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Treats for trash – Habituation of wild carrion and hooded crows (Corvus corone ssp.) to a novel token-exchange machine

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1. Introduction

1.1. The Crowbuddy Project

Over the past 42.000 years, strong interrelations have developed between humans and non-human animals (Baumann, 2023). Synanthropic animals, like many of the Corvidae family, have learned to adapt to human behaviour to, inter alia, maximize foraging success by following (disposed) human food sources. Carrion crows and hooded crows (*Corvus corone ssp.*) are found around the globe, even in the most urbanized areas, using their cognitive skills to get the most out of living in proximity to humans (Benmazouz et al., 2021; Greggor, Clayton, et al., 2016). Meanwhile, most human communities have shown little ingenuity in this regard beyond exploitative practices like hunting and domestication (Dhont & Hodson, 2019). By maintaining a rigid perception on how to benefit from animals around us, we have missed out on a non-invasive and sustainable option: Training wild animals to use their skills in a mutually beneficial human-animal-symbiosis.

Given that rapid human population growth and concomitant urbanization and ecosystem destruction does not only threaten our environment but our own health and, ultimately, survival, establishing new ways to better cooperate with nature and wildlife is essential (Rastandeh & Jarchow, 2021). Litter and waste, for example, pose an increasing risk to our environment that is potentiated in areas with high human population densities but is not yet fully understood in its scale (Ballatore et al., 2022). What is known, however, is that inappropriately disposed objects that contain potentially toxic components and microplastic, like cigarette butts, packaging and masks, have fatal consequences for both terrestrial and aquatic ecosystems (Jambeck et al., 2015; Qian et al., 2022). In Austria alone, a nationwide clean-up initiative by the federal environment agency in 2018 has led to more than 1,000 tons of collected litter, of which 26 tons were collected in Vienna (Stoifl & Oliva, 2020). If crows could learn that collecting and appropriately disposing of our litter is of advantage for them, they might be able to help us with this problem. It has already been shown that corvids are able to learn object exchange tasks (Dufour et al., 2011, 2020) and even to specifically exchange collected trash for a food reward in the course of some projects (e.g., “Corvid Cleaning”, Sweden; “Crowbox”, U.S.; “Birds for Change”, France). However, success with wild birds was scarce and scientific data that can help maximize success and efficiency of such projects by identifying the factors that influence the onset and transmission of this innovative behaviour in a population (or the absence of it) is lacking.

This explorative study aims at filling these gaps in knowledge and setting a basis for training free-living, unmarked carrion and hooded crows (and hybrids thereof [*Corvus corone ssp.*]; *C. c. corone* and *C. c. cornix* are widely considered as subspecies) of a population located at Zoo

Schönbrunn, Vienna (Austria). The zoo constitutes an attractive source of a large variety of foraging opportunities, particularly from animal enclosures and leftovers from visitors, as well as abundant breeding sites and is known to attract a large number of crows (Deventer et al., 2016; Miller et al., 2014; Uhl et al., 2019). Building upon the knowledge gained during this study, individuals will be trained to collect disposed items (i.e., trash) and exchange them for a food reward. This will not happen by direct contact with the trainer/observer, but by means of an AI-driven, self-sufficient apparatus, the Crowbuddy (see 2.2., designed by Gijs-Peter Kuijpers), which is placed in an unoccupied, fenced animal enclosure (see 2.1. and 2.4.2.). The enclosure is located on a wide, open square surrounded by several animal enclosures frequently visited by the crows as scavenging sites, which should facilitate the aggregation of large subgroups and social tolerance of conspecifics around the apparatus as shown in previous studies of the population (Kirchmeir et al., 2019; Miller et al., 2014; Uhl et al., 2019). Following a stepwise process of habituation (i.e., the decrease of an initial response towards a novel stimulus after repeated exposure, see 2.4.1.) to the Crowbuddy (which constitutes an unfamiliar, novel object), crows should learn that the apparatus represents a safe and stable food supply, setting the essential baseline for instrumental conditioning (i.e., final phase of establishing a cognitive behaviour-reward-connection). Factors that influence habituation, innovation, learning and behavioural transmission ought to be identified by mainly addressing the following research questions,

I. Will crows approach, interact with and/or exploit the apparatus and, if so, how will this change over time?
II. What influence will social context have on approaching and the behaviour towards and around the apparatus?
III. Will behaviour transmit across the population by social learning?
IV. What influence will human presence and behaviour have on the crows' behaviour towards and around the apparatus?

1.2. Innovation and diffusion by social learning

As the outcome of this and similar projects relies heavily on innovative behaviour and its diffusion (i.e., behavioural transmission by social learning), elaborating on innovation and the numerous factors influencing it is essential. Innovation is defined as the initial inception of a behavioural variant, the discovery of new information or the transfer of known behaviours into a novel context (Laland & Reader, 2010). According to anthropological frameworks by Brosnan & Hopper (2014), three key phases can be identified: 1.) Innovation as defined above, 2.) transmission/diffusion and 3.) preservation (i.e., the transformation of an innovation into a robust

behaviour within a social group). Innovation (and the subsequent spread of the new behavioural variant) constitutes one of the most fundamental human traits, but is also widespread in non-human animals across various taxa and appears to be especially prominent in primates and birds that have high relative brain volumes (Laland & Reader, 2010; Reader et al., 2016). Corvids particularly excel in telencephalic and associated pallial neuron number, likely driving their complex and flexible cognition (Ströckens et al., 2022) and their relative forebrain size is comparable to the prefrontal cortices of great apes (Olkowicz et al., 2016). It is therefore not surprising that Corvidae show the highest innovation diversity among passerines (Miller et al., 2016), as observed in New Caledonian crows (*C. moneduloides*), ravens (*C. corax*), American crows (*C. brachyrhynchos*), carrion and hooded crows (*C. corone ssp*) (Laland & Reader, 2010; Matzinger, 2015; Powell & Kelly, 1977; Taylor et al., 2010). High innovation rates may not only reflect complex cognition, but provide an important source of behavioural plasticity in rapidly changing, human-shaped environments, might supplement basic learning mechanisms and shape evolutionary processes (Aplin, 2016; Sih, 2013; Taylor et al., 2010).

Understanding innovation, especially in the domain of foraging (i.e., discovering and exploiting novel food sources), is crucial for shedding light on the various aspects that impact the onset of the here desired novel behaviour (i.e., exchanging trash for a food reward) and its diffusion. Foraging innovation is frequently observed in wild corvids (Logan et al., 2016; St Clair et al., 2016, 2018). It is, however, also a highly complex and multifaceted phenomenon, making it difficult to uncover influencing aspects in the wild, with a predictive framework for the underlying processes of successful diffusion of innovation and consistency across studies lacking (Aplin, 2016; Bandini & Harrison, 2020). Consequently, evidence is scarce (Aplin, 2016) and almost exclusively comes from experiments in captivity, which is why this study aims at contributing to filling these gaps in knowledge.

What are the driving mechanisms that make an individual an innovator or "producer" (i.e., an individual that produces novel information or behaviour) as opposed to a non-innovator or even a "scrounger" (i.e., an individual that exploits novel information generated by producers) (Arbilly et al., 2014; Miller et al., 2016; Mottley & Giraldeau, 2000)? Given the excellent cognitive basis of corvids to be innovators and the fitness benefits innovators may gain, one might conclude that innovation should happen as soon as an opportunity for it is provided. Although innovation may be highly adaptive under certain ecological conditions and aids in successfully occupying ecological niches, eliciting novel behaviour is also accompanied by some risk, as pointed out by Brosnan & Hopper (2014):

> *"[...] there may simply be high costs to innovating; a new solution may be equally (or more) likely to be detrimental than beneficial. For instance, a subordinate who lacks*

good access to food may eat something poisonous while trying out a novel food source. [...] A certain level of hesitancy to adopting novel behaviours is warranted."

Additionally, Reader et al. (2016) pointed out that innovators may not be able to protect the gain of their novel behaviour against scroungers, potentially lowering the benefits of innovation. Therefore, innovation should only appear in situations of necessity ("necessity drives innovation" hypothesis, Laland & Reader, 1999) or when the benefits apparently outweigh the risks (i.e., utility), rather than opportunistically (Lee, 2003; Morand-Ferron et al., 2011). Necessity cannot only arise from ecological factors – like lower abundance of familiar food sources or rapid environmental change - but also from individual factors like low social rank (Brosnan & Hopper, 2014), forcing individuals on the periphery of a social group to be innovative and overcome conservative tactics due to low competitiveness in regular foraging contexts (Caicoya et al., 2023). This is often the case for juvenile and sub-adult members of a social group, making age another central predictor of innovation, also due to increased explorative behaviour and neophilia (i.e., attraction to novel stimuli) in young individuals, as, for example, shown in common ravens (*C. corax*) and carrion/hooded crows (Brosnan & Hopper, 2014; Heinrich, 1995; Kawai, 1965; Miller et al., 2015; Morand-Ferron et al., 2011). This is not consistently true for all species, though, as starlings (*Sturnus vulgaris*) tend to be more innovative with higher social rank and juvenile monkeys of the family Callitrichidae are less innovative than their adult conspecifics (Boogert et al., 2008; Kendal et al., 2005; Miller et al., 2016). However, innovation is also not certain in situations of apparent utility, which might be linked to psychological limitations to innovation as reviewed by Brosnan & Hopper (2014). They identified 5 factors that might lead to individuals sticking with familiar behaviours they already use rather than implementing novel ones, of which two are especially relevant for this study: (1) neophobia and (2) conservatism. Neophobia (1), the fear of novel stimuli, is prominent in the Corvidae family (Brown & Jones, 2016; A. Greggor, 2016; Greggor, Jolles, et al., 2016; Miller et al., 2022; St. Lawrence et al., 2021) and may greatly impact the proneness to innovate (Reader et al., 2016). There is, however, great intraspecific variation in the degree of neophobia, with complex interrelations with ecology (e.g., degree of urbanization of the habitat), personality (axis of boldness-shyness & exploration-avoidance, cf. Réale et al., 2007), social context and rank within a social group (Brosnan & Hopper, 2014; Greggor, Clayton, et al., 2016; Miller et al., 2016, 2022; St. Lawrence et al., 2021), which is why it will be discussed separately in more detail in section 1.3. Conservatism (2), defined as the reluctance to find novel solutions when current strategies are sufficiently productive, may inhibit innovative behaviour as individuals try to avoid needless costs of failed exploration when there is no immediate necessity to innovate. Only when (socio-) ecological factors change in a way that makes known mechanisms insufficiently beneficial

(e.g., familiar food is no longer accessible due to environmental changes or monopolized by individuals with higher social rank), individuals “are driven beyond their inherent conservatism” (Brosnan & Hopper, 2014). It is therefore the internal, cognitive manifestation or result of an environment that does not demand innovation, possibly overshadowing benefits of a novel behaviour. The degree to which individuals tend to innovate is also tightly linked to their personality, as already indicated above in relation to neophobia and shown in common ravens (*C. corax*) and carrion/hooded crows (*C. corone ssp.*) by Miller, Schwab & Bugnyar (2016): Individuals with high exploration scores were significantly more likely to show innovative behaviour than their more avoidant conspecifics. Although innovators did not show significantly less neophobic tendencies, measured by latency to approach a novel apparatus (a common proxy for neophobia), than non-innovators, they were significantly more likely to manipulate the novel item. The paradox of explorative/innovative but, at the same time, neophobic species will be discussed further in section 1.3.

It is apparent that the mechanisms behind innovative behaviour are numerous and complexly intertwined, but for innovation to become a robust behaviour within a social group or population, it also must successfully spread by social learning (i.e., diffuse). Many members of the Corvidae live in complex social groups during at least some stages of their life history, as do non-breeding carrion and hooded crows, and frequently aggregate in social foraging events, independent of their current life history stage. Carrion and hooded crows also seem to show flexibility and adaptability concerning their social organization, with examples of shifting from territorial to cooperative breeding in individual populations, as observed in northern Spain and northern Scotland (Baglione et al., 2002; McIvor & Healy, 2015), further adding to the complexity of their social organization and cognition. According to the social intelligence hypothesis, complexity of social groups drives the evolution of cognitive complexity (Dunbar, 1998). In some corvids like ravens and carrion & hooded crows, complexity is enhanced by fission-fusion-dynamics (i.e., temporal variation in group size and composition leading to individual differences in vagrancy) and complex social layers (Boucherie et al., 2016; Loretto et al., 2017; Uhl et al., 2019). Consequently, learning socially by observing or copying others becomes more effective and may outperform asocial learning, represents a vital source of information without the risks of exploring and learning individually, facilitates acquisition of local knowledge by new or irregular members of the group and may greatly accelerate the transmission of novel behaviours (Allen et al., 2013; Aplin, 2016; Loretto et al., 2017; Templeton et al., 1999; Uhl et al., 2019). As generalist, social foragers, it plays a particularly important role in the acquisition of knowledge about (novel) food sources from conspecifics. However, social learning in carrion and hooded crows has received comparably little attention thus far, especially under

naturalistic conditions, and has been proposed to be investigated further in this particular study population as to add to knowledge gained from previous research (Miller et al., 2014, 2016).

The factors governing the diffusion of innovations appear equally complex as those related to the onset of it (and most factors impact both, e.g., conservatism), but can be pinpointed for carrion/hooded crows and the specific population in question by referring to a framework of 6 main factors proposed by Aplin (2016): (1) Transmission modes, (2), developmental constraints, (3) social learning biases, (4) social foraging strategies, (5) social networks and (6) population demographics. It should be noted that these factors are also interrelated. Transmission modes (1) greatly impact the speed and persistence of behavioural transmission, with horizontal transmission (i.e., within the same generation) leading to rapid diffusion within a social group and vertical transmission (i.e., from one generation to the next) facilitating persistence of the behaviour. As mentioned, the zoo constitutes an important scavenging and breeding site for a large number of crows with different levels of vagrancy, which could favour both rapid horizontal transmission due to more irregular visitors learning from residents (i.e., birds that utilize the zoo during the majority of the year; Uhl et al., 2019) as well as more robust, vertical transmission due to offspring learning from their parents and overlapping generation times, making it an ideal setting concerning population demographics (6). Although learning in crows is not restricted to a certain developmental period, developmental constraints (2) might arise due to age-related differences in fear responses towards novel stimuli (i.e., neophobia and neophilia) and proneness to explore, as already pointed out in the context of innovating, which can also influence the likelihood of copying novel, observed behaviour. Furthermore, social learning biases (3), i.e., internal learning rules that determine the socio-temporal context in which individuals (do not) learn, may greatly impact the likelihood of social learning, and can create mismatches that inhibit the spread of novel behaviours. It has, for example, been shown that the identity of the model (i.e., the observed individual) impacts the likelihood of the observer learning socially, with subordinates most likely copying explorative dominants in cooperatively breeding carrion crows (Chiarati et al., 2012). At the same time, subordinate individuals are often the ones that innovate because they are forced to do so to stay competitive (i.e., necessity to overcome conservatism), possibly creating such a mismatch stifling innovation. Also, social foraging strategies (4), like producer-scrounger-patterns, may greatly impact both the utility of innovation and its transmission. The payoffs for both producers and scroungers are negatively frequency dependent from the respective other tactic, which means that, for a novel behaviour to spread, an equilibrium that favours the tactic of producers must establish. In other words, producing must be more beneficial than scrounging or the innovative behaviour will disappear

(Arbilly et al., 2014; Mottley & Giraldeau, 2000). Given the vast food abundance at the zoo, pressure from scrounging might be mitigated and food monopolization may become rarer, which would favour the diffusion of exploiting the Crowbuddy and lower the risks and costs of innovating. Diffusion should also be favoured by the crows' social network (5) and the positive impact of fission-fusion-dynamics on behavioural transmission, as already mentioned in previous points, but may also change significantly depending on season, weather and temperature, as has been shown, inter alia, for our study population (Uhl et al., 2019). Consequently, it might also be the case that if only a few individuals of the population learn and perform the behaviour of disposing trash, fission-fusion-dynamics lower the chances for others to observe and socially learn the behaviour, as innovators might not always be residents (i.e., birds that utilize the zoo during the majority of the year) and thus, not always be around to learn from.

1.3. The role of social context

The highly complex and flexible social organization of carrion/hooded crows should, according to the social intelligence hypothesis, generally make them more successful learners in social compared to asocial contexts (Templeton et al., 1999). Consequently, social context plays an important role in innovation and diffusion. It has, however, already been discussed in relation to personality, social learning biases and social foraging tactics that the *quality* of social context is vital (section 1.1). While it is possible that the mere presence of a conspecific accelerates exploration of and decreases neophobia towards a stimulus, defined as social facilitation (Miller et al., 2014), and that social context generally increases risk taking ("risky shift phenomenon" described in humans, Bell & Jamieson, 1970; Chiarati et al., 2012; Kogan & Wallach, 1967), other studies have found that certain behavioural phenotypes may be inhibited in their exploration of novel objects by the presence of conspecifics, as shown in captive common ravens (Stöwe & Kotrschal, 2007). Additionally, combination of sexes, relatedness and rank seem to play a crucial role in whether social context is of facilitating or inhibitory nature (Stöwe et al., 2006) and it may be the case that only the presence of conspecifics individuals frequently associate with leads to attraction towards a stimulus (Kirchmeir et al., 2019; Scheid et al., 2007). A comparative study by Miller et al. (2015) on common ravens and carrion/hooded crows found that the presence of others increased the latency to approach novel food (i.e., neophobia), which could again be due to differences in rank (i.e., subordinates waiting for access) or simply waiting for others to take the risk first – a phenomenon the authors called "socially-induced neophobia". However, the presence of others increased interaction frequency with novel food and objects, indicating that once the birds overcame this "socially-induced neophobia", social context shifted from being inhibitory to being facilitating (Miller et al., 2015). In zebra finches, social context increased the latency to approach a novel object the first time the birds were

exposed to the novel stimulus, but accelerated habituation upon repeated presentation (St. Lawrence et al., 2021). Summing up all factors discussed, the effects of social context can vary, but inhibitory effects of social context in social species mostly seem to act on the individual level. Given the vast number of crows in the study population, the diversity of possible encounters due to fission-fusion-dynamics and the high levels of social tolerance and facilitation observed (also reflected in the high density of small territories [Kirchmeir et al., 2019]), facilitating effects of social context on exploring the Crowbuddy should outweigh inhibitory factors (Miller et al., 2014; Uhl et al., 2019).

1.4. Neophobia in an urban population

As pointed out in previous sections, the neophobic tendencies of individuals play a crucial role in innovation and diffusion and relations with life history stages, rank, social context, and personality have already been addressed. In a rapidly changing, human-shaped world, understanding neophobia and its socio-ecological correlates becomes increasingly important in order to understand why some species are more successful than others in adapting to the Anthropocene, but studies in the wild are scarce (Greggor, Clayton, et al., 2016; Greggor et al., 2014; Miller et al., 2022). In this current study, it is assumed that object neophobia (i.e., fear of the novel apparatus) will play a more crucial role than novel food neophobia, as the study population is constantly exposed to a variety of different food sources, most likely also containing the same or similar food provided during training. Also, according to a large-scale, multi-lab study by Miller et al. (2022) on socio-ecological correlates of neophobia in 10 corvid species, carrion crows show comparably little neophobia towards novel food while their neophobic response towards unfamiliar objects is among the highest, only surpassed by Eurasian jays, ʻAlalās and common ravens. It must be noted, however, that all study species except New Caledonian crows were held captive, which may have an impact on neophobia and behavioural flexibility.

One may argue that neophobia constitutes the counterbalancing weight to boldness, exploration and innovation, and that individuals must carefully decide for each novel situation whether to “add weight” to the one or the other side of the (metaphorical) scale in order to safely explore and exploit novel resources (Brosnan & Hopper, 2014; Greenberg & Mettke-Hofmann, 2001), as already indicated when discussing the possible costs of innovation (section 1.1.). This explains why the most innovative, explorative species often are, at the same time, the most neophobic ones, a phenomenon called “the innovation paradox” - with corvids being a showcase example (Forss et al., 2017; Greenberg & Mettke-Hofmann, 2001; Miller et al., 2016). Thus, neophobia and neophilia must not be perceived as a result of high or low scores on the personality axes of exploration-avoidance and/or boldness-shyness nor as two ends of a spectrum, but

as separate, distinct traits that may (but do not have to) be consistent over time and can act simultaneously (Forss et al., 2017; Greenberg & Mettke-Hofmann, 2001; Grunst et al., 2019, 2019; Miller et al., 2022; Réale et al., 2007; Weisstaub et al., 2006).

The innovation paradox can be put into a more tangible framework by contrasting two hypotheses: The Neophobia Threshold hypothesis (NTH) and the Dangerous Niche Hypothesis (DNH) (Greenberg, 2003; Miller et al., 2022). According to the NTH, ecologically plastic generalist species such as carrion/hooded crows should generally show lower neophobic tendencies than specialist species, as they rely on exploring various kinds of novel food sources, while the DNH postulates that higher frequencies of novelty encounters demand species to be more cautious due to the discussed risks of exploration (Greenberg, 2003; Miller et al., 2022). One can thus consider these two hypotheses on either side of the metaphorical scale mentioned in the preceeding paragraph, not as mutually exclusive concepts, and with complex interrelations with ontogeny (i.e., experience, particularly during developmentally sensitive periods) and ecology (Greenberg, 2003; Greenberg & Mettke-Hofmann, 2001; Miller et al., 2022). This complex balancing act makes neophobic explorers rely heavily on gaining social information from conspecifics, allowing for a reduction in neophobic responses to novel stimuli by learning socially (Forss et al., 2017). Thus, repeated exposure to and exploration of the Crowbuddy, particularly in a social context, should lead to a decrease in latency to approach and/or interact with the novel apparatus (i.e., habituation) (Greenberg & Mettke-Hofmann, 2001).

Urban environments constitute the ideal ecology to explore the counteracting cognitive processes explained by the NTH and DNH (Miller et al., 2022). On the one hand, highly urbanized populations, as is the study population, can show decreased neophobic responses towards anthropogenic objects compared to conspecifics living in suburban or rural areas, as has been shown, inter alia, in common myna birds (*Acridotheres tristis*), great tits (*Parus major*) and five corvid species (Jackdaws [*C. monedula*], Eurasian jays [*Garrulus glandarius*], rooks [*C. frugilegus*], carrion crows [*C. corone*] and magpies [*Pica pica*]) (Greggor, Clayton, et al., 2016; Grunst et al., 2019; Sol et al., 2011). This pattern can be explained by the frequent exposure of urbanized populations to a variety of novel (human-made) stimuli causing habituation, but also by cities constituting a low-risk, high-benefit habitat with less predation and higher food abundance than rural ecosystems, thus reducing the risks of exploration (Miller et al., 2022). This is especially true for our study population, as the zoo constitutes a large area (~ 17 ha) within the city limits. On one hand, food is abundant year-round and persecution is practically non-existent (Kirchmeir et al., 2019; Uhl et al., 2019). On the other hand, due to the high variety of resources to exploit, decreased neophobia might only occur for very specific novel situations while increasing in other contexts to balance risk and benefit. Urban corvids did not generally

show decreased neophobia compared to their rural conspecifics when exposed to an entirely novel item but approached human-made litter significantly faster than individuals in rural habitats (Greggor, Clayton, et al., 2016). These findings may, according to the authors, be explained by a cognitive generalization and categorization of objects that resemble potentially rewarding items (e.g., wrapping materials and foil that might contain leftovers) frequently encountered in cities, also enabling individuals to better identify such objects and quickly categorize novelty as (un)safe.

Comparing these different factors influencing neophobic tendencies in an urban setting also explains why findings on the effect of urbanisation on neophobia are often conflicting, as urban environments and thus, experiences in such may differ substantially and "tip the scale" in either direction – both on the population and on the individual level (Greggor, Clayton, et al., 2016).

Another central aspect of urbanisation is high human presence, which can potentially have various effects on exploration and overcoming neophobia. In this current study, visitor density at the zoo may impact behaviour around and towards the apparatus in a both facilitating and inhibitory manner. For example, high visitor density may lead to increased crow presence due to more opportunities to exploit food leftovers from humans or to be directly fed but may, at the same time, cause decreased interest in food provided at the Crowbuddy. High human presence can potentially also lower interest when it leads to less open space available for exploration. Additionally, human behaviour like making loud noises, approaching during exploration, or showing direct agonistic behaviours (chasing, "shooing") can, despite our population's familiarity with high human presence, negatively impact habituation (Clucas & Marzluff, 2012).

1.5. Research questions and predictions

Based on all findings and factors discussed, the following predictions could be made for the four research questions addressed in the Crowbuddy Project:

I. **Will crows approach, interact with and/or exploit the apparatus and, if so, how will this change over time?**

   Due to the strong tendency to innovate, particularly in the context of foraging, within the Corvidae family and the populations' highly urbanized nature and concomitant familiarity with human-made structures, we expect crows to quickly overcome neophobia and habituate to (i.e., approach and/or feed from) the apparatus. Consequently, we expect them to successfully reach the defined thresholds for completion of the habituation process and reach the final phase (i.e., instrumental conditioning) within the 4-month time frame of this study. Thus, frequency of crow presence and visits should increase

over time while latency to approach the Crowbuddy should decrease. After habituation, we expect crows to successfully learn to exchange trash for a food reward due to their innovative nature and capability to perform token-exchange tasks.

II. **What influence will social context have on approaching and the behaviour towards and around the apparatus?**

Given the species' general high sociality and the social tolerance and facilitation observed in the study population in previous research, we expect social context (i.e., number of individuals present on the square and around the apparatus, see ethogram) to have a positive effect on overcoming neophobia (i.e., decrease in latency to approach the Crowbuddy) and the frequency of Crowbuddy-visits (i.e., zone 1).

III. **Will behaviour transmit across the population by social learning?**

Due to fission-fusion-dynamics and the species general propensity to socially learn, we expect the exploitation of this novel food source to quickly spread across the population by social learning, showing in a rise in frequency and duration of crows inspecting conspecifics on the Crowbuddy as well as individuals visiting over time. After habituation, social learning and diffusion should have a similar effect on spreading the innovative behaviour of exchanging trash for a food reward.

IV. **What influence will human presence and behaviour have on the crows' behaviour towards and around the apparatus?**

We expect an effect of human presence and behaviour on crows' behaviour towards and around the apparatus. This will be investigated exploratively with no directional predictions due to the variety of possible effects discussed.

2. METHODS

2.1. Research population and site

This study was conducted at Zoo Schönbrunn (Vienna, Austria) on free-living, unmarked carrion and hooded crows (*Corvus corone ssp.*). The apparatus ("Crowbuddy", see 2.2.) was placed in an unoccupied, fenced animal enclosure on the square in front of the zoo's rainforest house (fig. 1) based on crow and human presence data collected during the baseline phase (see 2.3.).

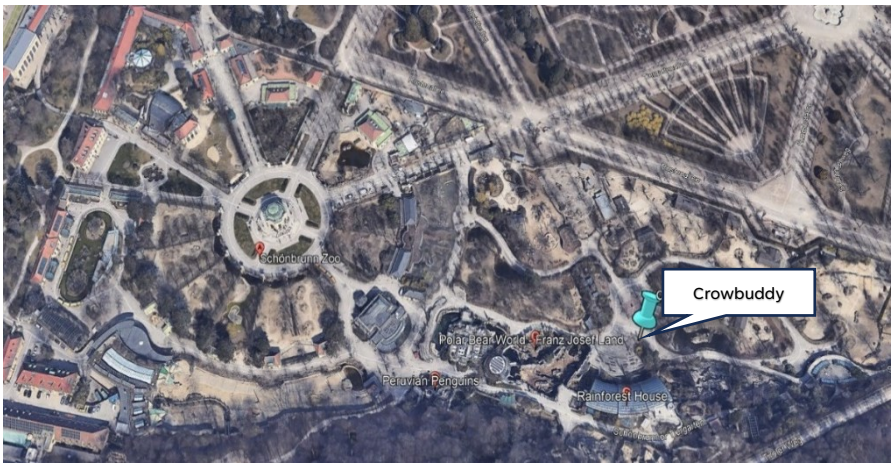

Figure 1: Bird view of the location of the apparatus "Crowbuddy" (blue pin) at the square in front of the Rainforest house at Zoo Schönbrunn, Vienna (Google earth screenshot, 28.06.2023).

2.2. The Crowbuddy – An autarkic "vending machine" for crows

Crows ought to exchange disposed objects (i.e., trash) for a food reward by learning to use an apparatus specifically designed for this purpose, the Crowbuddy (fig. 2A, designed by Gijs-Peter Kuijpers), allowing individuals to perform the behaviour without direct human contact via a fully automatic, autarkic system. As depicted in figure 2B, food rewards are placed in the food container on top of the apparatus after succesfull habituation. Crows can land on the landing site of the apparatus which has an opening to dispose collected trash. The object then falls onto the movable flap (horizontal, dotted line), as indicated by the top dotted arrow, and is scanned by the camare above the flap which is connected to the mainboard running the artificial intelligence (AI). The AI has been trained to distinguish artificial objects (e.g. bottle caps, cigarette butts, plastic pieces, masks) from nature (e.g. sticks, twigs, leaves, stones) via a Python code. After the scan is finished, both artificial and natural objects are disposed into the bin by the flap falling down (solid line) as indicated by the bottom dotted arrow. However, only artificial objects will be rewarded with food which will be dispatched from the food container into the feeder via a distributor wheel. The apparatus is powered by a photovoltaics panel on top which in turn powers a 12 volt car battery inside of the Crowbuddy, making it fully self-sufficient. The concrete base of the apparatus measures 100 × 100 cm, the apparatus itself 177 × 70/85 cm (without landing platform/with landing platform).

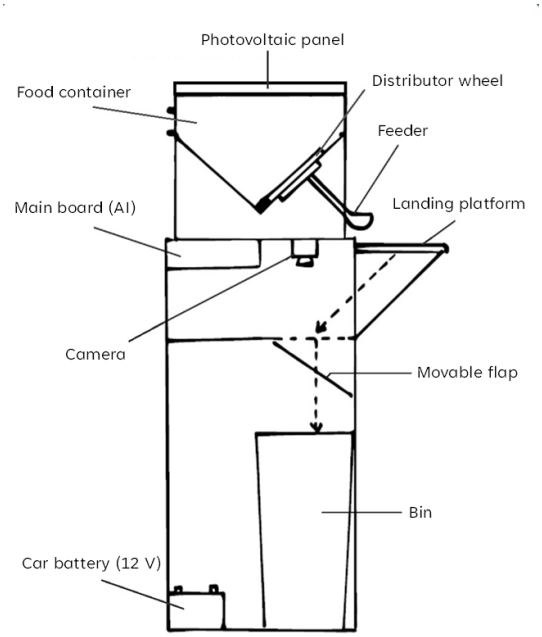

Figure 2 A) (left) and B) (right): A) The "Crowbuddy" (designed by Gijs-Peter Kuijpers, here with lid on landing platform) at its location during this study at Zoo Schönbrunn, Vienna (see 2.1.). Photo: Kristina Wastl. B) Diagram of the Crowbuddy (sideview) and its components.

2.3. Baseline and pilot phase

Preceding the main data collection (see 2.4.), baseline data collection and a pilot phase were conducted to assess a suitable location for the Crowbuddy, depending on space for the apparatus and exploration by crows as well as crow and human presence. This data was not included in the analysis.

2.3.1. Baseline data collection

Baseline data collection was conducted on 8 days from the 12th of April-28th of April 2022 in the early afternoon to determine a suitable location for the apparatus in terms of presence of crows, visitor density in relation to available space for the Crowbuddy and frequency of agonistic behaviour of visitors towards crows. Citizen science data on the population's spatial distribution at the zoo was provided by Stefanie Bachmann, MSc, gained from her master's project "Effects of resource availability and distribution on grouping dynamics and foraging strategies in an urban population of crows (*Corvus corone ssp.*)" (Supervision: Dr. Didone Frigerio, Dr. Palmyre H. Boucherie). This data underpinned the choice of 4 observational points and possible locations for the apparatus concerning high presence:

- Rainforest house square
- Small kid's playground with food stand

- Emperor's pavilion square
- "Jumbo" food stand

At each possible location, data was collected for 20 minutes each day, conducting scan sampling of crow and visitor presence at the on and offset as well as at 5 minute intervals of recording.

After evaluation of the collected data, the square in front of the zoo's rainforest house was chosen as the most suitable location for the Crowbuddy due to the highest number of crows present as well as the opportunity to place the apparatus in an unoccupied, fenced animal enclosure, enabling the crows to explore it without human interference.

2.3.2. Pilot phase

After choosing the final location for the Crowbuddy, shipment and technical maintenance of the apparatus postponed the onset of the study until beginning of September 2022. From the 5th of September-6th of October 2022, a pilot phase of data collection was conducted to establish the final recording protocol and ethogram.

2.4. Main data collection

2.4.1. Time frame, study phases and sample size

Data collection was conducted 3 days per week from the 25th of October 2022 until the 4th of March 2023 with interruptions due to technical maintenance of the Crowbuddy, resulting in a total sample size of 34 days. After the baseline and pilot phase (see 2.3), the main study was planned and conducted along 3 phases, constituting stepwise habituation to the Crowbuddy and leading up to the final phase of instrumental conditioning.

I.) Habituation phase 1 (Data collection day 1-19)

During this phase (25th of October 2022-8th of January 2023), individuals habituated to the apparatus by food being provided on the Crowbuddy (landing platform, feeder and on top of the apparatus) and in an approximately 2 m radius around it (i.e., zones 2 and 3, see fig. 4B) without crows having to perform a specific behaviour. This procedure was carried out to draw the crows' interest towards the enclosure of and the Crowbuddy itself and to establish a positive association with the apparatus (see 2.4.2 for observational protocol). This phase was concluded as soon as crows started feeding directly from the apparatus (i.e., Zone 1, fig. 4B).

II.) Habituation phase 2 (Data collection day 20-34)

Once crows started feeding directly from the apparatus (fig. 3), food was continuously removed from around the Crowbuddy (i.e., zones 2 and 3, see fig. 4B) and, on the

apparatus itself, from everywhere but the landing platform and feeder (fig. 2B) in a stepwise process (9th of January 2023-4th of March 2023). Hence, with each data collection day, food around the Crowbuddy became increasingly scarce and was eventually gone while it was abundant on the apparatus itself. By this, individuals learned that food is only provided directly on the Crowbuddy. As in Habituation phase 1, crows did not have to perform a specific behaviour to obtain food. This phase would have ended with crows stably visiting zone 1 for two consecutive data collection weeks, defined as at least 5 visits of zone 1 per data collection day.

Figure 3: Hooded crows (C. corone ssp.) obtaining treats from the Crowbuddy. Photos: Kristina Wastl.

III.) Training/Instrumental conditioning (not conducted)

This phase had the goal of crows learning that the Crowbuddy will only provide a food reward when a specific behaviour is performed. It was not conducted during this thesis as the defined threshold of the previous phase was not reached and starting the training prematurely might have had a negative impact on habituation reached thus far (see appendix for description of training procedure).

2.4.2. Data collection protocol (all phases)

Data collection was conducted in the early afternoon, starting between 12 and 2 pm, consisting of two video recorded data collection rounds of 30 minutes each with a 30-minute break in between. Videos were recorded with a Panasonic HC-X909 camcorder on a tripod. For each round, food (dog food, insect food and peanuts) was placed on and around the Crowbuddy (see 2.4.1 for phase specific details), marking the onset of the 30-minute recording. Before the placement

of food, date, time, weather, temperature, visitor density (see ethogram) and crow presence on the entire square where the apparatus is placed (360° scan sampling, fig. 4A) was assessed. Throughout the whole recording, behavioural sampling was conducted ad libitum and divided into behavioural bouts, as described in detail in the ethogram (Section 2.5, table 1). For standardized assessment of proximity to the Crowbuddy, three zones were defined around the apparatus (fig. 4B): Zone 1 represents the apparatus itself without its concrete base (see 2.2), but including the very top (i.e., the solar panel), zone 2 stands for an approximate 2 meter radius around the Crowbuddy inside the enclosure and zone 3 for the fence of the enclosure and 2 meters outside of it. All zones include trees and building structures within them.

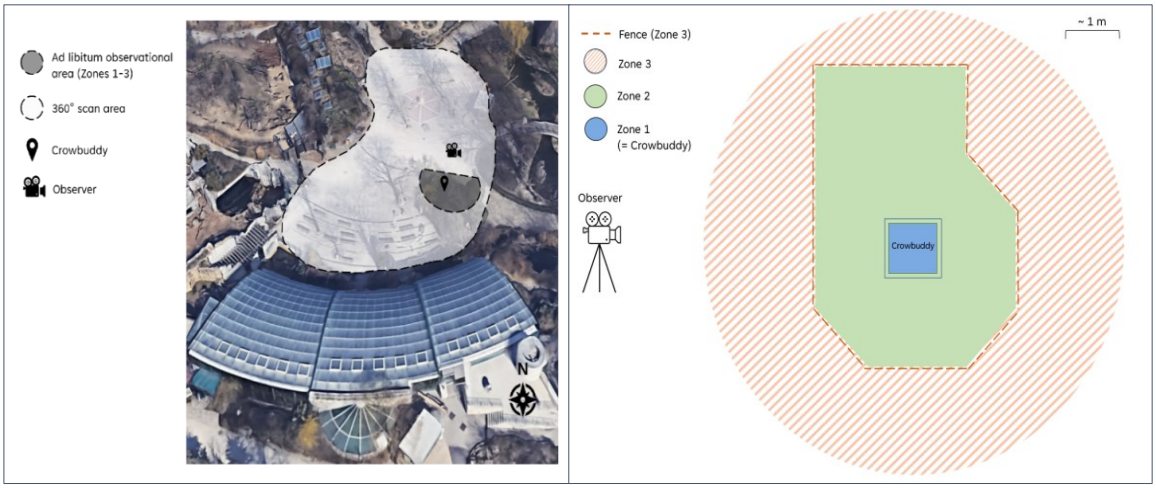

Figure 4 A) (left) and B) (right): A) Bird view of areas observed for ad libitum behavioural observation and scan sampling at Zoo Vienna, Schönbrunn; Ad libitum oversational area (Zones 1-3) = ~ 50 m², 360°-scan area = ~2200 m² (Google Earth screenshot, 01/2024). B) Camera position and predefined zones during data collection at. The Crowbuddy itself represents zone 1 (blue). Zone 2 (green) consists of the Crowbuddy's concrete base (blue solid line) and the inside of the enclosure (approximately 2-meter radius around the Crowbuddy). The fence of the enclosure (orange dashed line) and an approximately 2-meter radius around the enclosure represent zone 3 (orange striped). The camcorder was always placed at the same position in approximately 5-meter distance, using a drain cover as a landmark.

2.5. Analysis

2.5.1. Ethogram and coding

Recorded videos were coded with Solomon© coder (Péter, 2002) according to the ethogram in table 1, allowing for precise analysis of frequencies as well as durations and latencies associated with the predefined zones and respective behavioural bout (see appendix for screenshot of coding mask).

It should be noted that, as individuals were unmarked, crows that left the field of vision of the observer and returned later were counted as different crows. Due to this methodological limitation, frequency of *visits* (as opposed to presence, i.e., number of different *individuals* visiting,

see table 1) was preferred as a response variable in the statistical analysis. It should also be noted that only presence and visits of birds were assigned to individuals while all other behaviours were recorded as overall frequencies and durations.

Table 1: Precise ethogram of assessed behaviours and respective coding in Solomon©

Behaviour/Variable	**Definition** ("Individual" = crow [*Corvus corone, C. cornix*], "Novel object" = Crowbuddy)	**Coding (ad libitum if not stated otherwise) and additional information**
Presence & visits	**Ad libitum:** Individual lands in one of the 3 defined zones (see "Zone (1-3)" & fig. 4). **360° scan:** Individual landed in predefined area (fig. 4B) before or at onset of scan sampling (excl. flying individuals, also see "Social context"). During coding, each crow was assigned a random number (ID) for the duration of a behavioural bout. As long as the crow was in sight of the observer, all visits of different zones (i.e., when an individual moved between zones) was assigned to this individual allowing for an approximate differentiation between visits and presence. *Example: A crow enters zone 3 and is assigned ID #1. This crow then moves to zone 2 before it leaves the ad libitum observational zone and sight of the observer, leading to 1 visit in zone, 1 visit in zone 2 and an overall presence of 1 as it was the same individual. When the behavioural bout ends, all ID numbers were reset.*	Frequency + duration (s); Ad libitum for presence in defined zones + 360° scan at onset of recording (fig. 4A)
Social context	Social context (i.e., number of conspecifics present) was assessed as two different variables: 1.) Social context on the entire square where the apparatus was placed ("360° scan", fig. 4A) at the onset of each recording, counting all individuals present (excl. flying individuals). As this was assessed at the onset of recording before food was placed, this is a particularly useful proxy for social context for analysing its effect on latency to approach. **This variable is termed "360_SC" in statistical analysis.** 2.) Social context in the ad libitum observational area on the level of each behavioural bout (see "behavioural bout") by assessing the maximum number of individuals present simultaneously during a behavioural bout. This is a more accurate proxy for social context in terms of spatial and temporal proximity of individuals than the 360° scan. **This variable is termed "MaxSC" in statistical analysis.**	Frequency
Zones (1-3)	Zone 1: Directly on novel object (without concrete base), Zone 2: Inside enclosure of novel object, approximately 2-meter radius around NO, Zone 3: Fence of enclosure + 2-meter radius outside of enclosure; All Zones include trees and building structures within them. 0 = outside of any of the zones.	Reference point for associated behaviours
(Behavioural) Bout	To allow for more fine-grained analysis, ad libitum behavioural assessment was divided into behavioural bouts. A behavioural bout started when an individual landed in any of the predefined zones (see "Zone 1-3") and would end when there was no individual left in any of the predefined zones. Thus, a single recording session could potentially contain several behavioural bouts.	Latency to first behavioural bout, frequency and duration (s)
Manipulate novel object[1)]	Individual manipulates the novel object with its beak	Frequency + Duration (s)
Manipulate/eat food[1)]	Individual manipulates food with its beak and/or feeds on it	Frequency
Inspect novel object[1)]	Lateralized looking at (head tilts) and observing/scanning the novel object or detached parts of it for at least 3 seconds	Frequency + Duration (s)
Inspect Conspecific interacting with novel object[1)]	Lateralized looking at (head tilts) and observing/scanning another individual interacting with the novel object for at least 3 seconds	Frequency + Duration (s)
(Forced) Displacement	One individual causes another to move away, with or without directing agonistic or dominant behaviour (threats, dominant postures, vocalization) towards it; Dominant postures: See "SAD/Dominance display"	Frequency

Threat	One individual pecks at another individual with its beak, with or without physical contact;	Frequency
Kleptoparasitism/scrounging	One individual causes another to move away from a food source with or without directing aggressive or dominant behaviour (threats, dominant postures, vocalization) towards it or tries to steal food from the beak of another bird (successful or unsuccessful)	Frequency
Fight	One individual hits another with its feet and/or beak, with one individual jumping in the air and/or with one individual down on the ground and the other individual sitting on top	Frequency
SAD/Dominance display	Individual fluffs up head and leg feathers, often accompanied by vocalisation. Head is bowed down. Can be seen individually (SADs) or in the context of parallel walks (walking alongside another bird in close proximity).	Frequency
(Forced) Displacement by human	Human walks or moves in proximity (up to 2m) of an individual and/or human is clapping/"shooing", directly running towards individual, causing it to move away	Frequency
Threat by human	Human clapping, shooshing, directly running towards an individual	Frequency
Allopreening[1)]	Social grooming, one individual touches and/or runs its beak through the feathers of another individual	Frequency
Affiliative: Food[1)]	Individual touches another bird's beak and/or gives high pitched food calls with or without wing flapping to request a food item that is in the other's possession (begging) and/or individual transfers food to another bird (gift) and/or individuals share a food source (co-feeding)	Frequency, Co-feeding was assessed as event-frequency, not per individual participating
Contact sitting[1)]	One individual sits in immediate proximity to another bird (<5 cm, often directly touching)	Frequency
Location food taken: Feeder vs. platform	For food taken from zone 1, there was an additional assessment whether (1) the food was taken from the landing platform/from left and right to the feeder or (2) directly from the feeder of the apparatus (fig. 2B)	Frequency
Number of visitors	very low: <15 low: 15-29 medium: 30-44 high: 45-59 very high: >59	Number of visitors counted in the 360° scan area (fig. 4A)
[1)]If behaviour was interrupted for >5 seconds in the same spatial context (food source, individual, object), it was recorded again (e.g. Caching for 20 seconds, stops for 6 seconds, resumes caching = Caching coded with frequeny of 2)		

2.5.2. Statistical analysis

Inferential statistics were conducted in R (V. 4.2.3) using RStudio. Data was assessed to see if it meets the model assumptions using Schoenfeld residuals, the *vif* function (*car* package [Weisberg, 2019]) and the *diagnostic_fcns* function written by Roger Mundry. The best models were chosen by comparing AIC scores and performing full-null-model comparisons with a likelihood ratio test ($\chi 2$). Quantitative fixed effects were z-transformed in all models to allow for standardization and comparability. Descriptive statistics were calculated in Microsoft Excel. Both methods and results will be organized in the same manner according to topic rather than type of analysis, thus maintaining the same structure and organisation throughout the two sections. This leads to analysis conducted within the same models (i.e., models containing several

explanatory variables) still having distinct subsections, but only referencing the preceding subsection in which the model was first described.

I. Presence & visits across days and zones

i. Frequency of presence and visits across days and zones (all phases)

Frequency of the response variables presence (i.e., number of different individuals present) & visits (i.e., overall frequency of visits) were analysed fitting a Negative Binomial Generalized Linear Model (*lme4* package [Bates et al., 2015], *MASS* package [Venables et al., 2002]), due to its appropriateness for count data and overdispersion of our data set: *glm.nb(response ~ day + round + zone + visitor density + 360_SC + bout number)*. For this model, the 360° scan (i.e., number of crows present on the entire square at the onset of recording) was used as the sole proxy for social context as it can be expected that "Max SC" (i.e., maximum number of crows present simultaneously per bout) would increase with an increasing number of presence and visits (see ethogram). Due to the large similarity of results between the two response variables, only frequency of visits was plotted. Both variables were analysed at the level of a behavioural bout. Pairwise comparison of zones was conducted using the *emmeans* package (Lenth R, 2023; V. 1.8.9).

ii. Duration of overall presence (Zones 1-3) and per zone across days (all phases)

Duration of presence in zones 1-3 (overall time [s] individuals spent in the ad libitum area) was analysed fitting a Linear Mixed Effects model (*lme4* package [Bates et al., 2015], *MASS* package [Venables et al., 2002]), since the data was normally distributed and residuals were homoscedastic*: lmer(logDurationOverall ~ day + round + visitor density + 360_SC + Max_SC + (1 + day + 360_SC + Max_SC + visitor density + round PM2| bout number).*

Duration of zone-visits (seconds per individual, behavioural bout and zone) was analysed fitting a Linear Mixed Effects model (*lme4* package [Bates et al., 2015], *MASS* package [Venables et al., 2002]), since the data was normally distributed and residuals were homoscedastic: *lmer(logDurationPerZone ~ day + zone + round + visitor density + 360_SC + Max_SC + (1 + day + zone 2 + zone 3 + round PM2 + visitor density + 360_SC + Max_SC | bout number)*.

Pairwise comparison of zones was conducted using the *emmeans* package (Lenth R, 2023; V. 1.8.9).

iii. Crowbuddy (Zone 1) visits across days (habituation phase 2)

For the analysis of Crowbuddy (Zone 1) visits, only data from habituation phase 2 was used since this phase began with the first visit of the apparatus (day 20-34). The analysis was conducted fitting a Negative Binomial Generalized Linear Model (*lme4* package [Bates et al.,

2015], *MASS* package [Venables et al., 2002]), due to its appropriateness for count data and overdispersion of our data set: *glm.nb(Visits ~ day + round + bout number + Max_SC + 360_SC)*. Visitor density was excluded from this model given that its effect on overall visits was already analysed.

iv. Repeated visits & scavenging (all phases)

To get a glimpse of how individuals used different zones and how this changed over time, we compared both presence and feeding frequency to number of visits. Frequency of crow presence (i.e., number of individuals visiting) was deducted from frequency of visits (ΔPV) to obtain a proxy for (repeated) visits of different zones by same individuals within a behavioural bout (ΔPV > 0 = Individual visited more than one zone or moved between them) and was analysed inferentially. Frequencies of visits and frequency of feeding (i.e., obtaining a provided treat, see ethogram) were analysed descriptively to get a proxy for what zones were primarily used for (i.e., feeding or explorative purposes). ΔPV analysis was conducted fitting a Negative Binomial Generalized Linear Model (*lme4* package [Bates et al., 2015], *MASS* package [Venables et al., 2002]), due to its appropriateness for count data and overdispersion of our data set: *glm.nb(*ΔPV *~ day + zone + round + bout number + visitor density + 360_SC + Max_SC)*. Frequencies of feeding and visits were compared descriptively. Pairwise comparison of zones was conducted using the *emmeans* package (Lenth R, 2023; V. 1.8.9).

II. Social context

i. Effect of social context on latency to first approach (all phases)

Latency to the first crow visiting any of the predefined zones from the beginning of the recording (i.e., latency to the first behavioural bout) was analysed fitting a Cox Proportional Hazard Model (*survival* package [Therneau, 2023]) : *coxph(Latency ~ 360_SC + day + round + visitor density)*.

i. Effect of social context on duration of overall presence (Zones 1-3) and per zone across days (all phases)

The effect of social context on duration of overall presence (Zones 1-3) and per zone across days was analysed within the model described in section I.) ii.).

ii. Effect of social context on frequency of Crowbuddy visits (habituation phase 2)

The effect of social context on frequency of Crowbuddy visits was analysed within the model described in section I.) iii.).

iii. Effect of social context on ΔPV (all phases)

The effect of social context on ΔPV was analysed within the model described in section I.) iv.).

III. Social behaviours

i. Observing conspecifics – Social learning (habituation phase 2)

Social learning was assessed by recording frequency and duration of observing conspecifics at the Crowbuddy (i.e., in zone 1, see ethogram). Given that this behaviour was recorded as separate events between crows but not assigned to individuals as opposed to duration of presence and visits, the average per individual was calculated ($\frac{\Sigma\ Observing\ duration\ (s)\ per\ behavioural\ bout}{\Sigma\ Observing\ frequency\ per\ behavioural\ bout}$) for descriptive analysis. As zone 1 was first visited on data collection day 20 (habituation phase 2), only days 20-34 were included. Since observations of this behaviour were limited to this shorter time frame and highly clustered on certain days, the number and distribution of observations was not sufficient for inferential analysis.

ii. Agonistic and affiliative interactions (all phases)

Frequency of agonistic and affiliative interactions was analysed descriptively, comparing overall incidents across the whole course of data collection by zone.

IV. Explorative behaviour (all phases)

Explorative behaviour was assessed by descriptively analysing frequency and duration of manipulating and inspecting the Crowbuddy (see ethogram). Since this behaviour was recorded as separate events between crows but not assigned to individuals as opposed to duration of presence and visits, the average per individual was calculated ($\frac{\Sigma\ Inspect\ duration\ (s)\ per\ behavioural\ bout}{\Sigma\ Inspect\ frequency\ per\ behavioural\ bout}$) for descriptive analysis.

V. Human impact

i. Effect of visitor density on frequency of presence & visits (all phases)

The effect of visitor density on frequency of presence & visits was analysed within the model described in section I.) i.).

ii. Effect of visitor density on latency to first approach (all phases)

The effect of visitor density on the latency to the first approach of any of the predefined zones was analysed within the model described in section II.) i.).

iii. Agonistic behaviour by humans towards crows (all phases)

Agonistic behaviour by humans towards crows was analysed descriptively by assessing frequency of agonistic behaviour per data collection day.

3. RESULTS

3.1. Presence & visits across days and zones

3.1.1. Frequency of presence and visits across days and zones (all phases)

On both response variables presence (i.e., number of individuals present, "pr" when stating coefficients) and visits (i.e., overall frequency of visits, "v" when stating coefficients), day and zone had a highly significant effect ($p < 0.001$***), while there was no significant effect of round, bout and the number of birds present on the entire square at the onset of recording (i.e., 360°-scan). With time, presence and visits increased, with a slightly steeper increase of visits (fig. 5A, coef.: pr = 0.362, v = 0.443). Pairwise comparison of zones showed a highly significant difference between all zones for both variables ($p < 0.001$***, fig. 5B). Outer zones (i.e., zones with greater distance to the Crowbuddy) had significantly higher crow presence and visits than proximate zones (coef. with Zone 1 [Crowbuddy] as reference: Zone 2: pr =0.627, v = 0.619, Zone 3: pr = 1.966, v = 2.078). We also found a significant effect of visitor density on both variables (see section 3.5., "Human impact").

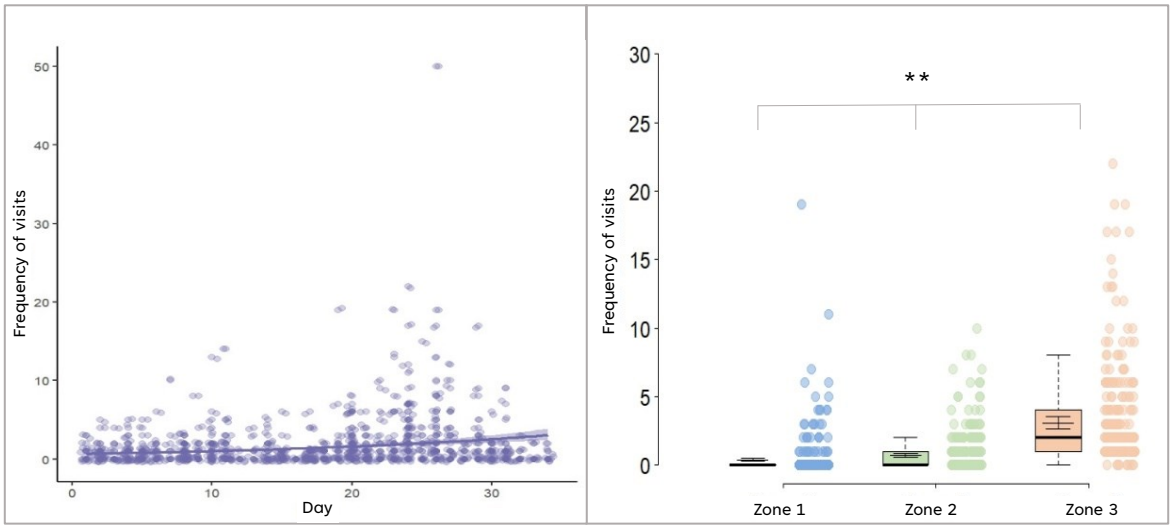

*Figure 5 A) (left) and B) (right): A) Plot of the Negative Binomial Generalized Linear Model, showing frequency of crow visits of the ad libitum observational area (Zones 1-3) across data collection days (1-34) with a confidence interval of 95%. Visits significantly increased over time ($p < 0.001$***). B) Plot of the Negative Binomial Generalized Linear Model, showing frequency of crow visits compared by zone. All zones differed significantly from each other ($p < 0.001$***), showing a rise of visits with distance to the apparatus.*

3.1.2. Duration of overall presence (Zones 1-3) and per zone across days (all phases)

Duration of overall presence (overall time [s] individuals spent in the entire ad libitum area) showed no significant effect of day, 360°-scan and visitor density, but a significant effect of

round, with crows tending to stay longer in the ad libitum observational area during data collection round 2 (p = 0.021*, coef.: 0.035). We also found a significant effect of social context ("Max SC") in the ad libitum observational area on duration of stays (see section 3.2., "Social context").

We found no significant effect of day (fig. 6A), 360° scan, round and visitor density on the duration individuals spent per zone, but a strong significant effect of zone (fig. 6B, p < 0.001***). Pairwise comparison of all three zones showed a significant difference of time spent between zone 1 and both zone 2 (p = 0.0028**, coef.: -1.308) and 3 (p < 0.001***, coef.: -1.554), while zones 2 and 3 did not differ from each other (p = 0.18, coef.: -0.246). Estimates indicate an increase of time spent with distance to the Crowbuddy (Zone 1 as reference; zone 3 [coef.: 1.554] > zone 2 [coef.: 1.308] > zone 1). There was also a strong significant effect of the number of conspecifics present simultaneously within a bout ("Max SC") on the time spent in each zone (see section 3.2., "Social context").

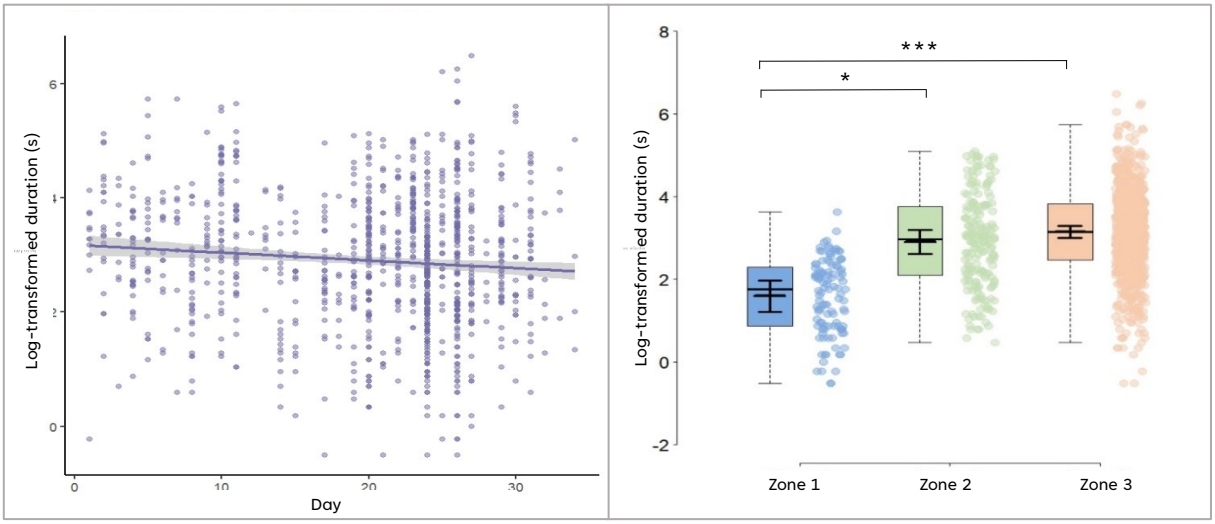

*Figure 6 A) (left) and B) (right): Plot of the Linear Mixed Effects Model, showing the log-transformed duration (s) individuals stayed within a zone across days with a confidence interval of 95 %. The effect of day on duration spent was not significant (p = 0.407). B) Plot of the Linear Mixed Effects Model, showing the log-transformed duration (s) individuals spent in the ad libitum observational area compared by zone. Pairwise comparison showed significant differences between zone 1 and both zones 2 (p = 0.0028**) & 3 (p < 0.001***), while zones 2 & 3 showed no significant differences (p = 0.18).*

3.1.3. Crowbuddy (Zone 1) visits across days (habituation phase 2)

The analysis of Crowbuddy (Zone 1) visits showed no significant effect of day (fig. 7), round, bout or the first 360° scan, but a highly significant effect of the number of conspecifics present simultaneously per bout ("Max SC", see section 3.2., "Social context"). Although day did not have a significant effect on Crowbuddy-visits, fig. 7 shows a peak in visits between day 24 and 27.

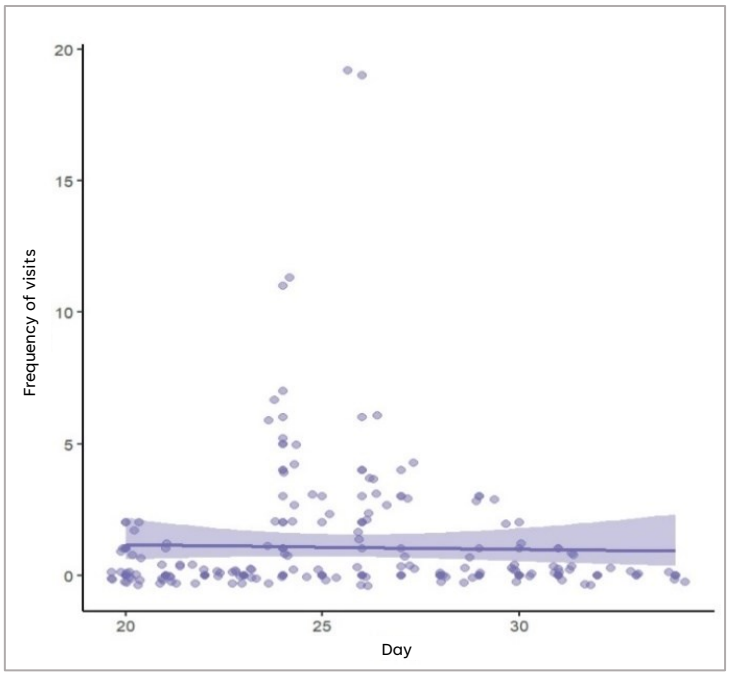

Figure 7: Plot of the Negative Binomial Generalized Linear Model, showing frequency of Crowbuddy (Zone 1) visits during habituation phase 2 (days 20-34) across days with a confidence interval of 95%. Day did not have a significant effect on frequency of visits ($p = 0.896$), but visits showed an irregular peak from day 24-26.

3.1.4. Repeated visits & scavenging (all phases)

We found a highly significant effect of day ($p < 0.001$***, fig. 8) and zone on ΔPV, while there was no significant effect of round, bout and the number of birds present on the entire square at the onset of recording (i.e., 360°-scan). Looking at the coefficients, ΔPV increased over time (0.441**)** and with distance to the Crowbuddy (Zone 1 as reference; Zone 3 [coef.: 2.381 > zone 2 [coef.: 0.174] > zone 1). Pairwise comparisons of zones showed significant differences between zones 1 & 3 ($p < 0.001$***, coef.: -2.381) and zones 2 & 3 ($p < 0.001$***, coef.: -2.207), while zones 1 & 2 did not show significant differences ($p = 0.75$, coef.: -0.174). We also found a significant effect of the maximum number of crows present simultaneously per bout (see section 3.2., "Social context").

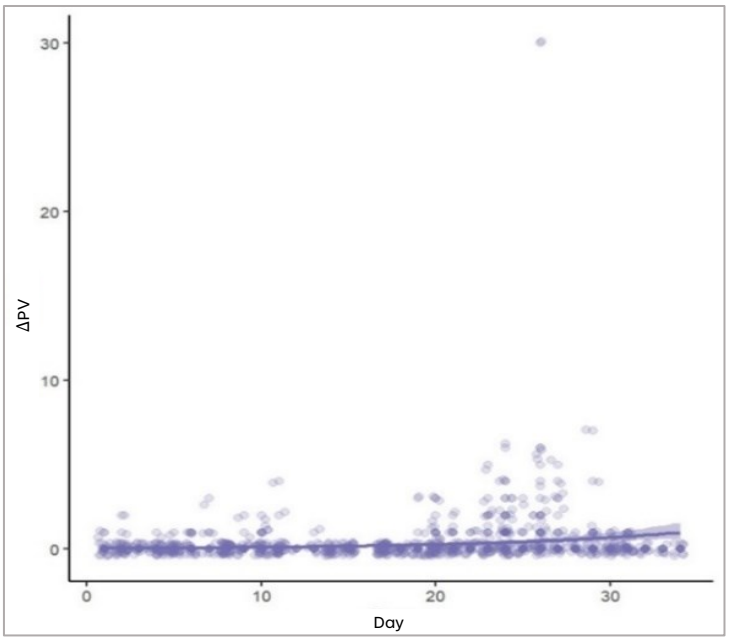

*Figure 8: Plot of the Negative Binomial Generalized Linear Model, showing ΔPV (= Visits - Presence) across days. ΔPV significantly increased across days (p < 0.001***, confidence interval = 95 %).*

Frequencies of feeding (i.e., obtaining provided treats) and visits were compared descriptively and showed substantial differences between zones and across days (fig. 9). It should be noted that although food quantity provided by the observer decreased with distance to the Crowbuddy over the time of data collection (see 2.4.1. for phase specific information), food was often dropped in outer zones by crows visiting and feeding from the Crowbuddy, leading to some treats still being available outside of zone 1 during habituation phase 2. During habituation phase 1 (data collection days 1-19), feeding and visits in zone 3 showed a mostly parallel pattern, with approximately half the frequency of feeding compared to visits on most days. After food was continuously removed from everywhere but the Crowbuddy (habituation phase 2, data collection days 20-34), visits to zone 3 still increased and even showed their highest peaks during this phase. In zone 2, frequency of visits and feeding were highly similar during habituation phase 1, while there were substantial differences during habituation phase 2. In Zone 1, frequencies for both parameters were almost identical from the first day of habituation phase 2 (i.e., first visit of zone 1).

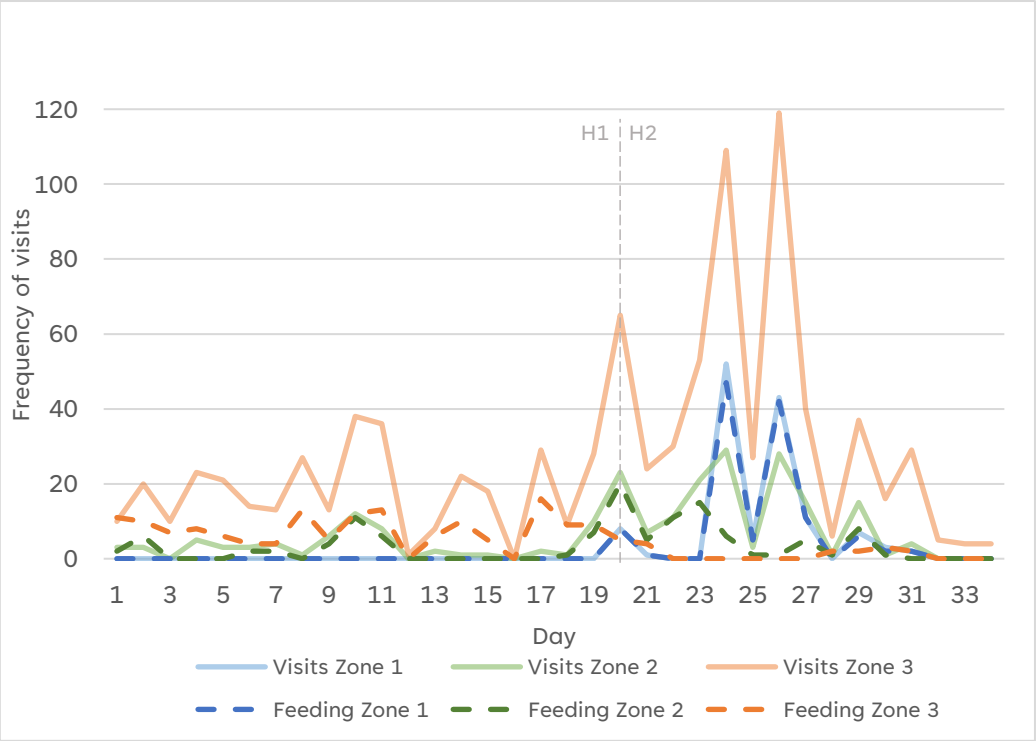

Figure 9: Frequency of crow visits and obtaining treats provided by the observer compared across days and zones. The dotted grey line indicates the end of habituation phase 1 (H1) and the beginning of habituation phase 2 (H2).

Food placed on the Crowbuddy was almost exclusively taken from the landing platform, and not from the feeder (fig. 10).

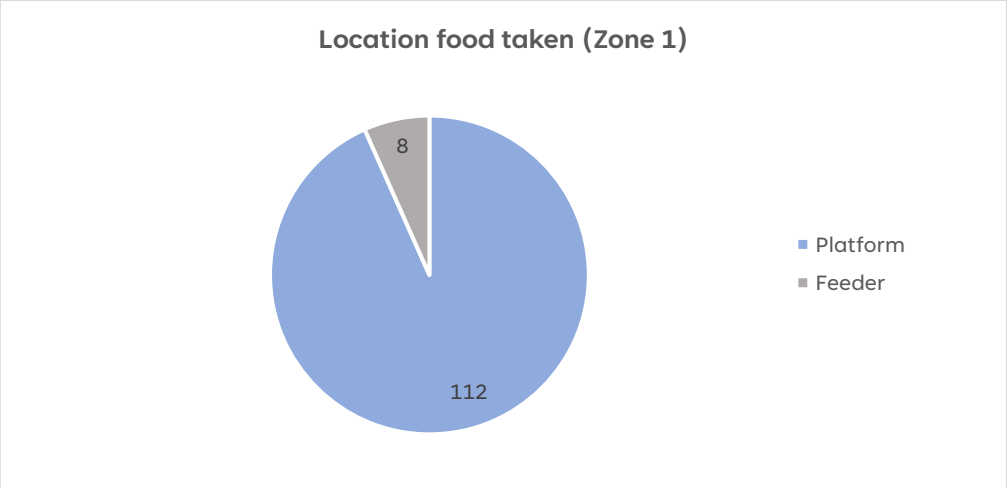

Figure 10: Comparison of the two locations where food could be taken from (platform and feeder, see 2.2.) when feeding in zone 1 (i.e., from the Crowbuddy). Crows showed high reluctance to take food from the feeder, with a 14-times higher frequency of obtaining treats from the platform.

3.2. Social context

3.2.1. Effect of social context on latency to first approach (all phases)

Latency to the first crow visiting any of the predefined zones from the beginning of the recording (i.e., latency to the first behavioural bout) did not significantly decrease over time, but we found a highly significant effect of the first 360° scan ($p < 0.001$***). Crows were more likely to approach the Crowbuddy faster the more conspecifics were present on the square (fig. 11, coef. = 0.681). We also found a weak significant effect of visitor density on latency to approach (see section 3.5., "Human impact").

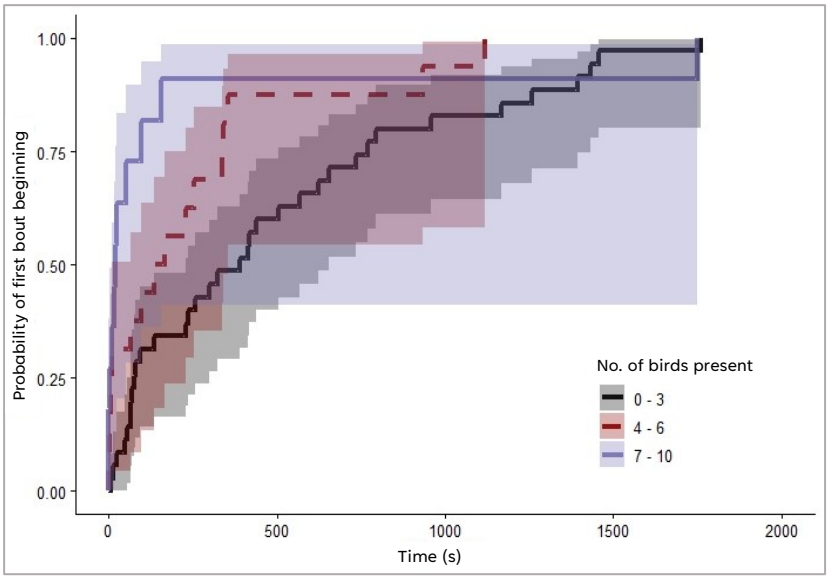

*Figure 11: Cumulative incident plot (Cox Proportional Hazard Model) showing the latency to the first approach of the Crowbuddy respective to the total recording length of one round on the x-axis (s) depending on crows present on the square during the first 360° scan. The y-axis represents the probability of the first behavioural bout beginning. The number of birds present during the 360° scan was transformed into 3 categories for better visualization (0-3 [black], 4-6 [red] and 7-10 [purple, 10 = maximum recorded]). Shaded areas represent the confidence intervals (95 %). The Cox Proportional Hazard Model showed a highly significant effect of social context on the latency to the first approach ($p < 0.001$***), indicating lower latencies with an increasing number of conspecifics present.*

3.2.2. Effect of social context on duration of overall presence (Zones 1-3) and per zone across days (all phases)

The analysis of duration (s) of visits per individual, behavioural bout and zone showed a significant effect of the maximum number of conspecifics present simultaneously within a bout ("Max_SC") on the duration spent in the ad libitum observational area ($p = 0.008$**). Estimates show a positive correlation between duration spent in each zone and number of conspecifics

present (coef.: 0.203). The same was true for the overall duration individuals spent in the entire ad libitum area (see 3.1.2., p = 0.004**, coef.: 0.255).

3.2.3. Effect of social context on frequency of Crowbuddy (Zone 1) visits (habituation phase 2)

We found a significant effect of the maximum number of conspecifics present within a bout ("Max SC") on frequency of Crowbuddy-visits (p < 0.001***). As depicted in fig. 12, visits to the apparatus tended to increase with the number of conspecifics present (coef.: 1.137).

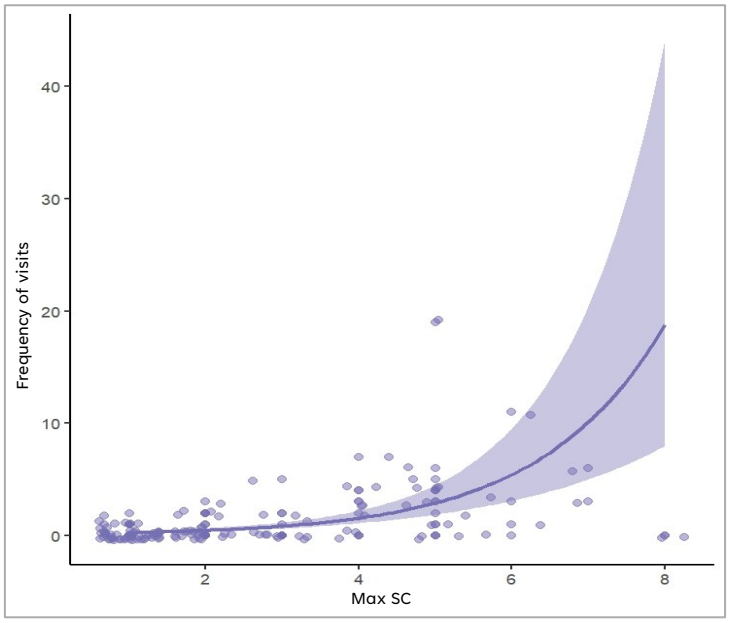

*Figure 12: Plot of the Negative Binomial Generalized Linear Model, showing the Impact of social context (Max_SC) on the frequency of Crowbuddy (Zone 1) visits. Crows were significantly more likely to directly visit the apparatus the more conspecifics were present in the ad libitum observational area (p < 0.001***).*

3.2.4. Effect of social context on ΔPV (all phases)

Analysis showed a highly significant effect of social context (max. number of crows present simultaneously per bout) on the probability of individuals (repeatedly) visiting different zones within a bout (p < 0.001***). With an increasing number of conspecifics present, ΔPV substantially increased (coef.: 0.995).

3.3. Social behaviours

3.3.1. Observing conspecifics – Social learning (habituation phase 2)

Interpreting the plots from descriptive analysis, the duration spent observing conspecifics tended to increase over time (fig. 13A). Observational behaviour varied substantially between zones, both concerning frequency and duration, as depicted in fig. 13B. Crows preferably used zone 3 for observational purposes while this behaviour was hardly observed in the other two zones. The one incident of a crow being in zone 1 and observing a conspecific was an individual sitting on the solar panel on top, inspecting another crow on the landing platform.

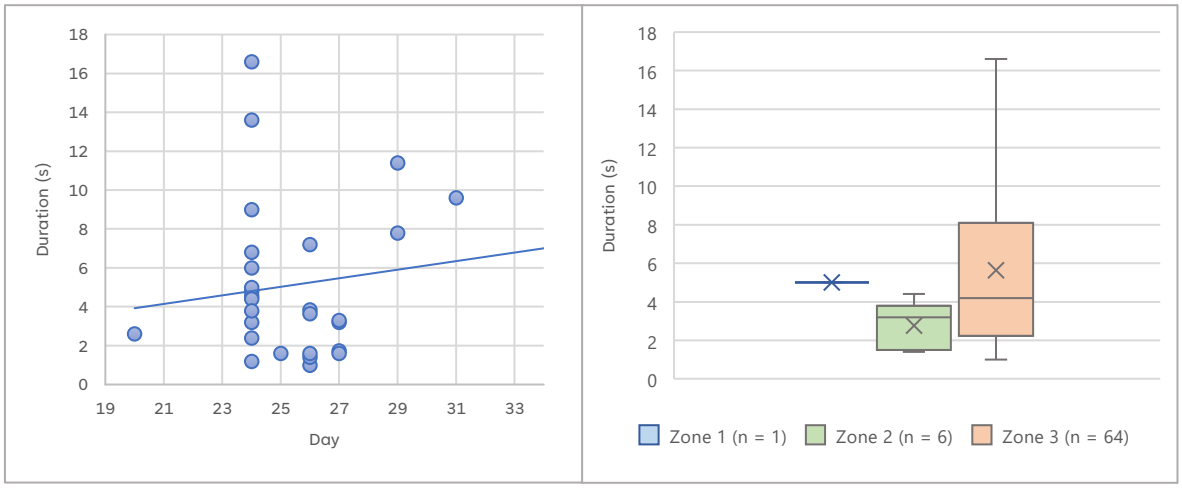

Figure 13 A) (left) and B) (right): A) Average time (s) spent observing conspecifics at the Crowbuddy over time. Time spent on this behaviour seems to have increased over time, but observations were highly clustered on certain days. B) Average time (s) crows spent observing conspecifics at the Crowbuddy compared by zone. Crows spent most time observing others from zone 3, while both duration and frequency decreased with proximity to the apparatus.

3.3.2. Agonistic and affiliative interactions (all phases)

Table 2: Total observation frequency of all assessed affiliative behaviours across zones. Overall incidents were low and almost exclusively comprised of sharing a food source (i.e., co-feeding).

Zone	Σ Affiliative - Food	Σ Contact-sitting	Σ Allopreening
1	5	0	0
2	3	0	0
3	3	1	0
Total	**11**	**1**	**0**

Affiliative behaviour towards conspecifics was hardly observed over the whole course of data collection (table 2). Food-related affiliative behaviour exclusively consisted of co-feeding and had the highest incidence in zone 1 in the form of sitting and feeding on the platform together.

Incidents of all agonistic, dominant and kleptoparasitic behaviours (A/D/K) besides (forced) displacement were low. However, the variety of A/D/K behaviours increased with distance to the Crowbuddy (i.e., Zone 3 > Zone 2 > Zone 1), while on the Crowbuddy, only kleptoparasitism in the form of (forced) displacement from food was observed (fig. 14 A+B). Incidents were generally lowest compared to visits in zone 2 (< 5 %) and almost exclusively consisted of kleptoparasitic behaviour. SADs/dominance displays (n = 2) and threats (n = 4) were solely observed in zone 3 with very low incidence. Fights were never observed in any of the zones. Percentually to visits, agonistic behaviour was highest in zone 1, showing almost double the amount compared to zones 2 & 3.

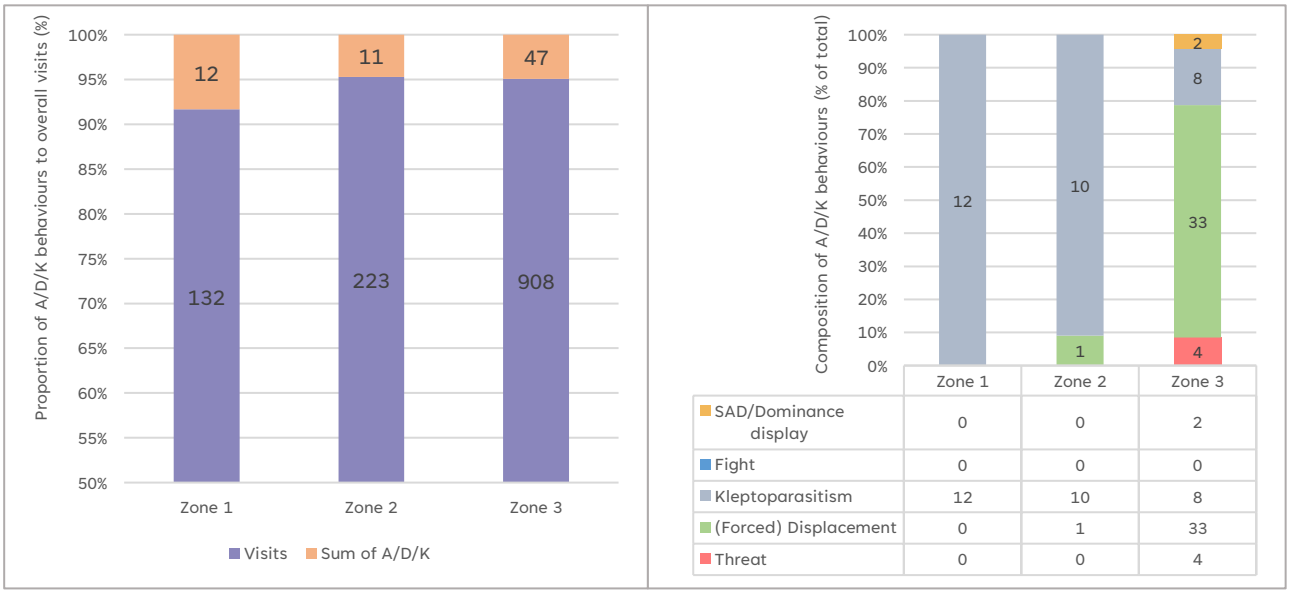

Figure 14 A) (left) and B) (right): Overall proportion of agonistic behaviours (A/D/K) to visits per zone. Incidents were generally low compared to visits but showed the highest percentual proportion in zone 1. The y-axis starts at 50% for better visualisation. B) Composition of agonistic behaviours compared by zone. The variety of behaviours shown increased with distance to the Crowbuddy, while agonistic behaviours in zones 1 & 2 almost exclusively comprised of food-related competitive behaviour (i.e., kleptoparasitism and scrounging)

3.4. Explorative behaviour (all phases)

Over the course of this study, no manipulation of the Crowbuddy was observed, while inspecting behaviour was observed regularly (n = 314). As depicted in fig. 15A, the time crows spent on inspecting the apparatus tended to increase slightly over time but varied substantially between zones (fig. 15B). Inspect behaviour was hardly observed in zone 1 while it strongly increased both in frequency and duration with distance to the Crowbuddy.

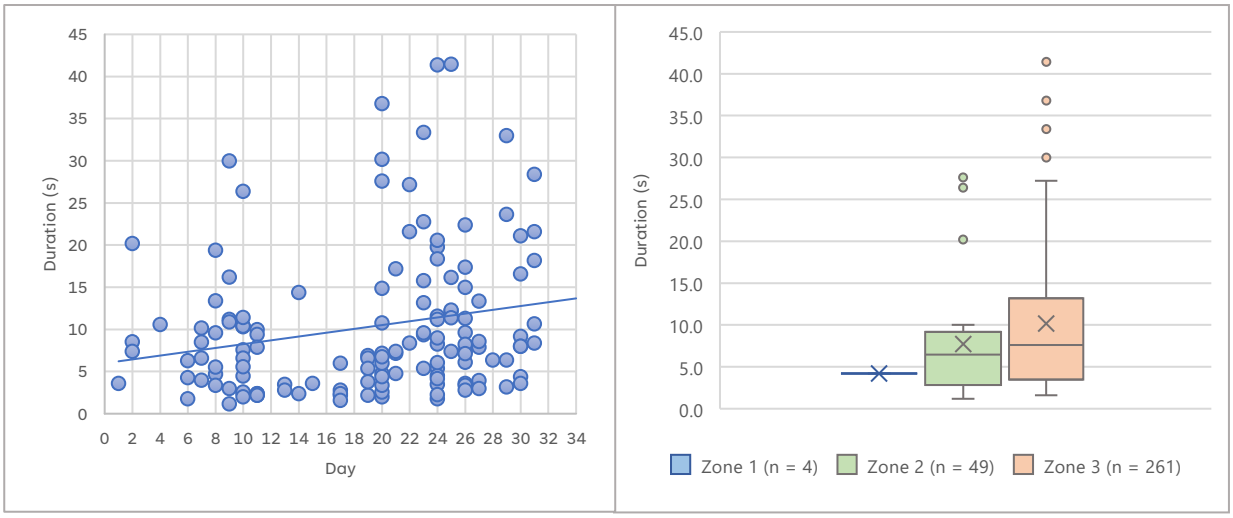

Figure 15 A) (left) and B) (right): A) Average time (s) spent inspecting the Crowbuddy over time. The time individuals spent on observing the apparatus appears to have increased over time, but it has to be noted that these values represent calculated average values and were not directly assessed per individual. B) Average time (s) spent inspecting the Crowbuddy compared by zone. Both duration and frequency of observing decreased with proximity to the apparatus.

3.5. Human impact

3.5.1. Effect of visitor density on frequency of presence & visits (all phases)

We found a significant effect of visitor density on frequency of presence (p = 0.0114*) and visits (p = 0.00414**). With an increasing number of visitors present, both variables tended to decrease (coef.: Presence = -0.159, visits = -0.192).

3.5.2. Effect of visitor density on latency to first approach (all phases)

Analysis of the effect of visitor density on the latency to approach of the ad libitum observational area showed a weak significant effect (p = 0.0245*). Crows tended to take more time until the first approach with an increasing number of visitors present (fig. 16, coef.: -0.406)

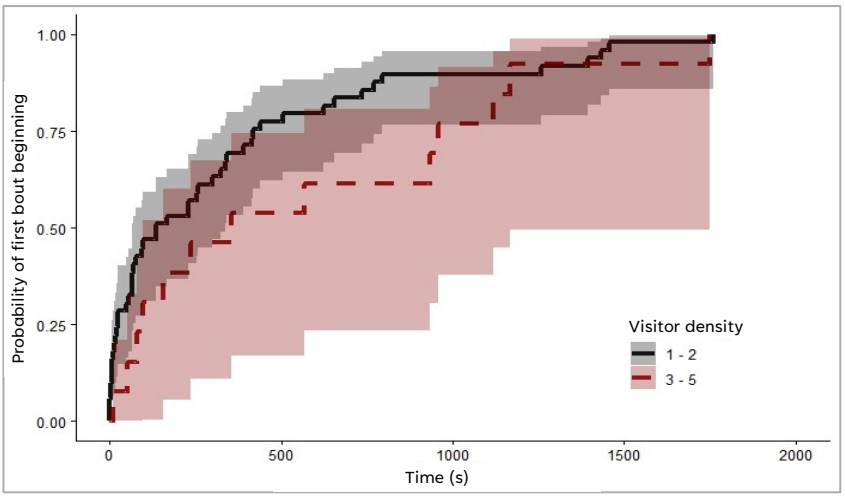

Figure 16: Cumulative incidence plot (Cox Proportional Hazard Model) showing the latency to the first approach of the ad libitum observational area respective to the total recording length of each round on the x-axis (s) depending on visitor density (Categories 1-5, 1 = very low, 2 = low, 3 = medium, 4 = high, 5 = very high) on the square at the onset of recording. The y-axis represents the probability of the first bout beginning. The 5 visitor density categories were merged into 2 (1-2 [black] and 3-5 [red]) due to very low incidents of densities 3 and 4 and for better visualization. Shaded areas represent the confidence intervals (95 %). The Cox Proportional Hazard Model showed a significant effect of visitor density on the latency to the first approach (p = 0.0245), indicating higher latencies with an increasing number of visitors present.*

3.5.3. Agonistic behaviour by humans towards crows (all phases)

Agonistic behaviour by humans towards crows around the Crowbuddy varied substantially across days (fig. 17) and analysis did not show any pattern linked to visitor density. Agonistic events almost exclusively consisted of (forced) displacement (n = 50), while a directed threat was only observed once.

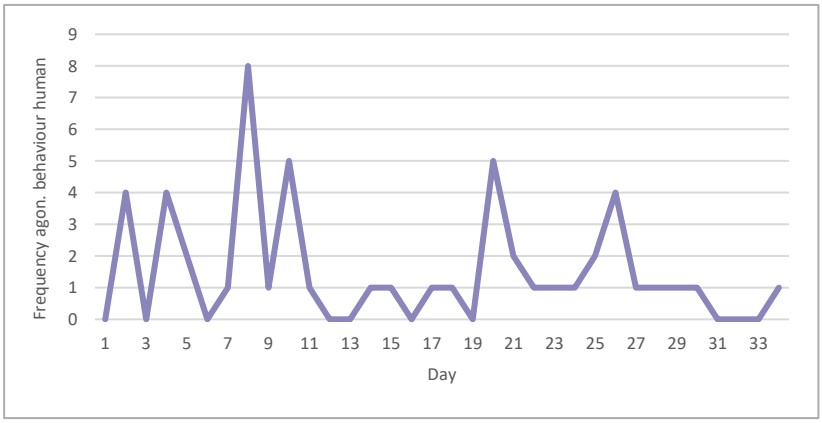

Figure 17: Sum of all agonistic behaviours by humans towards crows across days. Although observed frequently, it varied substantially between days. We did not find a correlation between frequency of agonistic behaviour and visitor density.

4. Discussion

The majority of our findings support our predictions in terms of directionality (i.e., positive or negative correlation, increase or decrease over time) but not concerning speed and degree of these effects to manifest. Notably, we observed slow and moderate habituation to the apparatus followed by a relatively stable neophobic response. Our findings provide evidence for conservatism, but also for social facilitation and the impact of human disturbance in a risky exploration context.

4.1. Neophobia & conservatism

Given the high degree of urbanisation and familiarity with human-made structures in our study population, the intensity of neophobic response towards the Crowbuddy was unexpected. Although we could confirm the predicted increase in presence and visits of the ad libitum observational area over time (Prediction I), this increase was more moderate and slower than anticipated. Consequently, defined thresholds to conclude habituation and to proceed to instrumental conditioning (i.e., learning to exchange trash for a food reward) were not met in the course of this study. Despite food abundance and quality being highest on the Crowbuddy (i.e., in zone 1) throughout data collection, and despite food being free to take, it took more than 2 months (20 data collection days) for crows to start directly feeding from the apparatus. Additionally, although overall presence and visits increased with time, they did not increase for zone 1 and decreased with proximity to the Crowbuddy (i.e., zone 1 < zone 2 < zone 3). When obtaining treats from the Crowbuddy, crows showed strong reluctance to take food from the feeder despite it containing proportionally higher amounts of highly preferred food (i.e., dog food) compared to the landing platform. Individuals were also more likely to repeatedly visit zone 3 compared to zones 1 & 2 during their stay in the ad libitum observational area, however, these results must be interpreted with caution as crows that left the field of vision of the observer and returned later during a behavioural bout were counted as different individuals due to the absence of individual markings. Similar patterns emerged concerning the duration individuals spent around the apparatus, with individuals spending significantly more time around than on the Crowbuddy. All of these results suggest strong neophobia related to the apparatus, which is underpinned further by the fact that latency to the first approach of the ad libitum observational area did not decrease over time.

Reasons for this avoidant response can be various and may act on the species, population, and individual level. One plausible explanation for the patterns observed is provided by the dangerous niche hypothesis (DNH, Greenberg, 2003) and the innovation paradox, highlighting the

complex reaction to novelty shown by some ecologically plastic generalists like crows, as pinpointed by Greenberg (2003):

> *"A bird that encounters more novelty may require the protection of heightened caution when exploring new objects and new foods, particularly if toxic foods or a high level of threat from predators characterize its environments. This has been the classic explanation for why some foraging opportunists, such as [...] ravens, show such high levels of neophobia [...] The hypothesis is that [the most innovative] species depend upon exploring new situations to survive, but they do so with a high level of fear and arousal, thus protecting themselves in the face of the potential, unknown dangers that are associated with novelty."*

While we assumed that the general neophobic tendency of crows would be less prevalent in our highly urbanized study population due to frequent exposure to human-made-structures, diverse, safe foraging opportunities, and low predation risk (Miller et al., 2022), it might, in fact, be the case that these regular novelty encounters elicit a stronger neophobic response towards objects that do not meet internalized rules for "safe-novelty generalization". In other words, although crows show strong opportunism and behavioural plasticity in certain contexts, high degrees of novelty that do not allow for sufficient risk-benefit-assessment due to a lack of similarity to previous experience (i.e., generalization) may elicit strong fear responses, leading to the phenomenon of neophobic explorers/innovators (i.e., the innovation paradox) (Brosnan & Hopper, 2014; Forss et al., 2017; Greenberg, 2003; Greggor, Clayton, et al., 2016). This is supported by previous findings on neophobia in highly urbanized corvids, showing that urban birds did not generally show lower neophobia compared to their rural conspecifics. However, they approached human-made litter significantly faster, implying a reduction in fear responses towards specific potentially rewarding items frequently encountered in urban habitats allowing for generalization (Greggor, Clayton, et al., 2016; Miller et al., 2022).

The classification of novelty in terms of risk and benefit by an individual is responsible for evoking curious or avoidant responses. The ambivalent reaction towards the Crowbuddy observed during this study might be due to the lack of utility in fully exploiting the apparatus, supporting the "necessity drives innovation" hypothesis (Laland & Reader, 1999; Morand-Ferron et al., 2011): Food abundance in the zoo is high year-round (Uhl et al., 2019), thus, the necessity for increased risk taking was not present for the crows in our study population since conservative tactics (i.e., familiar food sources) were sufficiently beneficial (Brosnan & Hopper, 2014; Reader et al., 2016). Hence, although food placed on the Crowbuddy elicited curiosity towards the apparatus, it was dampened by low utility and the simultaneous arousal of neophobia, as

explained by the two-factor-model on neophobia-neophilia by Russell (1973). The fact that crows did not habituate to taking food from the feeder within the study period further underpins this, as it appears that their moderate habituation was restricted to certain parts/areas of the Crowbuddy while others persisted in evoking a strong fear response.

Besides the influencing factors on the species and population level, individual factors may act on the propensity to explore and innovate. As already pointed out, experience may lead to generalization, allowing individuals to quickly categorize novelty as (un)safe based on previously encountered objects. This is both true on the population level, depending on the quality and quantity of novel stimuli provided by the environment (Miller et al., 2022) and transmission of information on these stimuli within a social group or population, as well as on the individual level, depending on experience gained during developmentally sensitive periods and individual space use (i.e., the range in which an individual may gain different experiences) which can be affected by behavioural type (Deventer et al., 2016). Additionally, position and rank within a social group, age, personality and vagrancy can significantly affect the subjective proneness and necessity to explore and innovate (Brosnan & Hopper, 2014; Caicoya et al., 2023; Heinrich, 1995; Kawai, 1965; Laland & Reader, 1999; Miller et al., 2015; Morand-Ferron et al., 2011). All of these factors have strong implications on successfully habituating crows to the Crowbuddy and may provide valuable insights into why certain behavioural patterns have emerged. However, they could not be addressed in this study as the birds were not individually marked, making it essential to enable individual recognition of crows in future studies.

4.2. Social facilitation & learning

As highly social and neophobic species, carrion/hooded crows are particularly reliant on social cues from conspecifics to better assess the risk of novel situations, potentially decrease their fear response and enable exploration by naïve individuals, as described by the social information hypothesis (Forss et al., 2017). Thus, they are drawn towards stimuli by the presence of conspecifics around them (Kogan & Wallach, 1967; Miller et al., 2014). It is therefore not surprising that we found strong evidence for increased interest/decreased neophobia towards the Crowbuddy due to social facilitation (Prediction II): With an increasing number of conspecifics present, crows were significantly faster to approach the ad libitum observational area, spent more time in the area (both concerning presence of different individuals and overall frequency of visits), were more likely to visit repeatedly (i.e., visit more than one zone) within a bout and, most importantly, were more likely to directly visit the Crowbuddy. Interestingly, social context on the entire square (360° scan) did not have a significant effect on any of these response variables except latency to approach, but social context in the ad libitum observational area (i.e.,

maximum number of crows present simultaneously per bout) did. This shows that the results on Crowbuddy-visits are not due to a general effect of numbers (i.e., the more crows that are present, the more crows will visit the apparatus) but due to a specific facilitation effect of conspecifics present in this closer spatial proximity. This is further underpinned by the fact that number of birds in the 360° scan had no effect on overall visits of the ad libitum observational area. Although some of these patterns could also be evoked by competition, e.g., competing for access and being displaced from one zone to the other, this can practically be ruled out due to the overall low incidence of agonistic behaviours (see 5.3.).

Since individuals in our study population were unmarked, precisely uncovering patterns of social learning and diffusion of foraging innovation across the population is difficult. However, the significant rise in presence over time (i.e., different individuals visiting per bout) implies that diffusion by social learning took place, as we would otherwise expect only visits (i.e., overall frequency of visits), not presence (i.e., different individuals visiting), to increase (Prediction III). Again, these results must be interpreted with caution due to crows leaving the field of vision of the observer and returning at a later point during a bout were counted as different individuals. Crows also observed conspecifics that visited the apparatus during habituation phase 2, with descriptive analysis suggesting an increase in time spent on this behaviour over time. However, although the duration of this behaviour was coded as separate events, it was not assigned to individuals (as opposed to duration of presence) and data points were highly clustered on certain days. Thus, we did not consider this variable suitable for inferential statistics. The clustered nature of the data does not necessarily mean that crows did not regularly observe conspecifics, as conservative coding and the difficulty of identifying observe/inspect behaviour, especially with an increasing number of birds present, may have led to a relatively small number of observations. Also, we cannot exclude the possibility that birds observed their conspecifics from a greater distance outside of the ad libitum observational area, which would not be included in our data.

Although indications for social learning were found, our data also implies that diffusion was limited: The difference between presence (i.e., number of different individuals visiting) and visits (i.e., frequency of overall visits; ΔPV = Visits – Presence) increased significantly over time, which could point towards some regular visitors increasingly exploiting this novel food source rather than rapid diffusion across the population, as in the latter case, one would expect ΔPV to remain relatively stable while presence and visits increase. The fact that the number of crows present on the square (360° scan) neither predicted presence nor visits further supports the assumption that there was a small part of the population that habituated to and increasingly used the apparatus. Assuming that this was the case, factors on both the individual and

population level could have led to these patterns emerging. Referring back to the "necessity drives innovation" hypothesis (Laland & Reader, 1999; Morand-Ferron et al., 2011), it is possible that some individuals of the population, besides the individual influencing factors already pointed out in section 5.1., found higher utility in overcoming their neophobia due to low social rank and/or poorer physical constitution. This, on the other hand, could have implications for the probability of social learning to occur: If only a couple of individuals show innovative behaviour because they are forced to overcome their conservative tactics, innate learning biases of observing conspecifics might put a cap on the diffusion of this behaviour (Aplin, 2016). In common ravens (*C. corax*), affiliation between the model and observer significantly impacts interest in observing the model's behaviour and individuals were more likely to pay attention to conspecifics of the opposite sex (Scheid et al., 2007). A study by Chiarati et. al (2012) showed that social rank of the model predicted social learning probability in wild carrion crows, with subordinate individuals being more likely to learn from explorative dominants than vice versa, which can create a negative relationship between innovation and diffusion probability (Morand-Ferron et al., 2011) and can be further enhanced by pay-off-biased learning (i.e., observing individuals seeing less utility in the behaviour than the model, Barrett et al., 2017). In addition, different vagrancies and space use of individuals (i.e., fission-fusion dynamics) can lead to innovators not always being around to learn from, which could serve as one of many possible explanations for the clustered nature of our data on observing conspecifics at the Crowbuddy as well as the overall variability of presence and visits across days (Deventer et al., 2016; Loretto et al., 2017; Uhl et al., 2019). Thus, it should be stressed again that enabling individual differentiation of crows in future studies is vital to gain deeper insight into the factors governing diffusion of innovation (or the absence of it) and investigating the assumptions made here.

4.3. Exploration & competition

Explorative behaviour towards the Crowbuddy was frequently observed, but only in terms of inspecting the apparatus while manipulation of it never occured during this study. The average time spent on inspecting the Crowbuddy appears to have slightly increased over time, although it must be noted that the same limitations apply to this behaviour as to observing conspecifics at the apparatus mentioned above: Inspect duration was coded as distinct events but not assigned to individuals, which is why the average per individual was calculated (see 4.4.). Thus, it is possible that certain crows inspected significantly more than others, increasing the average value. However, due to the large number of observations, these values should still provide an accurate enough proxy for explorative behaviour. The fact that inspecting the Crowbuddy was observed frequently while manipulation never occurred is another implication for neophobic tendencies, as already discussed in section 5.1. Although manipulation of objects with the beak

provides valuable information about the physical properties of items (Biddle et al., 2018), crows were strongly reluctant to do so and preferred observing the apparatus as a means of gathering information. They also preferred observing from a greater distance, with both frequency and duration decreasing substantially with proximity to the apparatus while hardly any inspect behaviour was shown when directly visiting the Crowbuddy (i.e., zone 1). However, this could (additionally) be due to more practical reasons: Zones 2 & 3 might simply provide a better view of the Crowbuddy, especially since these zones consisted of elevated structures like a fence and trees. Particularly zone 3, also containing an area separated from the Crowbuddy with a glass fence, was apparently perceived as the safest area for exploration. Independent of the study phases (i.e., differences in food availability within zones), crows tended to visit zone 3 frequently without being able to obtain a treat. In fact, the highest peaks in visiting frequency were observed during habituation phase 2, during which no treats were provided outside of zone 1. Zone 2 showed almost identical frequencies of visits and feeding during habituation phase 1, while the differences became larger after the first crows started to feed directly from the Crowbuddy (habituation phase 2). Zone 1, on the other hand, was never visited without obtaining a treat throughout habituation phase 2.

Putting this into context with our findings on inspect & agonistic/dominant/kleptoparasitic (A/D/K) behaviours, it appears that the outmost zone was readily visited without rewards present for explorative purposes. The zone became even more important once crows started to directly feed from the apparatus, which is also supported by the increase of duration spent in the ad libitum observational area with distance to the Crowbuddy. It should be noted, though, that the short duration of visits and inspect behaviour on the apparatus are most likely also due to limited space availability on the landing platform: Oftentimes, there was not a lot of time for individuals to stay and explore before being displaced by a conspecific. Although A/D/K behaviours had the highest total frequency in zone 3, crows showed the largest proportion compared to visits when on the apparatus while the variety of these behaviours increased with distance to the Crowbuddy. Both in zone 1 and 2, agonistic behaviours were generally rare and were almost exclusively related to food (i.e., kleptoparasitism), indicating that a) competition for gaining access to the apparatus was elicited, but to a very low degree and b) other social interactions became less important with proximity to the apparatus. Concerning point a), it appears that social tolerance of conspecifics in the study population was relatively high, underpinning previous findings (Miller et al., 2014) and aligning with our results on social facilitation. Given the vast area of the zoo and the high abundance of different scavenging opportunities (Uhl et al., 2019), overall low competitiveness around the Crowbuddy is expected. Competitiveness was only elicited during late points in habituation when presence and visits peaked. As

neophobia was prevalent throughout data collection, it is also plausible that observing others was of greater importance than competing, as obtaining information from conspecifics to reduce neophobia was continuously necessary. This servers as an explanation for b), since there is a fundamental trade-off between vigilance and other behaviours, such as exploration and social interactions (Dukas, 2009; Lima & Dill, 1990): Overall incidents of social behaviours were low compared to visits (affiliative behaviours hardly occurred at all) and the closer crows got the Crowbuddy, which elicited a strong fear response demanding vigilance, the less variety they showed in their social behaviours, focusing almost exclusively on competing for food. Zone 3 appeared to act as a "safe space", preferably used for exploration and occasional social interactions, probably due to the largest distance to the apparatus, elevated structures and being partly separated from the Crowbuddy by a glass fence, allowing for safe exploration.

Given the high proportion of kleptoparasitic behaviour in zone 1 & 2, it is essential to elaborate on possible reasons and limitations. Our definition of kleptoparasitism includes displacement and forced displacement from food as well actively stealing food from another individual's beak, however, the latter was hardly observed. These results thus portray competitive behaviour around food rather than active kleptoparasitism and scrounging. As pointed out before, limited space on the landing platform might force individuals to displace others to gain access, which would further support the notion that competition did not play a major role in the sense that it was rather elicited by spatial circumstances. In fact, scrounging was often observed in the form of individuals waiting for producers to drop food from the landing platform, which is not included in our data. Future studies should therefore separately assess competitive and scrounging behaviour combined with enabling individual recognition to potentially uncover emerging producer-scrounger patterns (Mottley & Giraldeau, 2000). Additionally, our findings suggest that the process of habituation might benefit from providing an enlarged landing platform and sufficient space containing elevated structures around the Crowbuddy, as this could aid in mitigating the risk of hostile conspecifics forcing individuals to put more energy into vigilance than exploration when close to the apparatus (Dukas, 2009; Forss et al., 2017). Thus, the goal of future studies should be to reduce the risk of exploration as far as possible, allowing for a shift on the spectrum of risk and benefit towards the latter and increasing the chances of overcoming neophobia.

4.4. Disturbance & distraction by humans

Our results suggest that prominent human presence constitutes a hindering factor during habituation (research question IV), as with rising visitor density, both bird presence and visits tended to decrease while the time it took crows to first approach the ad libitum observational area

increased. It thus appears that, despite the population's urban habitat and exposure to human activity, humans still pose a disturbance within a risky exploration context, demanding crows to shift their focus from exploration and scavenging towards vigilance (Clucas & Marzluff, 2012; Dukas, 2009; Forss et al., 2017; Lima & Dill, 1990). Although actual persecution and culling is rare in Vienna, particularly in the zoo (Kirchmeir et al., 2019), agonistic behaviour by humans towards crows is generally common, also along urban gradients (Clucas & Marzluff, 2012), and was frequently observed in the ad libitum observational, albeit with substantial variation across days. A directed threat was only observed once, however, visitors often approached crows during exploration eliciting a flight reaction or, as parts of zone 3 belonged to the common visitor area, overlooked them, forcing them to move. Although crows in the zoo are frequently observed feeding out of people's hands, having high tolerance for being in proximity and generally showing low fear of humans, this might not be applicable during situations of neophobia. The unpredictability of human behaviour could lower chances of crows overcoming neophobia by demanding more vigilance at the cost of exploration and adding to the subjective risk of the situation, similar to the trade-off discussed in the context of agonistic conspecifics. At the same time, it is possible that humans serve as a positive distraction, particularly after visiting food stands, as leftovers from visitors pose a welcome and frequent food source. Habituation progress would thus benefit from reducing human contact and disturbance as far as possible, particularly during phases when neophobia is still prevalent, which could be achieved by fencing off a wide enough radius around the Crowbuddy and/or placing signs, explaining how to best act around the apparatus so as to not disrupt exploration by crows.

4.5. Conclusion

In this explorative study, we aimed to train wild crows to use a novel token-exchange apparatus after a stepwise process of habituation, providing, for the first time, scientific data on the emerging patterns and potential factors governing innovation in the context of such projects. While habituation occurred, it did so to a moderate degree only. Evidence for neophobia was strong and exploration was stifled by high human presence. However, the study population might be subject to other socio-ecological factors that dampen the utility of fully exploiting the Crowbuddy and thus, the need to overcome conservative tactics. As a result, innovation was restricted to foraging innovation in terms of utilising a novel food source but did not extend to innovative token-exchange behaviour, as thresholds to proceed to the final training phase of instrumental conditioning were not met. However, indications for moderate diffusion by social learning and evidence for social facilitation were found. In light of the corvid family's ability to engage in token-exchange (Dufour et al., 2011, 2020), general propensity to innovate (Matzinger, 2015; Miller et al., 2016; Powell & Kelly, 1977; St Clair et al., 2016, 2018) and

anecdotal evidence from similar projects of successfully training them to exchange litter for a food reward (e.g., “Corvid Cleaning”, Sweden; “Crowbox”, U.S.; “Birds for Change”, France), it appears likely that crows have the capability to learn to use the Crowbuddy. Nonetheless, they move along the paradox of innovative explorers (Forss et al., 2017), and it might precisely be because of their impressive intelligence and complex cognition that they did not fully exploit the apparatus, as they carefully decide for each situation, impacted by manifold, complexly intertwined factors, whether the benefit outweighs the risk. Reducing factors that decrease the subjective perception of benefit, such as human disturbance and conditions that favour the threat posed by agonistic behaviours from conspecifics, should therefore be a point of focus in the future. Providing sufficient space to explore, both around and on the Crowbuddy, preferably containing elevated structures made of natural materials (e.g., wooden perches) and minimizing human interference (e.g., by fencing off a certain radius around the apparatus and/or installing signs providing information on proper behaviour around exploring crows) could help individuals to overcome their neophobia faster.

Although certain patterns could be uncovered and valuable insights were provided in this study, creating a solid stepping stone for future research, it has become clear that enabling individual recognition is absolutely essential to take a closer look at the complex network of factors governing habituation, neophobia, innovation and its diffusion - particularly since studies under naturalistic conditions are lacking (Aplin, 2016; Bandini & Harrison, 2020) and data from captivity must not portray realized innovation rates in environments under natural selection (Morand-Ferron et al., 2011). Individual differentiation of crows would thus allow us to generate much needed data that could provide insights into an abundance of factors that impact utility, proneness to innovate and diffusion by social learning, like personality and behavioural phenotypes (Grunst et al., 2019; Miller et al., 2016; Stöwe & Kotrschal, 2007), sex (Scheid et al., 2007), age (Heinrich, 1995), affiliation among conspecifics (Kirchmeir et al., 2019; Scheid et al., 2007) producer-scrounger patterns (Arbilly et al., 2014; Mottley & Giraldeau, 2000) and position and rank within a social group (Brosnan & Hopper, 2014; Caicoya et al., 2023; St. Lawrence et al., 2021). Additionally, long-term observations could aid in shedding light on possible influences of seasonality and breeding status (and concomitant changes in social structures and food availability; Kirchmeir et al., 2019; Uhl et al., 2019) transmission modes (Aplin, 2016) and different levels of vagrancy (i.e., fission-fusion dynamics; Loretto et al., 2017; Uhl et al., 2019) and uncover potential breaking points in habituation that change the effects and dynamics of social and ecological factors.

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7. Appendix

7.1. Abstract

During the Anthropocene, humans have altered earth in manifold and severe ways. Many of these alterations pose an increasing risk to the health of ecosystems and ultimately, our own survival, such as pollution of terrestrial and aquatic ecosystems by inappropriately disposed waste. The challenge of pollution is potentiated in urban areas with high population densities, but urban habitats also pose unique opportunities for establishing innovate strategies to confront it. One of these opportunities is the utilisation of the intelligence of synanthropic, non-human animals around us and creating mutually beneficial human-animal-relationships: Carrion and hooded crows (*Corvus corone ssp., Corvidae* family, *Passeriformes*) are known to thrive even in the most urbanized regions, using their complex cognition to maximize the benefits of living in proximity to humans by, inter alia, following human food sources. If crows could learn that collecting and disposing human-made trash is of advantage for them, they might be able to aid us in combating our pollution problem. Given that corvids show the highest innovation rate among passerines and are known to understand and perform token-exchange tasks, they possess the cognitive basis for learning to collect and appropriately dispose of litter and waste in exchange for a food reward. This, in turn, poses an opportunity for crows to extend their foraging repertoire (i.e., foraging innovation) and increase foraging success. Although some projects such as “Corvid Cleaning” (Sweden), “Crowbox” (U.S.) and “Birds for Change” (France) aimed at establishing this mutualistic relationship with corvids, success with wild birds was scarce and no scientific monitoring was conducted. Hence, scientific data that can help maximize success and efficiency of such projects by identifying the factors that influence the onset and transmission of this innovative behaviour in a population (or the absence of it) is lacking. In this study, we contributed to filling these gaps in knowledge and laid the foundations for a mutualistic relationship between humans and a wild, unmarked population of carrion/hooded crows located in Vienna, Austria. A fully autarkic “vending machine”, the Crowbuddy, was designed to provide a food reward when crows, in exchange, collect and dispose litter, excluding the necessity of direct human contact during the process. The current study focused on habituating these birds, which are both highly explorative and neophobic (a phenomenon called “innovation paradox”), to the apparatus by providing food on and around it, thus setting the necessary basis for future token-exchange-behaviour. The Crowbuddy was placed in an unoccupied, fenced enclosure at a popular scavenging site at Zoo Schönbrunn (Vienna). Using video recorded behavioural data collected over a period of 4 months, the following research questions were addressed: I.) Will crows approach, interact with and/or exploit the apparatus and,

if so, how will this change over time? II.) What influence will social context (i.e., the presence of conspecifics) have on approaching and the behaviour towards and around the apparatus? III.) Will behaviour transmit across the population by social learning? IV.) What influence will human presence and behaviour have on the crows' behaviour towards and around the apparatus? Our results show slow and moderate habituation to the novel apparatus, as crows took more than 2 months to feed directly from the Crowbuddy. This was followed by a relatively stable neophobic response, showing, inter alia, in no change in latency to approach the apparatus and no increase in direct visits of the Crowbuddy over time. We found indications for low to moderate behavioural diffusion across the population (i.e., transmission by social learning), but evidence for significant facilitating effects on habituation by the presence of conspecifics (i.e., social facilitation). The latter showed in a decreased latency to approach the Crowbuddy with an increasing number of crows present on the square where the apparatus was placed, an increased frequency and duration of visits of the area around the apparatus as well as an increased frequency of visits of the apparatus itself with an increasing number of conspecifics present simultaneously in proximity of the Crowbuddy. High human presence, on the other hand, appeared to have a dampening effect on habituation, as with increasing visitor densities, crows took longer to approach the Crowbuddy and, also, were less likely to approach at all. This study provides a stepping stone for future research to investigate the potential of mutually beneficial human-wildlife-interactions and sheds further light on neophobia, conservatism, the innovation paradox and certain socio-ecological factors governing these processes in an urban population of crows. Nonetheless, future research should aim at enabling individual recognition of crows as to uncover the roles of factors like age, sex, breeding status, social rank and behavioural type/personality.

7.2. Zusammenfassung

Während des Anthropozäns haben Menschen die Erde auf vielfältige und gravierende Weise verändert. Viele dieser Veränderungen stellen ein zunehmendes Risiko für die Gesundheit der Ökosysteme und letztlich für unser eigenes Überleben dar, wie etwa die Verschmutzung terrestrischer und aquatischer Ökosysteme durch unsachgemäß entsorgten Abfall. Die Herausforderung der Verschmutzung wird in urbanen Gebieten mit hoher Bevölkerungsdichte verstärkt, doch städtische Lebensräume bieten auch einzigartige Chancen zur Etablierung innovativer Strategien zu ihrer Bekämpfung. Eine dieser Chancen ist die Nutzung der Intelligenz synanthroper, nicht-menschlicher Tiere um uns herum und das Schaffen von wechselseitig vorteilhaften Mensch-Tier-Beziehungen: Aas- und Nebelkrähen (*Corvus corone ssp.*, Familie *Corvidae*, *Passeriformes*) sind bekannt dafür, selbst in den am stärksten urbanisierten Regionen

zu gedeihen und nutzen ihre komplexe Kognition, um die Vorteile des Lebens in der Nähe von Menschen zu maximieren, indem sie unter anderem menschlichen Nahrungsquellen folgen. Wenn Krähen lernen könnten, dass das Sammeln und Entsorgen von menschengemachtem Abfall vorteilhaft für sie ist, könnten sie uns helfen, unser Verschmutzungsproblem zu bekämpfen. Angesichts der Tatsache, dass Corviden die höchste Innovationsrate unter den Passeriformes zeigen und bekannt ist, dass sie Token-Exchange-Aufgaben (also ein Objekt gegen ein anderes eintauschen) verstehen und durchführen können, besitzen sie die kognitive Basis um zu lernen, Müll und Abfall zu sammeln und im Austausch gegen eine Futterbelohnung angemessen zu entsorgen. Dies wiederum bietet den Krähen die Möglichkeit, ihr Nahrungsspektrum zu erweitern (foraging innovation) und ihren Erfolg bei der Nahrungssuche zu erhöhen. Obwohl einige Projekte wie „Corvid Cleaning“ (Schweden), „Crowbox“ (USA) und „Birds for Change“ (Frankreich) darauf abzielten, diese besondere mutualistische Beziehung zu Corviden aufzubauen, war der Erfolg mit Wildvögeln gering und es gab keine wissenschaftliche Begleitung der Projekte. Daher fehlt es an wissenschaftlichen Daten die helfen können, den Erfolg und die Effizienz solcher Projekte zu maximieren, indem jene Faktoren identifiziert werden die das Auftreten und die Übertragung dieses innovativen Verhaltens in einer Population (oder dessen Fehlen) beeinflussen.

In dieser Studie trugen wir dazu bei, diese Wissenslücken zu schließen und die Grundlagen für eine mutualistische Beziehung zwischen Menschen und einer wilden, unmarkierten Population von Aas- und Nebelkrähen in Wien, Österreich, zu legen. Ein vollständig autarker „Futterautomat“, der Crowbuddy, wurde entwickelt um eine Futterbelohnung bereitzustellen, wenn Krähen im Austausch dafür Müll sammeln und entsorgen, ohne dass direkter menschlicher Kontakt während des Prozesses erforderlich ist. Die aktuelle Studie konzentrierte sich darauf diese Vögel, die sowohl hochexplorativ als auch -neophob sind (ein Phänomen, das als „Innovationsparadox“ bezeichnet wird), an den Apparat zu gewöhnen (Habituierung), indem Futter direkt auf und in der nahen Umgebung des Apparats bereitgestellt wurde, um so die notwendige Basis für zukünftiges Token-Exchange-Verhalten zu schaffen. Der Crowbuddy wurde in einem unbewohnten, eingezäunten Gehege an einem beliebten Platz für die Futtersuche im Zoo Schönbrunn (Wien) platziert. Anhand von videoaufgezeichneten Verhaltensdaten, die über einen Zeitraum von 4 Monaten gesammelt wurden, wurden die folgenden Forschungsfragen untersucht: I.) Werden sich Krähen dem Apparat annähern, damit interagieren und/oder ihn nutzen, und wenn ja, wie wird sich dies im Laufe der Zeit verändern? II.) Welchen Einfluss hat der soziale Kontext (d.h., die Anwesenheit von Artgenossen) auf die Annäherung und das Verhalten an/um den Apparat? III.) Wird sich das Verhalten durch soziales Lernen innerhalb der Population ausbreiten? IV.) Welchen Einfluss hat menschliche(s) Präsenz und Verhalten auf das Verhalten der Krähen um den Apparat?

Unsere Ergebnisse zeigen eine langsame und moderate Habituierung an den neuartigen Apparat, da die Krähen mehr als 2 Monate benötigten, um direkt vom Crowbuddy zu fressen. Darauf folgte eine relativ stabile neophobe Reaktion, die unter anderem in keiner Veränderung der Latenz zur Annäherung an den Apparat und keinem Anstieg der direkten Besuche des Crowbuddy im Laufe der Zeit zum Ausdruck kam. Wir fanden Hinweise auf eine niedrige bis moderate Verhaltensdiffusion innerhalb der Population (d.h. Übertragung durch soziales Lernen), aber Beweise für signifikante förderliche Effekte auf die Habituierung durch die Anwesenheit von Artgenossen (social facilitation). Letzteres zeigte sich in einer verringerten Latenz zur Annäherung an den Crowbuddy mit zunehmender Anzahl an Krähen, die auf dem Platz anwesend waren, auf dem das Gerät platziert war, einer erhöhten Häufigkeit und Dauer der Besuche im Bereich um den Apparat sowie einer erhöhten Häufigkeit der Besuche des Apparats selbst, je höher die Anzahl an Artgenossen war, die gleichzeitig in der Nähe des Crowbuddys anwesend waren. Starke menschliche Präsenz schien hingegen eine dämpfende Wirkung auf die Habituierung zu haben, da die Krähen mit zunehmender Besucherzahl länger brauchten, um sich dem Crowbuddy zu nähern, und die Wahrscheinlichkeit, dass sie sich annähern, generell gesunken ist. Diese Studie bietet einen Ausgangspunkt für zukünftige Forschungen zur Untersuchung des Potenzials von wechselseitig vorteilhaften Mensch-Wildtier-Interaktionen und gibt wertvolle Einblicke in Neophobie, Konservatismus, das Innovationsparadox und bestimmte sozial-ökologische Faktoren, die diese Prozesse in einer urbanen Krähenpopulation steuern. Nichtsdestotrotz sollte zukünftige Forschung darauf abzielen, eine individuelle Erkennung der Krähen zu ermöglichen, um die Rollen von Faktoren wie Alter, Geschlecht, Fortpflanzungsstatus, sozialem Rang und Verhaltenstyp/Persönlichkeit aufzudecken.

7.3. Solomon® coding mask

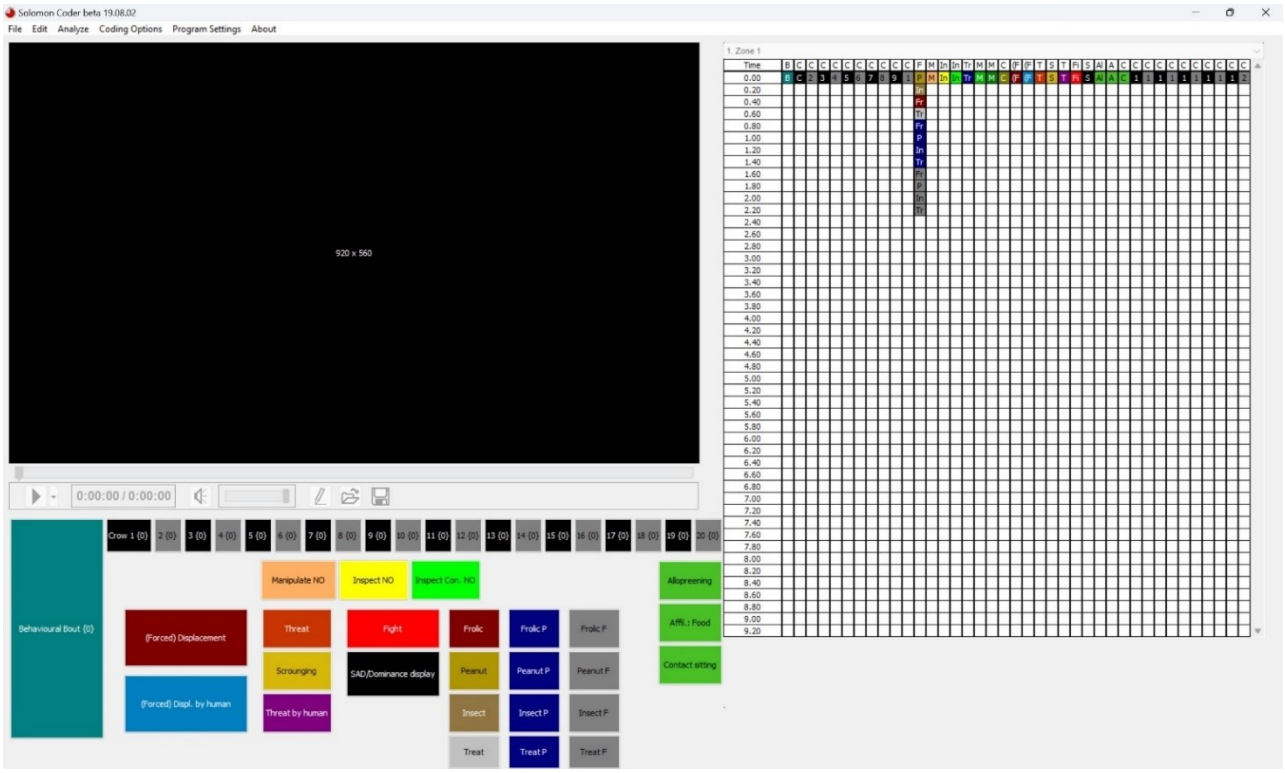

Figure 18: Screenshot of the Solomon® coding mask used to precisely code all behaviours associated with zone and behavioural bout.

7.4. Training procedure for final phase (not conducted)

To establish the connection between behaviour (i.e., putting an object into the designated opening of the apparatus at the landing site, see fig. 2B) and reward, an object (e.g., a crown cap) is placed near the designated opening of the apparatus. As soon as an individual (accidentally) pushes the object into the opening (e.g., during landing or exploratory behaviour), the apparatus will provide a reward. When this happens repeatedly, individuals should learn that the event of objects falling into the opening leads to a food reward.