.). A GLMM was done to test the predictions of whether sex (female/ male), age (sub adult/ adult), social status (breeder/ non-breeder), coping style (fast/ slow coper), diet (vegetarian/ meat or mixed) and risk of area (low/ medium/ high) influence the use of areas. A generalized linear mixed models (GLMMs) implemented in the GLMM ADMB module were used (H. Skaug, D. Fournier, A. Nielsen, A. Magnusson and B. Bolker, R package version 0.6.3.). Parameters were estimated by maximum likelihood using the Laplace approximation to evaluate the marginal likelihood (Skaug & Fournier, 2005). All tests were two-tailed and the alpha level was set at 0.05 (Fraiser & Bugnyar, 2011). As all of the collected data were count data of observations, the data were zero inflated. For all GLMMs, the individual crows were entered as random factors and zero-inflated GLMMs with binomial error structures and a logit-link functions were used. Akaike's information criteria (AIC) values were used to select the best (most parsimonious) model (Burnham & Anderson, 2004) and the model containing the smallest AIC value was therefore taken into account (i.e., the best compromise between accuracy and precision) (Vanpe et al., 2009).

3. Results

3.1. Observational studies

3.1.1. Sex ratio and age class of marked crows

A total of 115 crows were caught, marked and released during the project. From the 115 marked crows, 66 (63.5%) were males and 38 (36.5%) were females (see Figure 3a). The age class of the crows was estimated from the colour of the inside of the bill (see Marking procedure) resulting in 98 (85%) sub adults, 11 (9.5%) adults and 6 (5.5%) juveniles (see Figure 3b). 91 (79%) crows were seen at least one more time following marking and 35% were seen five or more times.

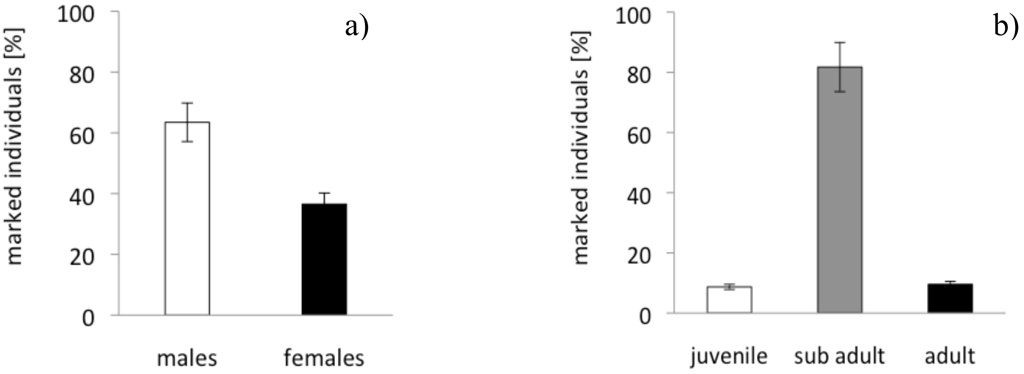


Figure 3: a) sex ratio and b) age class of marked crows (n=115).

3.1.2. Unmarked crows versus marked crows

Over 2222 scans, a total of 4858 crows were recorded, with a mean of 2.2 crows recorded per scan and 48.6 crows per observation round. 55% of unmarked crows could be observed in eastern and 44.5% in western part of the Zoo. Similarily, 57.1% and 42.9% of marked crows were observed in eastern and western part. No significant difference (Two sample Kolmogorow-Smirnow test, p=0.627) in use of areas between unmarked and marked crows was found (see Figure 4). Respectively marked crows are representative for the whole population of crows living within the area of Vienna Zoo and used for further analysis.

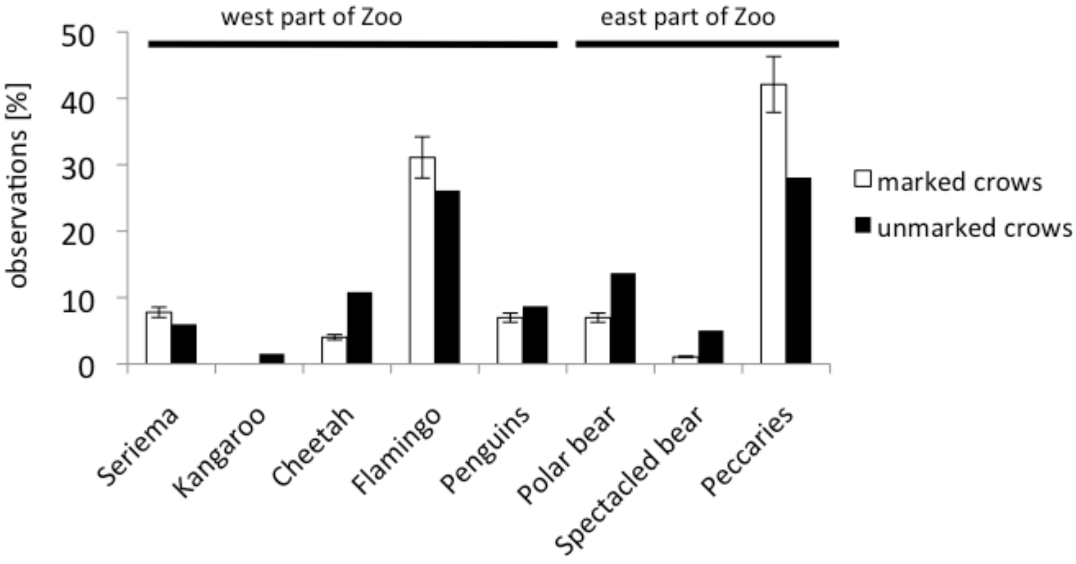


Figure 4: Use of areas by marked and unmarked crows.

3.1.3. The foraging behaviour of marked crows

Observed activities inside and outside the enclosure were foraging, carrying food, watching others and searching for food. The most frequently occurring behaviours during focal observations were searching (46.3%), feeding (27.7%) and watching others feed (15.2%). Food sources recorded were visitors leftovers, natural sources, zoo animal food: meat and zoo animal food: no meat. Zoo animal food: no meat was consumed more (45.7%) than zoo animal food: meat (21.6%) or visitors leftovers (23.7%) (see Figure 5b).

Juveniles spend more time (48.1%) searching for food then sub adults and adults (41.8%) (see Figure 5a). Sub adult crows (25.7%) ate visitors leftovers more frequently then adults (6%), but no significant influence of sex ratio and age class was found in foraging behaviours and diet of marked crows (R, zero-inflated GLMM, $p<0.05$, for details see Appendix 3).

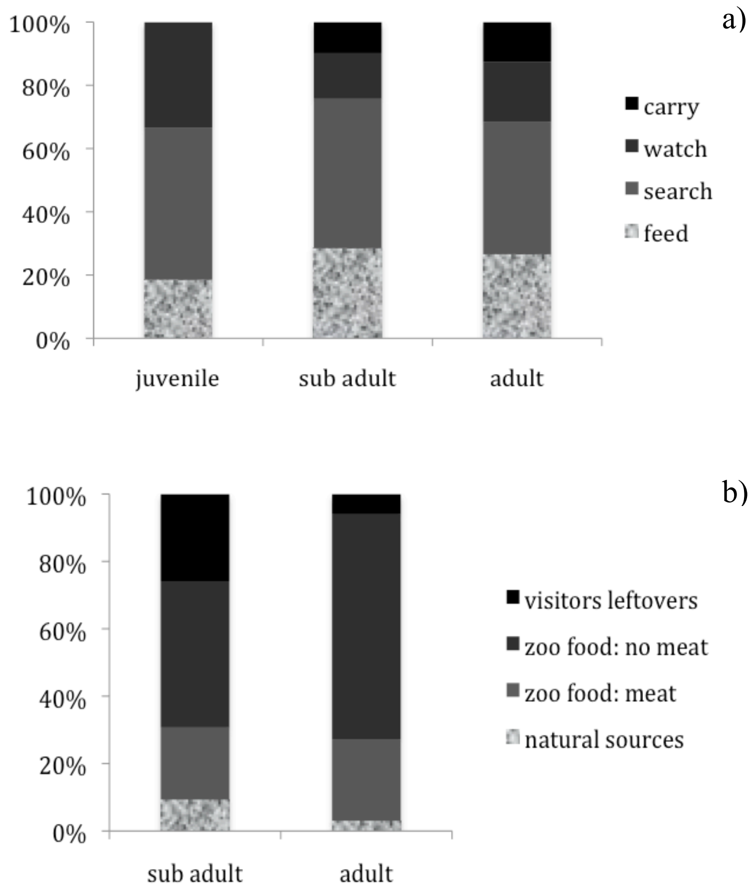


Figure 5: There was no significant influence of sex ratio and age class in a) the foraging behaviours and b) diet of marked crows.

3.1.4. The use of east and west parts by individual crows in Vienna Zoo

Figure 4 and 7 show preferences for certain areas of the Zoo by crows on a group level. On an individual level, the different use of parts of the Zoo becomes even more pronounced (see Figure 6). A total of 829 focal observations of 41 individuals shows that only a few individuals (2.5%) were using the eastern and western part at similar rates. The other individuals stayed either in the east (21.51%) or the west (18.44%) and thus appear to prefer one area over another. A significant difference in the use of eastern and western areas of the Zoo (R, zero-inflated GLMM, p=0.0116, for details see Appendix 3) was found. The results also show a significant intercation between social status (breeder/ non-breeder) and the use of eastern and western part of the Zoo (R, zero-inflated GLMM, p=0.00024, for details see Appendix 3).

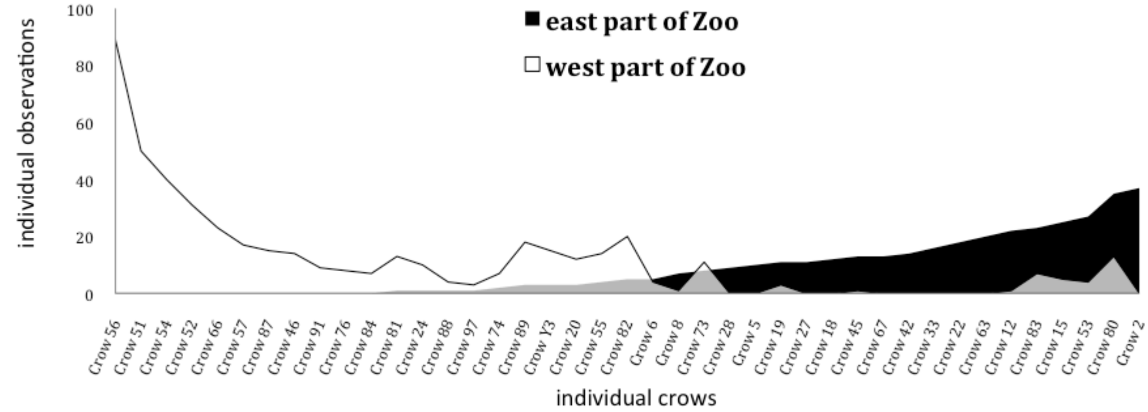


Figure 6: Use of east and western part of the Zoo and the individual allocations of single crows.

Figure 7 shows that breeders were found more often in the western part of the Zoo ($x^2_1=133$, $p \leq 0.0001$), whereas non-breeders used both areas. The area of the flamingos was used by breeders and non-breederes, whereas in the peccaries areas mostly non-breeders were found (R, zero-inflated GLMM, p≤0.0001, for details see Appendix 3) .

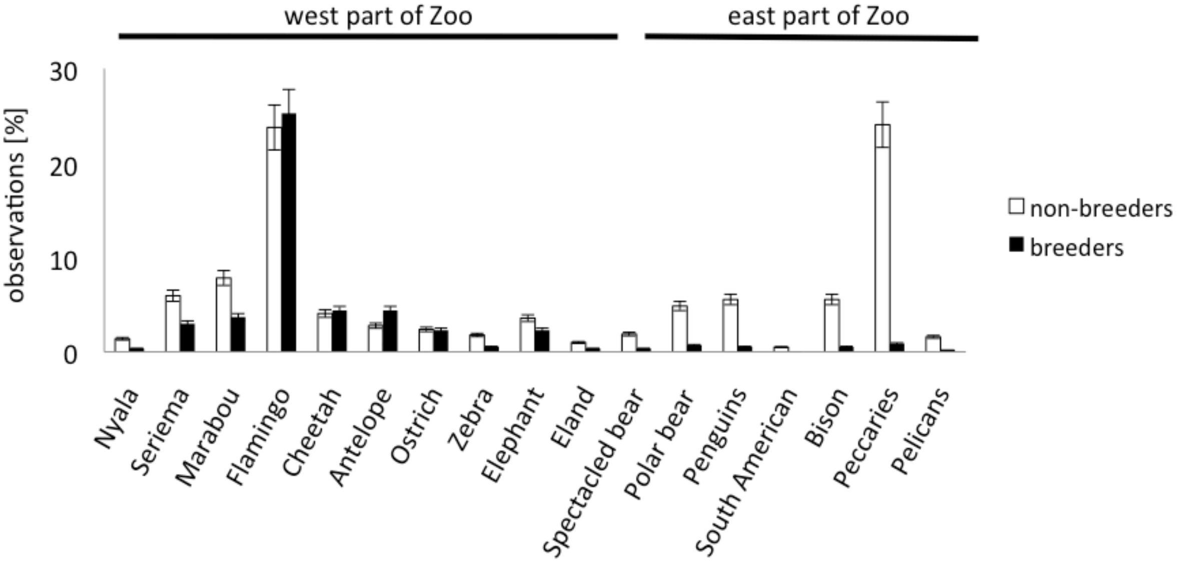


Figure 7: The use of areas is different, depending on social class (breeders/ non-breeders).

3.1.5. The use of areas by breeders

Six marked crows were identified as being paired breeders. Other breeding pairs were observed, but because only one partner was marked, they were not used for further analysis.

Breeding pair 56/ 51 had their nesting site in the flamingo location, where they successfully reared three chicks. Accordingly they were sighted in that area 85.4% (crow 56) and 90% (crow 51) of the time (see Figure 8a). Breeding pair 54/ 52 had their nest in the area of the nyala, where they successfully reared two chicks. Both spent most of their time within the area of their nesting site (crow

54 (52.5%) and crow 52 (58.1%)) (see Figure 8b). The partners in the breeding pair 32/ 81 had nested in an unknown location, but were defined as being a breeding pair (for criteria see 2.4.2 Focal sampling). Interestingly in this case, one crow spent most of its time in the area of the flamingos, whereas the other crow mainly used the polar bear area (see Figure 8c). Breeding pair 32/ 81 shows that breeding pairs do not have to have the same foraging areas. Two of the three breeding pairs used only the eastern part of the Zoo and one pair used both areas.

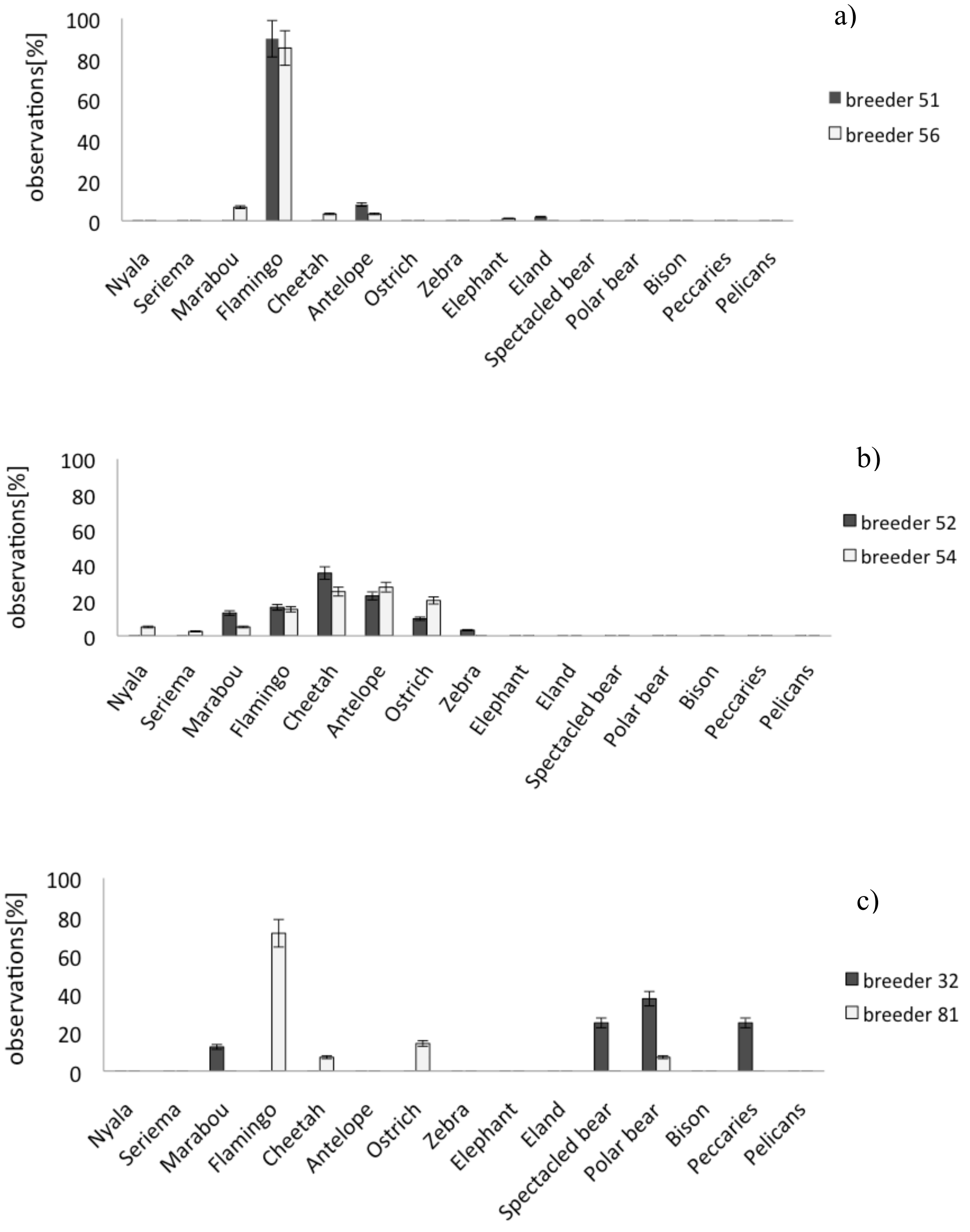
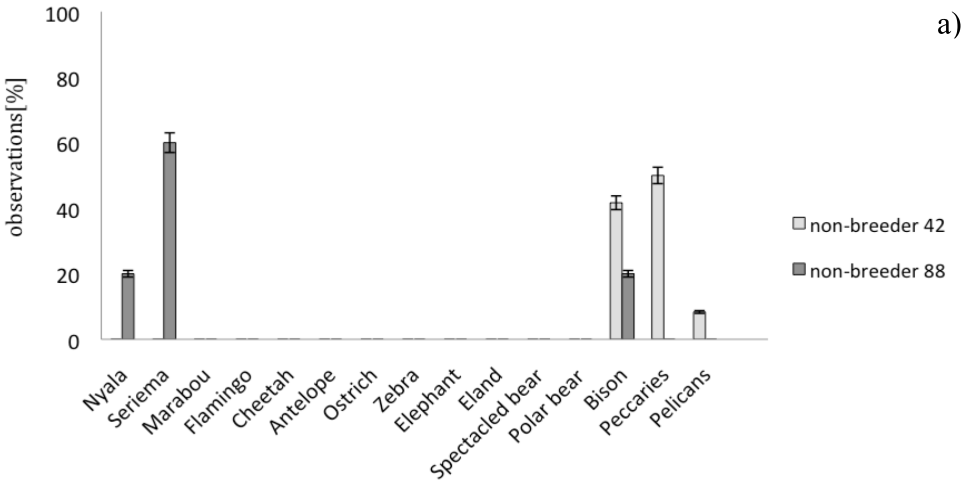


Figure 8: Use of areas of 3 different breeding pairs - a) crow 51 paired with 56, b) crow 52 paired with 54 and c) crow 32 paired with 81.

3.1.6 The use of areas by non-breeders

To illustrate the use of areas for feeding, six randomly chosen crows were taken and the individual patterns were analyzed in detail. Crow 80 was one of the most observed non-breeders and was mostly seen around the peccaries in the east of Zoo (58.3%) and only 20.8% of the time in the west, around the flamingo enclosure. Female non-breeder 2 and male non-breeder 42 were both found 100% of the time in the eastern part of the Zoo. Crow 6 was observed in both the flamingos in the west (40%) and the peccaries in the east (40%). Crow 15 was observed primarily around the peccary enclosure in the east of the Zoo (83.4%), but was also seen around the marabou enclosure in the west (16.6%). Crow 88 was observed 80% of the time in the west and only 20% of the time in the east (see Figure 9a and 9b).



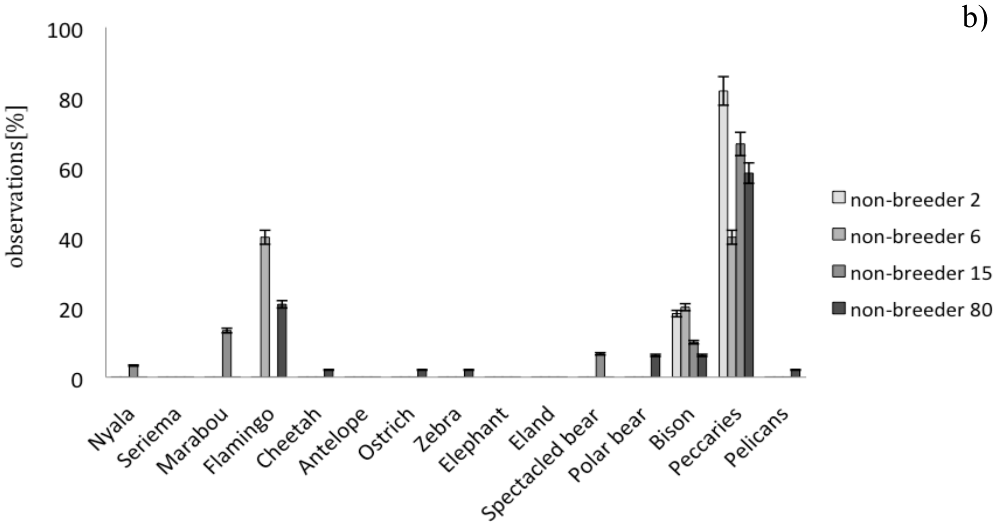


Figure 9: Individual use of areas of a) two female non-breeders and b) four male non-breeders, showing they are using the eastern and the western part of Zoo Vienna.

3.2. Experimental studies

3.2.1. Tonic Immobility

A tonic immobility test was performed on 104 out of the 115 marked crows. 71 (68%) of the crows turned around within zero to five seconds after being released and were considered fast copers. 21 (26%) of the crows did not flip over on their own and stayed immobile for the whole sixty seconds, and so are considered slow copers (see Figure 10). Within five to fifty-five seconds, only 6 (6%) of the crows are turned over on their own.

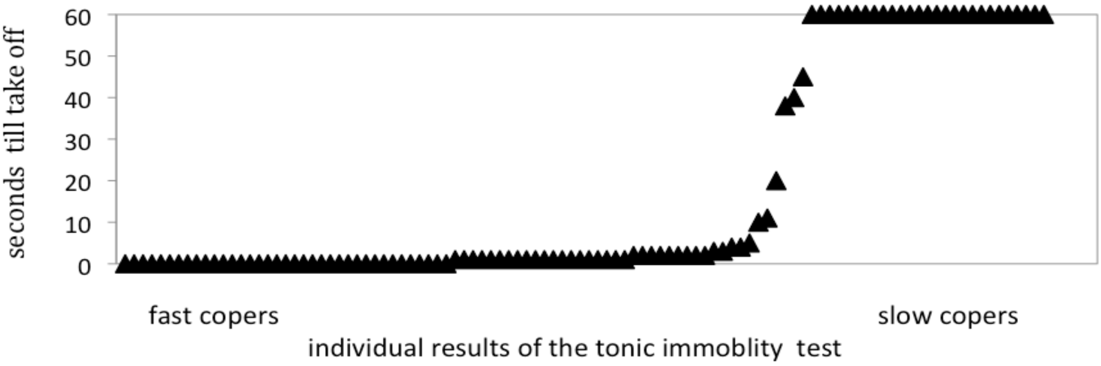


Figure 10: Seconds till the crow took off in the tonic immobility test done with all marked crows.

Of the 38 tested females, 28 (73.7%) were fast copers and 10 (26.3%) were slow copers. Of 66 tested males, 45 (68.2%) were fast copers and 17 (25.8%) were slow copers (see Figure 11a). Of the 99 tested non-breeders, 66 (71%) were categorized as being fast copers and 27 (29%) as slow copers and of 9 tested breeders, 8 (89%) were categorized as being fast copers and only 1 (11%) as slow coper (see Figure 11b). As shown in Figure 13a, no significant difference was found for either sex or social status (t-test, p>0.05). Hence, neither sex nor social status affects the results of the tonic immobility test. If a crow was caught again, a second tonic immobility test was performed and compared with the result of the first to get an idea about the consistency over time. Of 15 the crows that were recaught and retested, 14 (93.3%) crows showed no significant difference in the performance (paired t-test, p>0.05).

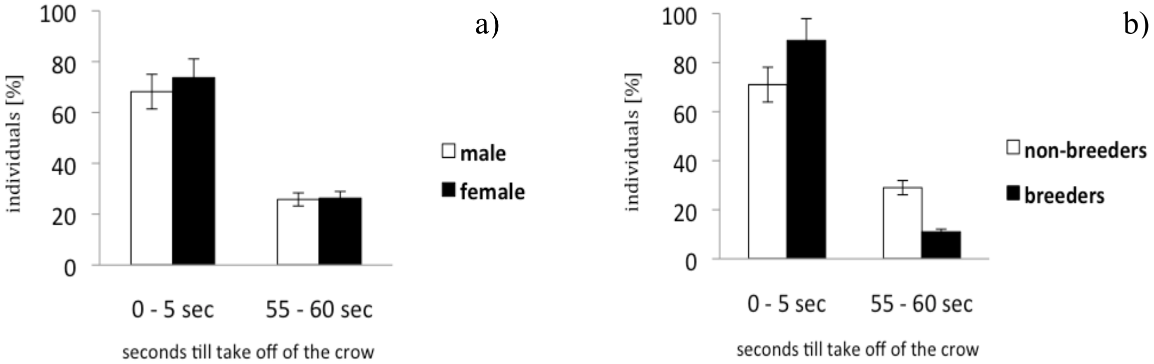


Figure 11: Influence of a) sex ratio and b) social class on tonic immobility.

3.2.2. The use of the Zoo areas depending on the coping style

All areas differ in two main points. First, some areas house predators and therefore provide high quality food sources, but also increased risk during foraging. Second, some areas are highly frequented by crows, whereas others are not. To test if the use of specific areas was influenced by variables such as danger due to predators in the enclosures or density of crows a zero-inflated GLMM was performed in R (for details see Appendix 3). Results did not show any significant influence of risk, due to predators presence (zero-inflated GLMM, $p>0.05$), but a significant effect of crow density was found (zero-inflated GLMM, $p<0.05$). The birds within high crow density areas are significantly more likely to be slow copers (zero-inflated GLMM, $p=0.0021$). This indicates that slow coping crows use the social context as foraging factor.

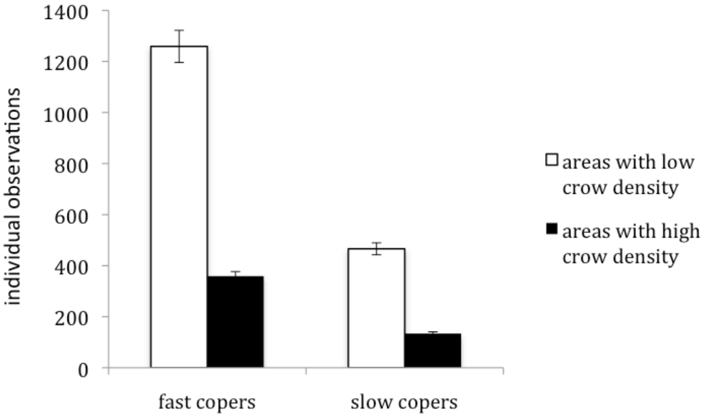


Figure 12: Observations of fast and slow copers at areas of high and low crow density.

3.2.3. Novel object exploration experiment

In the course of four months (from July to November 2010), no crows particiapted in the experiments in any of the three locations. For example, they did not appraoch the box with food inside, search for food hidden under cups or pull a string. Accordingly this experiment was stopped due to time constraints (data collection should be finished within six to eight months).

4. Discussion

4.1. Study population

During the catching period, a mean of 38.3 crows per month was marked and a total of 2222 scan observations with an average of 48.6 crows observed per round were recorded. Scans were completed throughout the Zoo to cover as much of the area as possible. Scans showed that marked and unmarked crows were present at the same sites and in similar frequencies indicating that the wild crow population in Vienna Zoo is well represented by the marked birds. Crows were mainly feeding on food provided by the Zoo to zoo animals. This means humans cause the high density of crows. The age class distribution was 80% sub adults, 10% adults and 10% juveniles. These results are roughly consistent with reports for another free-living corvid species in Austria - common ravens (Braun et al., 2012). The social structure therefore seems to be quite unaffected by the high density. The sex ratio was slightly biased towards males (3:2), which is possibly due to catching primarily during breeding season, where the female usually remains in the nesting area (particularly during incubation time in April/ May). A similar picture has been shown for ravens foraging in a local zoo, where one partner showed up at feeding sites and carried off consecutive loads of food towards territory and nest (Braun et al., 2012). In Vienna Zoo crows were mainly found in the enclosures of ommnivorous and/ or vegetarian species, whereas in comparison, other studies under similar conditions, such as at Cumberland Gamepark in Gruenau, Austria, showed that wild ravens concentrated particularly on the enclosures of the wolves and the wild boars (Braun et al., 2012). This suggests that ecological conditions, such as co-feeding with potential predators, may influence the individuals' decision whether or not to scrounge for food when there is competition. Social conditions, on the other hand, may affect the means of gaining food possessed by others and may thus, to a large extent, determine the profitability of scrounging (Bugnyar & Kotrschal, 2002). In this case neither sex ratio nor age class had an influence on diet choice.

However, clear preferences for particular feeding areas, that essentially divided the Zoo into an eastern and western part, were found. One factor influencing this preference may be the social status as breeders were found mostly in the east and non-breeders in both parts. A possibility for differences relating to social status could be due to location of the nesting sites. In general, such a proportion and behavior from breeders and non-breeders is also supported by a study about marked free-ranging ravens. In this case, non-breeders typically arrived at the study site at dawn and left for the night roost around sunset, whereas territorial breeders visited the park only occasionally, notably during the morning feeding of the zoo animals (Braun et al., 2012). Another possibiltiy could be that in the east, the availability of nesting sites was limited. As Vienna Zoo is extensively covered with trees, this might be very unlikely. Furthermore, the Zoo borders directly with the surrounding park area, therefore another explanation for this bias could be that breeders foraging in the east might have their nest site outside the Zoo and are not marked. This possibility might occur due to constraints during catching of the birds. It is also known that the crows are roosting in the wood above the Zoo and therefore the non-breeders are sharing an area where the exchange of information about feeding sites can take place. As suggested by the information centre hypothesis (Ward & Zahavi, 1973), the roosting areas may be the place to gain all the needed information. Marzluff et al. (1996) and a similar study in hooded crows (Sonerud et al., 2001) provide good experimental evidence for information exchange at communal corvid roosts (Wright et al. 2003). It was found that when naïve birds were released at roosts, they followed knowledgeable birds to carcasses, whilst when released away from roosts, they were rarely sighted at such carcasses (Marzluff et al., 1996). Therefore, the breeders could be excluded from such an exchange of information and limited to only using known areas as foraging ground. However, due to the relatively small area covered by the Zoo, it is unlikely that information exchange is playing a crucial role.

4.2. Tonic immobility

A second factor influencing the crow distribution for specific areas may be the coping style, measured with the tonic immoblity test. Tonic immobility testing has frequently been used to characterize individuals along a bold-shy continuum in order to determine one factor of the birds' personality. During the tonic immobility testing, which has the advantage of being a highly standardized protocol, the experimenter sitting still and in a crouched position lowered the possible influence of experimenter presence on the behaviour of the crows. A tonic immobility study with hens (*Gallus gallus domesticus*) showed that the subjects were unaffected by whether or not the experimenter wore spectacles or sunglasses, or whether the experimenter remained visible or retreated out of the bird's sight after inducing tonic immobility (Jones, R.B., 1989). The results in the crows were clear cut, with individuals either turning around within one to five seconds or individuals staying immobile for a maximum of 60 seconds. Repeated tests on the same individual also gave the same result. The results of the tonic immobility and the characterization as bold or shy birds, was neither influenced by age class nor social status. Interestingly, fast copers were found in several areas, whereas slow copers were found particularily in those areas where there were many other crows present. This indicates that slow coping crows may seek the company of others and rely on the presence of conspecifics when foraging in specific areas. Marzluff and Heinrich (1991) also came to the conclusion that group formation may benefit ravens in overcoming food defence, but may also lead to increased competition (Heinrich et. al, 1998).

4.3. Novel object exploration

It was very difficult to get the crows used to the new feeding situations that were experiementally designed to test novel food exploration. During the three months in which the three novel food situations were presented once a day for 30 minutes, no crow approached any task. Some crows sat in the area and watched the food, but none every took it. There may be differing reasons for this. On the one hand, the tasks might have been too novel, and the crows may have needed a much longer habituation time to get over their neophobia. As claimed by Stoewe et al. (2006), the delay of approach to novel objects when together with conspecifics could be due to an increase in neophobia and thus even lead to inhibited approach to, and intake of, novel food. This is also supported by a studies with schooling fish, such as chum salmon (*Oncor hynchus keta*) (Ryer & Olla, 1991). On the other hand, it could have been that the experimental areas were not good locations for such tests. Care was taken not to include locations inside strictly defended breeding territories, where access to the obejcts would have been limited, or those in close proximity to visitors which could have disturbed the birds. Although this part of the study did not work out, these pilot experiments still give good insight for future field experiments in this area or in general with free-ranging corvids.

4.4. General discussion

The management of "undesirable species" is one of the major biodiversity concerns relating to urban ecosystems (Savard et al., 2000). This can be extremely challenging because the complexity of underlying ecological relationships can make the outcome of management interventions difficult to predict (Davison et al., 2011; Delahay et al., 2009). Quite a few studies during the last decade have concentrated on research into the ecology of such species to figure out which management solutions could be of use. For example, the monk parakeet (*Myiopsitta monachus*) is a generalist parrot species of South America and is known of being an agricultural pest. The species was introduced in Spanish cities like Barcelona between 1992 and 1994 (Bucher et al. 1990). A study conducted in Barcelona with this species showed that they are most likely to roost in urban parks with edible plants and palms. It was illustrated that the distance from nests to the nearest urban park averaged less than 500 m. These findings suggested that limiting the number of available nesting sites in close distance to possible foraging habitats could lead to limiting the population (Sol et al., 1997).

Within Vienna Zoo, this does not seem to be a reasonable solution as the number of breeders compared to non-breeders is relatively small. The amount of food provided by the visitors and the Zoo staff as well as the area on its own seem to offer all factors that a non-breeder flock needs to establish. The vicinity of the woods for night roosting may also play an important role (Wright et al., 2003).

Results from the present study indicate that slow coping crows may need other crows to be present, which increases opportunities for social learning. The finding that no crows participated in the experimental set-up highlights the neophobia of this species. Therefore the Zoo may need to investigate a new feeding system, which is unpredictable and consists of a variety of new feeding structures that would prevent the crows from having immediate access to all provided food sources. It might also reduce the competition between crows and zoo animals over food sources. For the Zoo animals, this may also result in valuable enrichment.

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7. Appendix

7.1. Appendix 1

Table 3: Data taken during scan sampling observations.

Date	Diverse	Description
Round number	Morning	0900 hours to 1100 hours
	Lunch	1300 hours to 1500 hours
	Evening	1800 hours to 2000 hours
Weather	Sunny	Blue sky, no clouds around
	Cloudy	Cloudy, but no rain
	Rainy	Rain
Temperature	Cold	>10°C
	Warm	10–20°C
	Hot	<20°C
Location of crows	Ground level	Within 1.5 meters distance to the ground (including a fence and different structures like stones, stairs and big roots)
	Off ground	More then 1.5 meters away from the ground
	Inside enclosure	Inside or on the fence of an enclosure
	Outside enclosure	Outside the fence of an enclosure
Behaviour	Searching	Digging in/on substrate/ moving around on the ground, head generally directed towards ground
	Watching	Remaining stationary, either on or off ground, alert (feathers upright) or passive (feathers smooth, relaxed posture), may be looking around the surrounding area, not directly food related
	Eating	Consuming food item, food disappears into bill, includes food storing in throat pouch
	Carrying	Holding food item visibly in bill and moving from one location to another, on or off ground
	Special	Any other food related, but rare behaviour (e.g. caching)
Quality of food	Human leftovers	Visitors feeding on crows, visitors leftovers

	Natural sources	Food sources outside the enclosure, but not human related
	Zoo animal food: meat	Food from Zoo animals found inside the enclosure, meat only
	Zoo animal food: no meat	Food from Zoo animals found inside the enclosure, vegetables only
	Not Visible	The food source was unable to identify properly
Species identification	Not Visible	
	Hooded Crow	Corvus corone cornix: more grey feathers then Carrion
	Carrion Crow	Corvus corone coroen: completely black feathers
	Carrion/ Hooded Hybrid	Carrion/ Hooded hybrid: mix of both subspecies
Nearest neighbour	>1 metre	
	1-3 metre	
	>3 metre	
Number of visitors	No Visitors	
	Small No.	5-10 within view distance
	Medium	10-25 within view distance
	Large No.	More than 25 in view distance
Activity level of visitors	Quiet	Normal speaking and observing animals in the enclosures
	Moving	Normal speaking and others moving along the enclosures
	Noisy	Noisy, children playing, fast moving everywhere

7.2. Appendix 2

Table 4: Individual data of all marked birds including subspecies, social status, age, sex, tonic immobility results and individual preferences.

Bird	**Species**	**Social Status**	**Age**	**Sex**	**Tonic Immobility**	**Individual Preference**
1	Carrion crow	breeder	adult	m	-	N
2	Carrion/ Hooded Hybrid	non-breeder	sub adult	m	1:00	E
3	Hooded crow	non-breeder	sub adult	f	0:11	N
4	Hooded crow	non-breeder	sub adult	f	-	N
5	Carrion crow	non-breeder	sub adult	m	00:20	E
6	Hooded crow	non-breeder	adult	m	00:40	E/W
7	Hooded crow	non-breeder	sub adult	f	-	N
8	Hooded crow	non-breeder	adult	m	0:45	E
9	Carrion/ Hooded Hybrid	non-breeder	adult	m	1:00	N
10	Hooded crow	non-breeder	sub adult	m	0:02	N
11	Carrion/ Hooded Hybrid	non-breeder	sub adult	m	-	N
12	Carrion/ Hooded Hybrid	non-breeder	sub adult	m	1:00	E
13	Carrion/ Hooded Hybrid	non-breeder	sub adult	m	0:01	N
14	Hooded crow	non-breeder	sub adult	m	0:02	N
15	Carrion crow	non-breeder	sub adult	m	1:00	E
16	Carrion/ Hooded Hybrid	non-breeder	sub adult	m	0:02	N
17	Hooded crow	non-breeder	sub adult	m	0:01	N
18	Carrion crow	non-breeder	sub adult	m	1:00	E
19	Carrion/ Hooded Hybrid	non-breeder	sub adult	m	1:00	E
20	Carrion/ Hooded Hybrid	non-breeder	sub adult	f	1:00	W
21	Carrion/ Hooded Hybrid	non-breeder	sub adult	f	0:01	N
22	Carrion crow	non-breeder	adult	m	-	E
23	Hooded crow	non-breeder	sub adult	f	0:01	N
24	Hooded crow	non-breeder	sub adult	m	0:38	W
25	Carrion/ Hooded Hybrid	non-breeder	sub adult	f	0:01	N
26	Hooded crow	non-breeder	sub adult	f	0:01	N
27	Carrion/ Hooded Hybrid	non-breeder	sub adult	f	1:00	E
28	Carrion/ Hooded Hybrid	non-breeder	sub adult	f	0:03	E
29	Carrion/ Hooded Hybrid	non-breeder	sub adult	m	0:01	N
30	Hooded crow	non-breeder	sub adult	f	0:02	N
31	Hooded crow	non-breeder	sub adult	m	0:01	N

32	Hooded crow	breeder	sub adult	m	0:01	N
33	Carrion/ Hooded Hybrid	non-breeder	sub adult	m	0:01	E
34	Carrion/ Hooded Hybrid	non-breeder	sub adult	f	0:10	N
35	Hooded crow	non-breeder	sub adult	m	0:01	N
36	Carrion/ Hooded Hybrid	non-breeder	sub adult	m	0:03	N
37	Hooded crow	non-breeder	sub adult	m	0:01	N
38	Carrion/ Hooded Hybrid	non-breeder	sub adult	m	0:04	N
39	Carrion/ Hooded Hybrid	non-breeder	sub adult	f	1:00	N
40	Carrion/ Hooded Hybrid	non-breeder	sub adult	f	0:00	N
41	Carrion/ Hooded Hybrid	non-breeder	sub adult	f	0:01	N
42	Carrion/ Hooded Hybrid	non-breeder	sub adult	f	1:00	E
43	Carrion/ Hooded Hybrid	non-breeder	adult	m	1:00	N
44	Carrion/ Hooded Hybrid	non-breeder	sub adult	f	1:00	N
45	Hooded crow	non-breeder	sub adult	m	1:00	E
46	Carrion/ Hooded Hybrid	non-breeder	sub adult	m	0:00	W
47	Carrion/ Hooded Hybrid	non-breeder	sub adult	f	0:02	N
48	Carrion/ Hooded Hybrid	non-breeder	sub adult	m	1:00	N
49	Hooded crow	non-breeder	sub adult	m	0:01	N
50	Hooded crow	non-breeder	sub adult	f	0:00	N
51	Hooded crow	breeder	sub adult	m	0:00	W
52	Hooded crow	breeder	sub adult	m	0:01	W
53	Hooded crow	non-breeder	sub adult	m	0:01	W
54	Carrion/ Hooded Hybrid	breeder	sub adult	f	0:00	W
55	Hooded crow	non-breeder	adult	m	0:00	W
56	Carrion/ Hooded Hybrid	breeder	sub adult	f	1:00	W
57	Hooded crow	non-breeder	sub adult	m	1:00	W
58	Hooded crow	non-breeder	sub adult	m	0:00	N
59	Carrion/ Hooded Hybrid	non-breeder	sub adult	m	0:00	N
60	Carrion/ Hooded Hybrid	non-breeder	sub adult	m	1:00	N
61	Hooded crow	non-breeder	sub adult	m	0:01	N
62	Hooded crow	non-breeder	sub adult	f	1:00	N
63	Carrion/ Hooded Hybrid	non-breeder	sub adult	m	0:02	E
64	Carrion/ Hooded Hybrid	non-breeder	sub adult	f	0:01	N
65	Carrion/ Hooded Hybrid	non-breeder	adult	m	0:01	N
66	Carrion/ Hooded Hybrid	non-breeder	sub adult	m	0:00	W
67	Carrion/ Hooded Hybrid	non-breeder	sub adult	f	0:00	E
68	Hooded crow	non-breeder	sub adult	m	1:00	N

69	Carrion/ Hooded Hybrid	non-breeder	sub adult	f	0:01	N
70	Hooded crow	non-breeder	sub adult	m	0:00	N
71	Hooded crow	non-breeder	sub adult	m	0:02	N
72	Hooded crow	non-breeder	sub adult	f	0:00	N
73	Carrion/ Hooded Hybrid	non-breeder	sub adult	m	0:00	E/W
74	Carrion/ Hooded Hybrid	non-breeder	sub adult	f	0:00	W
75	Hooded crow	non-breeder	sub adult	f	0:00	N
76	Carrion/ Hooded Hybrid	non-breeder	sub adult	m	0:00	W
77	Hooded crow	non-breeder	sub adult	m	1:00	N
78	Carrion/ Hooded Hybrid	non-breeder	adult	m	0:00	N
79	Hooded crow	non-breeder	adult	m	0:00	N
80	Carrion/ Hooded Hybrid	non-breeder	sub adult	m	1:00	E
81	Carrion/ Hooded Hybrid	breeder	adult	m	0:00	W
82	Carrion/ Hooded Hybrid	non-breeder	sub adult	f	1:00	W
83	Hooded crow	non-breeder	sub adult	f	0:00	E
84	Hooded crow	non-breeder	sub adult	m	0:00	W
85	Carrion/ Hooded Hybrid	non-breeder	sub adult	f	0:00	N
86	Hooded crow	non-breeder	sub adult	f	0:00	N
87	Carrion/ Hooded Hybrid	non-breeder	sub adult	m	0:05	W
88	Hooded crow	non-breeder	sub adult	f	0:42	W
89	Carrion/ Hooded Hybrid	breeder	sub adult	m	0:00	W
90	Carrion/ Hooded Hybrid	non-breeder	sub adult	m	0:00	N
91	Hooded crow	non-breeder	sub adult	m	1:00	W
92	Hooded crow	non-breeder	sub adult	m	1:00	N
93	Carrion/ Hooded Hybrid	non-breeder	sub adult	f	1:00	N
94	Carrion/ Hooded Hybrid	non-breeder	sub adult	m	0:00	N
95	Hooded crow	non-breeder	sub adult	m	0:00	N
96	Carrion/ Hooded Hybrid	non-breeder	sub adult	m	0:02	N
97	Carrion/ Hooded Hybrid	non-breeder	sub adult	m	0:02	E/W
98	Hooded crow	non-breeder	sub adult	f	0:00	N
99	Carrion/ Hooded Hybrid	non-breeder	sub adult	m	0:00	N
100	Carrion/ Hooded Hybrid	non-breeder	sub adult	f	0:00	N
101	Carrion/ Hooded Hybrid	non-breeder	sub adult	m	0:00	N
102	Carrion/ Hooded Hybrid	non-breeder	sub adult	f	0:00	N
103	Carrion/ Hooded Hybrid	non-breeder	sub adult	m	0:00	N
104	Carrion/ Hooded Hybrid	non-breeder	sub adult	m	0:00	N
105	Carrion/ Hooded Hybrid	non-breeder	sub adult	f	1:00	N

106	Carrion/ Hooded Hybrid	non-breeder	sub adult	f	0:00	N
107	Carrion/ Hooded Hybrid	non-breeder	sub adult	m	0:00	N
108	Carrion/ Hooded Hybrid	non-breeder	sub adult	m	1:00	N
109	Carrion/ Hooded Hybrid	non-breeder	sub adult	f	0:00	N
110	Carrion/ Hooded Hybrid	yearling	juvenile	m	too young	N
111	Carrion/ Hooded Hybrid	yearling	juvenile	m	too young	N
112	Carrion/ Hooded Hybrid	yearling	juvenile	m	too young	W
113	Too young for identification	yearling	juvenile	f	too young	N
114	Too young for identification	yearling	juvenile	?	too young	N
115	Carrion/ Hooded Hybrid	yearling	juvenile	?	too young	N

7.3. Appendix 3

Table 5: All tested models describing the response during foraging situations (feed, search, watch, carry) correlating to individual fixed variables such as age class and sex.

Response variable	Estimate Std. SE t P
Feed Nbinom dispersion parameter: 403.43 Zero-inflation: 1e-06 Log-Likelihood: -947.765	Estimated Std. SE t P (Intercept) -2.6558 0.3640 -7.30 2.9e-13 *** Agejuvenile -0.4944 0.6339 -0.78 0.44 Agesubadult 0.1015 0.3270 0.31 0.76 Sex male 0.0606 0.2012 0.30 0.76
Search1 Nbinom dispersion parameter: 403.43 Zero-inflation: 1e-06 Log-Likelihood: -1365.53	Estimated Std. SE t P (Intercept) -1.8801 0.2293 -8.20 2.4e-16 *** Age juvenile 0.0752 0.3656 0.21 0.837 Age sub adult 0.0505 0.2113 0.24 0.811 Sex male -0.2042 0.1211 -1.69 0.092 .
Search2 Nbinom dispersion parameter: 403.43 Zero-inflation: 1e-06 Log-Likelihood: -1365.56	Estimated Std. SE t P (Intercept) -1.8295 0.0881 -20.76 <2e-16 *** Sex male -0.2103 0.1152 -1.82 0.068 .
ANOVA (search2, search1)	NoPar LogLik Df -2 logQ P.value 1 5 -1365.6 2 7 -1365.5 2 0.06 0.97045
Watch Nbinom dispersion parameter: 403.43 Zero-inflation: 1e-06 Log-Likelihood: -597.393	Estimated Std. SE t P (Intercept) -3.49590 0.55151 -6.34 2.3e-10 *** Sex male 0.32266 0.31788 1.02 0.31 Age juvenile 0.96207 0.71913 1.34 0.18 Age sub adult -0.00576 0.48504 -0.01 0.99
Carry Nbinom dispersion parameter: 403.43 Zero-inflation: 1e-06 Log-Likelihood: -434.345	Estimated Std. SE t P (Intercept) -3.4192 0.4302 -7.95 1.9e-15 *** Sex male 0.0432 0.2501 0.17 0.86 Age juvenile -16.1580 1706.6000 -0.01 0.99 Age sub adult -0.1558 0.3831 -0.41 0.68

Table 6: All tested models describing the response of food (visitors' leftovers, natural sources, Zoo food: meat or Zoo food: no meat) correlating to individual fixed variables like age class and sex.

Response variable		**Estimate Std.**	**SE**	**t**	**P**	
Human leftovers		Estimated Std.	SE	t	P	
Nbinom dispersion parameter: 403.43	(Intercept)	-6.1919	1.4823	-4.18	3e-05 ***	
	Sex male	-0.0892	0.7558	-0.12	0.91	
Zero-inflation: 1e-06	Age juvenile	-12.0500	532.5600	-0.02	0.98	
Log-Likelihood: -312.929	Age sub adult	0.6281	1.3169	0.48	0.63	
Natural sources 1		Estimated Std.	SE	t	P	
Nbinom dispersion parameter: 403.43	(Intercept)	-4.820	1.808	-2.67	0.0077 **	
	Sex male	-2.149	0.950	-2.26	0.0237 *	
Zero-inflation: 1e-06	Age juvenile	-11.207	496.890	-0.02	0.9820	
Log-Likelihood: -134.183	Age sub adult	-0.677	1.610	-0.42	0.6743	
Natural sources 2		Estimated Std.	SE	t	P	
Nbinom dispersion parameter: 403.43	(Intercept)	-5.533	0.860	-6.43	1.3e-10 ***	
	Sex male	-2.081	0.884	-2.35	0.019 *	
Zero-inflation: 1e-06						
Log-Likelihood: -134.415						
ANOVA		NoPar	LogLik	Df	-2 log Q	P.value
(natural sources 2, natural sources 1)	1	5	-134.41			
	2	7	-134.18	2	0.464	0.7929
Zoo food: meat		Estimated Std.	SE	t	P	
Nbinom dispersion parameter: 403.43	(Intercept)	-9.411	3.220	-2.92	0.0035 **	
	Sex male	0.231	1.381	0.17	0.8674	
Zero-inflation: 1e-06	Age juvenile	-11.025	1130.600	-0.01	0.9922	
Log-Likelihood: -259.372	Age sub adult	0.533	2.384	0.22	0.8232	
Zoo food: no meat		Estimated Std.	SE	t	P	
Nbinom dispersion parameter: 403.43	(Intercept)	-4.588	1.226	-3.74	0.00018 ***	
	Sex male	0.531	0.702	0.76	0.44914	
Zero-inflation: 1e-06	Age juvenile	-14.678	648.410	-0.02	0.98194	
Log-Likelihood: -506.769	Age sub adult	-0.604	1.031	-0.59	0.55823	

Table 7: Best model describing the response variable sights and the interaction of east/ west use of the zoo correlating to the fixed individual variable social status (breeder/ non-breeder).

Response variable	Factors	Estimate Std.	SE	t	P
Sights Negative binomial dispersion parameter: 0.72882 Zero-inflation: 0.32384 Log-likelihood: -440.961	*Intercept*	1.921	0.424	4.53	5.8e-06 ***
	East/ west	1.417	0.561	2.52	0.0116 *
	Social status	-0.100	0.456	-0.22	0.8259
	Interaction east/ west: social status	-1.861	0.614	-3.03	0.00024 **

Table 8: Best model describing the interaction of frequnzy and sights. Response variable sights and the frequenzy of sightings correlating to the fixed individual variable like fast or slow coper.

Response variable	Factors	Estimate Std.	SE	t	P
Sights Negative binomial dispersion parameter: 0.1413 Zero-inflation: 1e-06 Log-likelihood: -1172.07	*Intercept*	-2.691	0.225	-11.99	<2e-16 ***
	frequenzy many	2.008	0.235	8.55	<2e-16 ***
	fast_slow slow coper	0.461	0.382	1.20	0.23
	Interaction frequenzy many: fast_slowslow_coper	0.775	0.412	1.88	0.06.

Table 9: Best model describing the response variable sights and the frequenzy of sightings in high frequented areas correlating to the fixed individual variable like fast or slow coper.

Response variable	Factors	Estimate Std.	SE	t	P
Sights Negative binomial dispersion parameter: 0.16187 Zero-inflation: 1e-06 Log-likelihood: -555.23	*Intercept*	-0.470	0.205	-2.29	0.0218*
	fast_slow slow coper	1.042	0.339	3.07	0.0021**

7.4. Appendix 4

Table 10: Training phase set-up for a 4-day session (with 5 replicas)

	Location 1 (Flamingo)	**Location 2 (Seriema)**	**Location 3 (Peccaries)**
Day 1	Box task	String pulling task	Cups task
Day 2	String pulling task	Cups task	Box task
Day 3	Cups task	Box task	String pulling task
Day 4	Food only	Food only	Food only

Table 11: Experimental phase set-up for a 3-day session (with 8 replicas)

	Location 1 (Flamingo)	**Location 2 (Seriema)**	**Location 3 (Peccaries)**
Day 1	Box task	String pulling task	Cups task
Day 2	String pulling task	Cups task	Box task
Day 3	Cups task	Box task	String pulling task

7.5. Appendix 5

Deutsche Zusammenfassung

Rabenkraehen (*Corvus corone corone, C. c. cornix*) sind Nahrungsgeneralisten und dadurch in grossen Gruppen im Areal des Schlossparkes und des Tiergartens Schoenbrunn zu finden. Anekdoten berichten davon, dass Kraehen regelmaessig mit den Besuchern, sowie den Tieren des Tiergartens waehrend ihrer Nahrungssuche interagieren. Das Ziel dieser Studie war zu erforschen, welche Strategien und individuelle Praeferenzen/ Techniken die Kraehen zum Nahrungserwerb anwenden und welche Gebiete sie dafuer aufsuchen. Die Tiere wurden in Reusenfallen gefangen, vermessen, gesext und individuell am Fuss markiert. Zusaetzlich durchlief jedes Tier einen tonischen Immobilitaets Test, um sein Verhalten in einer unangenehmen Situation zu messen und eine Einteilung in langsam und schnell reagierende Individuen zu treffen. Markierte Voegel wurden dann ueber einen Zeitraum von fuenf Monaten taeglich beobachtet. Die Resultate zeigen deutlich, dass die Kraehen Praeferenzen fuer bestimmte Gebiete und auch Gehege haben. Interessanterweise haengen diese Praeferenzen mit dem sozialen Status des Tieres, sowie seiner individuellen Reaktionsgeschwindigkeit in der tonischen Immobilitaet zusammen.

7.6. Appendix 6

Curriculum vitae

Personal data

Name	Martina Schiestl
Born	21.12.1983, Innsbruck, Austria
Citizenship	Austria
Email	martina.schiestl@univie.ac.at

Education

2013	Workshop on conflict management, Vienna/ A
2013	Behavior, cognition and training seminar with Dr. Sophia Yin, Vienna/ A
2013	Practical Animal Training Workshop, Vienna/ A
2012	Animal Welfare Seminar: emotion, cognition and behavior, Edinburgh/ UK
2012	Bird Welfare and Behavior Seminar, Copenhagen/ DK
2011	Strahlenschutz Grundausbildung, Seibersdorf/ A
2011	Advanced Animal Trainer Workshop, Chessington / UK
2008-2013	Master Neuro-, Behavior- and Cognitive Biology, University of Vienna, Austria Master thesis “Personality and Foraging strategies in free ranging crows (*Corvus corone corone, C.c. cornix*)” under supervision of Prof. Thomas Bugnyar
2003-2008	Bachelor Biology, University Innsbruck, Austria
1998	Graduation Economic school, Innsbruck, Austria

Career

2011-today	Animal trainer, Department of Cognitive Biology, University Vienna/ A
2010-2011	Biology teacher, High School Dr. Rampitsch, Vienna/ A
2008-2010	Educational consultant and animal keeper, Tiergarten Schoenbrunn, Vienna/ A
2007	Freelancer for Zoo Vienna to author a didactical proposal, Vienna/ A
2007	Foster mother and field assistant in the migration of northern bald ibis, A/ G/ I
2006	Research assistant and animal keeper in the Wildlifepark Rosegg, Carinthia/ A
2003	Cetacean research with Tethsys Research Institute in the Meditearranen Sea/ I
1999-2008	Various occupations (sales assistant, secretary, doctors’ assistant, receptionist and waitress)

Publications and Presentations

Schiestl, M., Miller, R., Bugnyar, T. Individuality and foraging strategies in free ranging crows (C.c corone, C.c. cornix) - in prep.

Miller, R., Schiestl, M., Whiten, A. Bugnyar, T. Social influences on learning in free ranging crows (C.c.corone, C.c.cornix) - in prep.

Poster at the Artenschutztage in the Vienna Zoo/ A (August 2011), Individuality and foraging strategies in wild ranging corvids (C.c. corone)

Poster at the Corvid Symposium, Lund/ SW (August 2012), Personality and foraging strategies in wild ranging corvids (C.c. corone)

Invited talks in the parrot shelter (ARGE Papageien) in Vienna/ A (2012, 2013), Animal training using positive reinforcement techniques; How to deal with aggression in parrots

Invited talks at the Bird welfare and behavior seminar, Copenhagen (April 2012), Animals in science - training for research; A comparative study about touchscreen training in kea, ravens and pigeons

Talk at the Ecology and Behavior conference, Rennes/ F (May 2011), Individuality and foraging strategies in wild ranging corvids (C.c. corone)

Additional skills

Languages: German (native speaker)
English (fluent in spoken and written)
Italian (extended knowledge)

Computer experiences: ECDL (Office)
Fidelio
Gastro-Dat
Profi-Med
Medical net
Solomon coder
SPSS and R

Driving license B (since 15-02-2002)

Member in the Austrian Biologist Association (ABA)
Member in the International Avian Trainer Association (IAATE)